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# **Preface**

The largest genus of marine invertebrates and likely of marine invertebrates, *Conus* also presents arguably the most challenging taxonomy and nomenclature. Van Mol, Tursch and Kempf's (1967) assessment, "Une grande confusion systématique règne au niveau spécifique," remains true not only because of the very large number of species (about 500), but also because:

- 1) Within-species variation is extensive and betweenspecies differences are often difficult to detect.
- 2) Many new species continue to be described, and almost all of these descriptions are unconvincing, because they:
- a) Fail to assess intraspecific variation in objectively described traits; and
- b) Fail to present adequately clear, quantitative comparisons with the most closely related species.
- 3) The original specimens on which many species were based—now known as "type" specimens—no longer exist, or their whereabouts are unknown to specialists.

Our intentions as authors of this work are to:

- 1) Survey all available nominal taxa in *Conus*, including synonyms and homonyms;
- 2) Discuss objectively and consistently each valid recent species, to describe these and to differentiate them from their most similar congeners;
- 3) Illustrate photographically in colour the shells of all valid recent species, including examples of intraspecific variation;

- 4) Summarize present knowledge of the appearance, radular teeth, habits and habitats of living animals;
- 5) Show on maps the presently known geographic distributions of species;
- 6) Illustrate some nominal taxa of uncertain validity (Appendix 1); and
- 7) Illustrate a selection of *Conus* specimens that the authors have not been able to identify with known species (Appendix 2).

This work has both benefited and suffered from the collaborative efforts of amateur and professional malacologists, the spectrum spanned by the authors. We have benefited from the generosity of several amateur collectors who have provided material for study, locality data for geographic distribution studies, photographs of living animals, observations of the natural history of animals, and discussions of these problems. In addition, some dealers of specimen shells have also provided information.

For convenience, we have divided the work among three volumes, of which this is the first. It covers *Conus* of the tropical Indo-Pacific region, where more than half of all known species occur. The second volume will cover the tropical Atlantic and Eastern Pacific Oceans as well as temperate-zone species of *Conus* throughout the world excl. Australia and New Zealand. The first two volumes contribute especially to understanding marine biodiversity, as *Conus* is probably the most diverse of all genera of invertebrates in the sea.

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# Introduction

More than any other genus of shelled molluscs, *Conus* has for centuries held the attention of a remarkably diverse array of enthusiasts: shell collectors, naturalists, artists, shell dealers, and even molecular biologists.

Aristotle must have known the common Mediterranean species of this far-flung genus, but we know of no specific allusions to it in the surviving research results of the earliest known invertebrate zoologist. The oldest known written record of Conus is that of Belon (1553) which included an illustration in wood-cut, and by 1700 a good deal was known about various aspects of the genus. Fossil Conus were recognized by the mid-16th century by Aldrovandi ([1522-1605]; published posthumously in 1648), an originator of the concept of the natural history museum. Rembrandt made an etching of Conus marmoreus in 1650. Swammerdam ([1637-1680] 1669, 1737), illustrated a sectioned shell of Conus and described the very thin inner shell walls. Bonanni's (1684) illustrations of Conus are clearly recognizable to species. Before the end of the 17th century Lister (1688) published the first monograph devoted to molluscan shells, and Rumphius (published posthumously in 1705) recorded the first human fatality from Conus venom.

The shells of *Conus* were prominent in Rumphius's D'Amboinsche Rariteitkammer (1705) and in other natural history folios that appeared throughout the early and mid-18th century (e.g., Seba, 1734-1765; Regenfuss, 1758). These illustrated, often in colour, specimens in the natural history "cabinets" amassed by royalty and the wealthy in 18th-century Europe, and some of the *Conus* species acquired such names as "*cedonulli*" (matchless) and "*gloria maris*" (glory-of-the-sea). This must have helped to promote interest.

Argenville (1742) devoted several pages of text and 3 plates to *Conus* in the next great compendium on "conchyliologie." In the next decade Adanson (1757), in a large volume on the molluscs of Senegal, included 15 pages of detailed descriptions and one plate of 8 species of *Conus* (not all from Senegal) and illustrated features of external anatomy. In the same decade Linnaeus's binominal system of nomenclature characterized *Conus* as we now know the genus, and provided a firm footing for biological classification that soon gained wide acceptance.

The first detailed anatomical study of *Conus* was made by G. S. Poli (1746-1825), perhaps before the end of the 18<sup>th</sup> century, because his comparable work on bivalves appeared in 1791-1795. However, the remarkably accurate coloured illustration of *Conus* anatomy was not published until 1826, after his death (Kohn, 1992).

At the turn of the 19th century, when J.B.P. Lamarck switched allegiance from botany to zoology, he turned after two short studies of land snails to intensive study of fossil *Conus* in France (Lamarck, 1803), including paleoecologi-

cal and biostratigraphic interpretations. In 1810, he reviewed all known recent and fossil *Conus* species. Lamarck well recognized the extent and diversity within the genus (he listed 181 recent and 9 fossil species in the 1822 edition of his invertebrate zoology monograph). And, as later recounted by Kiener (1845), he marvelled at the attractiveness of the genus to so many people despite its geometric simplicity and constancy of shell form:

"Le genre Cônc est, comme l'a dit Lamarck, le plus beau, le plus étendu et l'un des plus considérables de la classe des Univalves. C'est celui qui renferme les coquilles les plus précieuses et en même temps les plus remarquables, soit par la régularité de leur forme, soit par l'éclat et l'admirable varieté de plusieurs d'entre elles. Aussi sont-elles trés-recherchées des amateurs." (Kiener, 1845)

We now know that the genus *Conus* has had an equally remarkable evolutionary history. Stanley (1979: Fig. 9-4) suggested that it is the most rapidly evolving of all prosobranch gastropod groups, and Kohn (1990) documented a preliminary, broad-brush pattern of its history from the fossil record.

Conus must truly be a genus that has mastered the game of evolution. Today we recognize more than 500 living species, primarily tropical but successful in a remarkable diversity of marine environments, from the intertidal zone to continental slopes, and many apparently maintaining genetic continuity across the vast expanses of the Indo-Pacific zoogeographic realm. The genus has accomplished this diversification with remarkable variation on the theme of simple conical or biconic shell geometry christened by Linnaeus and appreciated by Lamarck and Kiener.

The seemingly continuous variation continues to attract and vex collectors and students both on scientific and esthetic grounds, and it challenges the efforts of taxonomists to classify the species within the Linnacan system of nomenclature. We have written this book to assist these efforts by evaluating available systematic data on the Recent *Conus* species of the vast Indo-Pacific biogeographic realm. This information derives almost entirely from shells, and this book is thus firmly in the tradition of our 18th-century predecessors mentioned above. In the accounts of each species, we summarize information about other characters, including anatomy, natural history, reproductive biology, and distribution, but the application of additional character sets, e.g. from molecular biological study, awaits the next generation of researchers.

# The Origin and Evolution of Conus

The durable shells of *Conus* are well suited to long-term preservation after death of the animal, and as might be expected the genus has a very respectable fossil record. Since the first three described by Gustavus Brander in 1766, well over 1,000 fossil species have been given available

names. Many of these are likely synonyms of others, but this is very hard to determine in the fossil record as it is impossible to learn about living animals and populations.

Our present knowledge of the fossil record (Kohn, 1990) indicates that *Conus* originated in Lower Eocene time, about 50-55 million years before present (mybp). The most probable ancestor was a turrid, but it is not yet possible to be any more specific than that. The oldest *Conus* fossils are known from England (*C. concinnus* Sowerby) and France (*C. rouaulti* d'Archiac). The terrestrial fossil record of tropical and subtropical terrestrial plants indicate that at the time, the climate of Europe was much warmer than today.

Once it originated, Conus diversified rapidly. More than 100 Eocene species have been described, most from the mid and late divisions of this epoch. During this time, Conus rapidly extended its geographic range as well. Most Middle Eocene species are European, but the genus also spread to present-day Egypt, Nigeria, Pakistan, and southeastern and western North America. Fewer species (about 60) are known from the Oligocene (25-38 mybp), a cooler epoch that saw general declines in diversity of shelled marine animals. One or more major radiations of Conus occurred in the Miocene epoch (5-25 mybp), from which about 350 species are described, most from Europe and the Indo-Australian region. The Miocene radiations may be the source of some modern species, but diversity again declined in the Pliocene (2-5 mybp; 152 species recorded), another cool epoch with generally reduced invertebrate diversity. The apparently very rapid increase during the Pleistocene epoch (0.01-2 mybp), leading to the present extremely high diversity particularly in the Indo-Pacific region, may reflect a real increase in speciation rates or an artifact of the geologic record.

# The Place of Conus Among the Gastropod Molluscs

Conus is the type genus of the Conidae, validly established as a family by John Fleming in 1822. The Conidae together with the Turridae and Terebridae constitute the Superfamily Conoidea (Ponder and Warén, 1988), often also known as the Conacea or Toxoglossa. It in turn belongs to the Order Caenogastroda (or Neogastropoda) in the Subclass Prosobranchia of the Class Gastropoda.

Some classifications combine the Conidae and Turridae as a single family; the superfamily then contains only two families. Turridae and Conidae are certainly the most similar of the three family-group taxa, and the distinction between them is nebulous. Conidae is probably monophyletic in the strict sense: "a group of species that includes an ancestral species and all of its descendants" (Wiley, 1981). However, the ancestor of Conidae was most likely a turrid, and Turridae (excluding Conidae) would thus be paraphyletic: a group that includes the most recent common ancestors but not all of its known descendants (Farris, 1974).

Taxonomic convenience rather than evolutionarily consistent logic thus plays a role in the separation of Conidae and Turridae. These two are the largest family-group taxa

of prosobranch gastropods. Conidae includes more than 500 extant species, and Turridae may have that many genera and ten times as many species!

The distinction between Turridae and Conidae is based on the following criteria (from Kohn, 1990): Partial resorption of the inner walls of the shell, a hallmark of *Conus* (Kohn et al., 1979), also occurs in *Conorbis* and *Hemiconus* (the two genera besides *Conus* in the Conidae), but not in *Cryptoconus* (Turridae). The spire and aperture in *Cryptoconus* each comprise about half the total shell length, while the spire of *Conorbis* is always shorter than the aperture length. In Conidae, the shell form is approximately conic or biconic, and the sides of the aperture are generally parallel. In this book we include the one extant species of *Conorbis* (*C. coromandelicus*), but we exclude the extinct genus *Hemiconus* as well as species of *Conus* known only as fossils.

# The Infrageneric Classification of Conus

The classification scheme for all animals accepted today originated in the tenth edition of Linnaeus's *Systema Naturae per Regna tria Naturae* (1758). Linnaeus established the genus *Conus*, in which he included 35 species and three infraspecific forms.

Linnaeus subdivided *Conus* into four infrageneric groups, indicated in the original work by 1-4 asterisks. Because these were not latinized genus-group names, they have no status in nomenclature (ICZN Opinion 124). However, they represent the original attempt to subdivide the genus, and they help us to interpret Linnaeus's nominal species because they complement the species descriptions. Linnaeus's infrageneric groups serve to convey an impression of the shape of the shell. They may be translated as follows (Dillwyn, 1817; Dodge, 1953):

- Truncate, or spire almost truncate.
- \*\* Pyriform, base rounded, subcylindrical, body whorl one and one-half times as long as the spire.
- \*\*\* Elongate, base rounded, the body whorl twice as long as the spire.
- \*\*\*\* Ventricose, with a wide aperture.

Although the second and third categories appear to differ quantitatively, the distinction is not as useful as it may seem. Spire height is difficult to measure accurately, and it also varies considerably among individuals of a species, both inherently and due to erosion of the shell.

The original Linnaean subdivisions of *Conus* remained unchanged in the 12<sup>th</sup> (Linnaeus, 1767) and 13<sup>th</sup> (Gmelin, 1791) editions of the Systema Naturae, although the number of species recognized jumped to 157 in Gmelin's edition. In an English update of Gmelin's work, Dillwyn (1817) distributed the 160 species he considered valid among the four original Linnaean subgroups.

In other 18th-century treatments of the entire genus, Martini and Chemnitz (1773-1795) subdivided 180 recognized species into five subgroups. These were not latinized,

and the entire work has been rejected for nomenclatural use as it was not consistently binominal (ICZN, 1958). Equally detailed, and presently more important because its new species names are taxonomically available, was the Bruguière-Hwass monograph of Conus, published in France in 1792. It treated 147 species, of which 109 Recent species, 14 Recent infraspecific taxa, and 2 fossils were given nomenclaturally available names for the first time. Here the genus was subdivided into three groups based on a new shell character, coronation or tubercles on the shoulder, as well as shell shape:

Genus	Subgenus	Type Species	Examples of other species
Conus			
	Conus	litteratus Linnaeus	virgo Linnaeus, generalis Linnaeus
	Dendroconus	<i>striatus</i> Linnaeus	stercusmuscarum Linnaeus, betulinus Linnaeus, gubernator Linnaeus
	Textilia	bullatus Linnaeus	textile Linnaeus, aulicus Linnaeus
	Theliconus	nussatella Linnaeus	glans Hwass, terebra Born
	Leptoconus	amadis Gmelin	australis Holten
Coronax	is		
	Coronaxis	bandanus Linnaeus	marmoreus Linnaeus
	Puncticulis	arenatus Hwass	cedonulli Linnaeus
	Tuliparia	tulipa Linnaeus	
	Cylindrella	sulcatus1 Hwass	
	Conilithes	antidiluvianus Brugui	ère

Shell coronate (38 species)
Shell conical, spire smooth (73 species)
Shell cylindrical, spire smooth (36 species).

As in the case of Linnaeus's infrageneric groups, these have no status in nomenclature, but they usefully complement the species diagnoses.

In both his first account of the entire genus and the later treatment in his invertebrate zoology textbook, Lamarck (1810, 1822) used the presence or absence of shoulder coronation as the only subdividing character, with 44 coronate and 137 non-coronate Recent species.

In the first to attempt to divide the Linnaean genus *Conus* into smaller taxa that now have available genus-group names, Montfort (1810) introduced four new genera and retained *Conus* as a fifth. Each was identified by a type species:

Genus	Type Species	
Cylinder	textile (Linnaeus)	
Rollus	geographus (Linnaeus)	
Hermes	nussatella (Linnaeus)	
Rhombus	imperialis (Linnaeus)	
Conus	generalis Linnaeus	

Swainson (1840) returned to a two-subdivision scheme, formalizing Lamarck's two groups as the genera *Conus* and *Coronaxis*, each with five subgenera. Except for *Conus* s.str., all of the subgenera were given new names.

The 1840's saw the publication of two major iconographics of *Conus* with colour illustrations of much improved quality, by Reeve (1843-1849) and Kiener (1845-1850). These works treated much larger numbers of species (334 and 347, respectively), but neither attempted subdivision of the genus. Thus as the number of *Conus* species recognized increased, by 1850 infrageneric classification of *Conus* was either becoming simplified or being omitted. Linnaeus's arrangement had lost favour, and Montfort's and Swainson's met with little acceptance. These authors had not attempted the increasingly difficult task of fitting all of the known species into their schemes.

Complexity at the genus level returned with Mörch in 1852, who, drawing partly on the earlier works mentioned, published an arrangement of the Conidae consisting of 11 genera. Conus s. str. and Chelyconus each contained two subgenera, so Mörch employed a total of 15 genus-group names. He took four of them from Swainson (Coronaxis. Cylindrella, Dendroconus and Leptoconus) and two from Montfort (Cylinder and Hermes). Except for Conus s.str. the rest were new:

Genus	Subgenus	Type Species
Conus		
Ounus	Stephanoconus	regius Gmelin <sup>2</sup>
	Puncticulus	arenatus Hwass in Bruguière
Coronax	ás	The state of the contract of the contract of the state of
Cylindre	lla	
Nubecui	la <sup>3</sup>	[geographus Linnaeus]*
Lithocor	nus	leopardus (Röding) <sup>4</sup>
Rhizoco	nus	[miles Linnaeus]
Chelyco	nus	[ermineus Born] <sup>5</sup>
	Pionoconus	magus Linnaeus
	Phasmoconus	radiatus Gmelin
Cylinder	e	
Hermes		

<sup>\*</sup> Square brackets indicate type by subsequent designation.

<sup>1</sup> Originally as "C. asper Chemnitz."

<sup>&</sup>lt;sup>2</sup> Originally as "C leucostictus Hwass."

<sup>&</sup>lt;sup>3</sup> Originally introduced by Herrmannsen (1846).

<sup>&</sup>lt;sup>4</sup> Originally as "C. millepunctatus Lamarck."

<sup>&</sup>lt;sup>5</sup> Originally as "C. testudinarius Hwass."

In the following year H. and A. Adams proposed a new scheme with four genera, three of which were subdivided into subgenera, for a total of 11 subgroups, if nominate subgenera are counted only once. Five of these were adopted from Swainson and five, including *Nubecula* Herrmannsen, from Mörch.

In the 1850's as in the previous decade, authors who considered large numbers of individual species (e.g., Sowerby, 1857-1858; Crosse, 1858) did not attempt subdivision of the genus, and this practice continued throughout the remainder of the 19th century (Chenu, 1859; Weinkauff, 1874; Tryon, 1884). Only Fischer (1887) divided *Conus* into four subgenera; these were subdivided into 11 sections that were not given genus-group names.

Few 20th-century studies have attempted to treat the entire genus, with very disparate infrageneric classifications. The trend to subdivision seems to have been climaxed by Cotton (1945) whose system contains 29 genera arranged in 14 groups of 1-3 genera each. He proposed that these groups "may even represent subfamilies." Marsh (1964) employed a similar set of 3l genus-group names but considered them subgenera of Conus. Japanese workers (e.g., Kira, 1965) have also used a similar set but typically raised them to genus level. Based on radular tooth form, Azuma (1964) subdivided the genus into 6 major groups, one of which was further divided into 4 subgroups. These were not given formal nomenclatural status, however. The most recent subdivision is that of da Motta (1991), comprising eight genera and 60 subgenera; he does not include nominotypical subgenera.

In the most ambitious attempt to date to provide a descriptive and taxonomic account of the entire taxon, Walls [(1979)] did not attempt subdivision of *Conus*. Other late 20th-century taxonomic analyses of the genus as a whole also eschew subgenera: Tomlin's (1937) catalogue, continued as computerized print-outs by Kohn et al. (1992); Kohn's (1963-1992) chronological treatment of the nominal species described between 1758-1840; and Coomans, Moolenbeek and Wils' alphabetical revision of Recent species only, covering species-level names beginning with the letters a-e (1979-1986). The absence of formal infrageneric taxa also characterizes most recent regional treatments of *Conus*, for example Kay (1979); Röckel, Rolán and Monteiro (1980); Estival (1982); Vink (1984-1992).

More than 90 genus-group names have now been proposed in the family Conidae as here considered (Emerson and Old, 1962; Kohn, Kim, Pointer, Riggs, Dang, and Swarthout, 1992). The classifications employing different subsets of these vary widely. Schemes based on shell shape and sculpture, shell colour pattern, and radular tooth characters are inconsistent and incongruent. The message this fact conveys to us is that they do not represent useful genus-level classifications but are likely based rather on attributes more appropriate to the species level. In this work we thus follow the practice of Powell (1966), Dance (1974), and most of the recent authors cited above; see also Kohn (1990), and assign to *Conus* all extant species of the Coninae (sensu Thiele, 1929; Wenz, 1942) except for *Conorbis*. We believe this conclusion corresponds most closely with the

modern concept of the genus (Wiley, 1981; Mayr and Ashlock, 1991), one species or a monophyletic group of species separated from related comparable units or genera by a decided morphological gap.

# The Species-level Classification of Conus

In number of species, *Conus* is probably the largest genus not only of marine gastropods but of marine animals. It is thus a major contributor to biodiversity in the sea. Unfortunately, taxonomic knowledge of the genus precludes an accurate estimate of the number of extant species. About 20 years ago, Kohn (1976) estimated 400 ± 200 living species. In this book we recognize 318 in the Indo-Pacific region.

The total number of described or nominal species is more accurately known. Tomlin's (1937) catalogue included about 2,700 Recent and fossil species described prior to 1937; about 100 omitted by Tomlin have been discovered subsequently, but 30 names should be deleted from Tomlin's list. These include species in Turridae, misidentifications, misspellings, and *nomina nuda* (Kohn et al., 1992). Since 1936, more than 600 *Conus* species have been described, the majority since 1970.

Surprising numbers of new species of Conus continue to be described. The average number of new species descriptions per year was rather constant at 6-7 between 1940 and 1970. In the 1970's the average jumped to 13/year, and to 17/year in the 1980's. Thus far in the 1990's the average is 23/year. As in the case of ancient species it is often difficult to determine whether a new nominal species represents a "real" biological species in nature or hitherto unappreciated morphological variation within a previously described species.

The concept of the species has many interpretations, and a detailed discussion of the variations would be out of place here. As Wiley (1981) stated,

"Experts with different groups of organisms frequently employ different criteria in determining the species status of populations. They do this because the biological attributes of various groups may be quite different. What may seem like local demic variation to an ichthyologist may indicate distinct species to an entomologist (or vice versa). Thus, there is no substitute for knowing as much about the biology of the organisms as possible."

As is the case with most organisms, we lack the necessary information to apply the **biological species** concept (a species is a group of interbreeding populations that do not interbreed with other such groups), or the **evolutionary species** concept (a species is a lineage of ancestor-descendant populations separate from other such lineages and with its own history and evolutionary tendencies) (Wiley, 1981). To solve the practical problems of characterizing species and of identifying specimens to species, we thus resort primarily to the **morphological species** concept, a species is a group of organisms or populations separated from other such groups by distinct morphological discontinuities. If, in the characters we can analyze, such discontinuities are absent between two suspected species, that is if the variation

is continuous or the differences transitional, we conclude that there is only one species. In contrast, if two distinct forms occur sympatrically without intergrades, we conclude that they are different species. In cases of uncertainty, we have decided to unify rather than separate such taxa.

Virtually all new species descriptions of Conus are inadequate by modern standards, mainly because they fail to address the likely range of intraspecific variation in the characters on which the nominal species is based. Worse yet, many publications that introduce new species fail to describe even a minimum number of characters in ways that other workers can evaluate them. An important reason for the failures of these new species introductions is that most are published privately in the "grey literature" rather than in normal, recognized scientific journals devoted to systematic studies, and they are thus not subjected to the normal peer review procedures that determine acceptability in the modern scientific literature. For some reason, many authors of new species of Conus have failed to understand that there is no honour, distinction, or virtue in describing a new species. Rather the author gains only a responsibility, "a heavy responsibility, for the author of a new species stakes his/her reputation on his/her defense of the new name as denoting a real, previously undescribed species, representing breeding populations of many individuals, outside the range of variation of all previously described species" (Kohn, 1980).

#### How to Use This Book

This book is in the tradition of 18th- and 19th-century iconographies that treated the genus as a whole, such as those of Martini and Chemnitz, Hwass and Bruguière, Kiener, Reeve, and Sowerby. We have discussed them briefly above in the section on infrageneric classification. Like these predecessors, we have relied primarily on shell characters for the distinction of species. We depart from them mainly in two directions. First, we address the extent of intraspecific variation, especially of shell characters that vary continuously such as size, shape, and sculptural and colour pattern features. In this way, we have tried to convey an appreciation of within-species variation contrasted with between-species differences. Second, we incorporate information on external anatomy, radular teeth, geographic distribution and aspects of natural history such as habitat and reproductive habits.

In addition to these efforts, we have adopted several other procedures that we hope will ensure a high level of accuracy:

- 1. We have examined all original descriptions of Recent Indo-Pacific *Conus* species, and we have deposited photocopies of these in a chronological file in the SMNS, so they will be readily accessible to future workers.
- 2. We have examined and photographed type specimens of as many species as possible. One set of colour photographs of type specimens is in the SMNS, and a computerized list of diapositives of type specimens in SMNS, MNHN, and the University of Washington is available from the authors upon request.

3. In the case of species tending toward polymorphism rather than continuous variation of shell characters, we describe and illustrate the different recognized forms.

## Geographic Scope of the Book

To determine the geographic scope of this work we define Indo-Pacific using the terminology of Springer (1982): "The Indian Ocean, including contiguous seas, and the Pacific Ocean as far east as Easter Island, but excluding the area occupied by the coast and offshore islands (Guadalupe, Revillagigedos, Clipperton, San Felix, San Ambrosio, Juan Fernandez, etc.) of the Western Hemisphere." The South African Province is also excluded. The largest of the marine biogeographic provinces, the Indo-Pacific is a vast region, encompassing one-fourth of the world's ocean area, and it is probably home to more than half of all living species of *Conus*.

# Species Accounts in the Systematic Section

We begin the systematic section with *C. marmoreus* Linnaeus, 1758. This was the first species of *Conus* listed by Linnaeus, and it is the type species of the genus, by the subsequent designation of Children (1823).

Because a phylogenetic classification of the genus has not yet been attempted, we lack an objective sequence in which to present the species. As discussed above in the section on infrageneric classification, various authors have attempted groupings based on shell characters, but these vary considerably and they are mutually incongruent. None has resulted in a satisfying scheme, and all leave species that cannot be unequivocally assigned to only one of the groups. H.C. Weinkauff's clear statement of this remains as correct today as in 1874:

"Ich betone ausdrücklich, dass ich diese Gruppierung nur als eine künstliche angesehen wissen möchte, die ich einer Anordnung nach dem Alphabet vorziehe, die aber noch gar viel zu wünschen übrig lässt, um befriedigend zu sein. Es liegt dies in der Natur der Gattung, die bei aller Übereinstimmung im Grossen, doch eine Menge kleiner Verschiedenheiten besitzt. So gibt es eine Anzahl Arten, die sich jeder Gruppierung widersetzen und eine grössere Anzahl von so vagen Merkmalen, dass sie sich ebensogut in einer anderen Gruppierung unterbringen liessen, ja selbst in einer dritten oder vierten."

Our solution to this problem has been to eschew infrageneric groups but to adopt an order of presentation that to the extent possible groups similar species together, both in the text and the illustrations. We hope that this approach will facilitate comparisons by the reader. All nominal species are easy to locate, because the Index lists all species-group names in alphabetical order. There valid species are readily identified by bold type, while junior synonyms and *nomina dubia* are in lighter type.

The heading of each species account indicates the original author of the species and the year of publication. This

is followed by references to illustrations in this book, including colour photographs of shells (on Plates 1-73), colour patterns of foot and siphon, drawn from life (Plates 74-76), colour photographs of living animals (on Plates 77-84), and range maps (Maps 1-136).

Most of the photographed shells are in the collections of major museums, the majority in the SMNS. In all, we include photographs of specimens from 21 museums and 52 private collections, identified in the captions of the plates. All photographs without attribution in the captions are of specimens in the Röckel collection in the SMNS. In the photographs we tried to compromise between illustrating specimens in actual size (as in Kiener and Reeve, for example), and making all of the figures the same size (as in Walls, for example). The first method uses a great deal of space and makes very small specimens unrecognizable, while the second gives an erroneous concept of the real size of the shell. In this book, the illustrations of larger specimens are reduced more than those of smaller specimens. In this way, relative but not absolute sizes are maintained. The actual length of each shell as well as its locality of origin is indicated in the accompanying caption.

Returning to the species entries in the text, the synonymy that follows the heading includes citations of the original description of the species and the first publication of each subsequent nominal species-group taxon now considered to be a synonym or infraspecific taxon.

Types: The present status of the type specimen or specimens is then indicated, including size (length x maximum diameter, to the nearest 0.5 mm) and present location of the types (excluding paratypes) of all nominal species listed in the synonymy. If a holotype, lectotype, or neotype has been designated by a prior worker, we indicate the appropriate term. In some cases, we know of the existence of a type series but no single type specimen has been designated. We refer to this material as "type" if we assume the type series consists of only one specimen, and as "syntypes" if to our knowledge the type series contains more than one specimen. We do not construe this listing of syntypes as fixing any specimens as holotypes or lectotypes. This is in accord with Article 72b (vii) of the International Code of Zoological Nomenclature (ICZN, 1985). If type specimens have not been fixed, we cite the original illustration of a syntype as original figure."

**Type Localities:** Either cited in the original descriptions or designated subsequently, type localities are given next, verbatim in quotation marks, for the valid species as well as for the synonyms and infraspecific taxa. If no type locality has been designated, this entry is omitted.

Range: Geographic ranges are given in different styles, depending on the range. Broad ranges are indicated as the western-to-eastern and northern-to-southern limits, e.g., "Western Thailand to Solomon Is., Taiwan to Australia. Narrower ranges are given more fully, e.g., "Hawaiian Archipelago, Fanning Is. and Eniwetok, Marshall Is." Each accompanying map includes the range of 1-3 related species. They are distinguished on the maps by lines of different intensities. The information on ranges is syn-

the sized from literature records judged trustworthy by the authors, museum collections, and personal communications to the authors. Doubtful records are excluded; unverified but likely correct reports which we have no reason to doubt are indicated as "probable."

**Description:** Shell shape and sculpture are described first, with the following order of characters: Assumed range of adult size and weight, shape of last whorl, form of shoulder, height and shape of spire, size, number and sculpture of whorls of larval shell, outline and sculpture of teleoconch sutural ramps, and sculpture of last whorl. We have not included the number of teleoconch whorls, because *Conus* shells have indeterminate growth, and the number of whorls increases with growth and age.

The characterizations, described more fully in the Glossary section below, are accompanied by a box containing the range of morphometric data measured on a sample of usually 10-20 specimens. These include shell length (L), relative weight (RW), relative diameter (RD), position of maximum diameter on the last whorl (PMD), and relative spire height (RSH). The boxes are positioned so as not to interrupt the narrative descriptions, but the information they contain provides the bases for the descriptors used there. These data are particularly important because the shells of Conus offer the viewer a number of optical illusions, especially when a shell is viewed in the usual manner from the aperture side with the axis of coiling vertical and the apex up. For example, the form of the spire affects the viewer's subjective impression of the relative diameter of the last whorl; a last whorl surmounted by a high, concave spire appears narrower than the same last whorl with a low, convex spire.

The description continues with shell colour pattern. The pigments of *Conus* shells are deposited in different shell layers, and in at least some cases it is apparent from the shell surface that some are deeper than others. For this reason the innermost, or ground colour, is given first, followed by the colours and patterns of the more external or overlying layers. The terms used to indicate colour pattern elements are defined in the Glossary below.

The colour pattern of the last whorl is described before the spire, because the last whorl is the most conspicuous aspect of most *Conus* shells. Finally, the thickness, surface texture and opacity as well as colour of the periostracum is described.

The colour pattern of the externally exposed parts of the body is described next, and it is keyed to the colour photographs of living animals and the drawings of exposed soft parts by Mrs. Chaberman. Other sources of these descriptions are colour photographs generously provided to the authors by J.C. Estival (New Caledonia) and Mrs. Gloria Pearson (Marshall Islands), and unpublished observations of A. J. Kohn. While this information will be of little use to the reader who has only an empty shell, it will be helpful to those who wish to identify living animals without abusing or killing them, and it is sometimes important in distinguishing closely related species.

Where information on radular tooth form is known, it is summarized next.

In our descriptions, knowledge of some characters is based on the study of fewer specimens than of others. In particular, the accounts of adult shell characters usually synthesize study of many specimens, based mainly on the large collection in the SMNS. The accounts of body colour pattern, larval shell, and radular teeth are necessarily usually based on fewer specimens. In addition, many of the descriptions of body colour patterns are based on photographs, the colours in which vary depending on the type of film, light source, and degree of expansion of the animal. We thus have less confidence that they reflect a real range of intraspecific variation. However, much of the information we present on the colours of animals and on radulas has not been published before, in some cases it may help in species determinations, and it forms a base for future studies.

Habitat and Habits: Knowledge of the habitats of most Conus species is limited to the depth range in which specimens have been collected, so bathymetric information is given first. This is followed by more specific notes on habitats where data exist, including the type and diversity of substratum and the animal's relationship to it. This includes, for example, whether it is typically epifaunal, in algal turf, under coral heads, in sand, etc. Where additional knowledge of the natural history of Conus species exists, it is usually limited to feeding and reproductive activities, and these are briefly summarized, with reference to the original reports in case the reader wishes further details.

Where information on reproductive biology, including spawning sites, egg capsules and developmental mode, is known, this is summarized, primarily based on the comparative studies of Kohn and Perron (1985, 1994).

**Discussion:** The first part of each Discussion concerns how to distinguish the focal species from the species most similar to it. This matches the order in which species are presented in the book, in that the comparisons are always made with species that have been described earlier in the text. For example, *C. coronatus* (no. 23) precedes *C. abbreviatus* (no. 21), so the comparison between the two is in the Discussion of *C. abbreviatus*, and the account of *C. coronatus* indicates that they will be compared in that Discussion.

The second part of the Discussion emphasizes withinspecies rather than between-species aspects, including justifications for use of the specific name and for synonymized nominal species, and the presence of morphological variants. We apply subspecies status only to well characterized variants with a definite, rather broad, and well-known geographic range. In cases of morphological variants whose ranges are very restricted, and in cases of within-population variation, we use the term "form." In the terms of the International Code of Zoological Nomenclature, such names are "infrasubspecific" and as such have no nomenclatural status; they "are excluded from the species group and the provisions of the Code do not apply to them" (Art. 45 (c)).

# Glossary

# The Shell Characters and Character States Used in This Book

#### Introduction

The challenging task of identifying specimens to species depends completely on a clear recognition of the characteristics of the specimens. For this reason, we use this section to describe in detail the characters and their states used in this work. Most of these characters are also illustrated in text figures.

While some characters have discrete states (e.g., shoulder with or without tubercles) most characters of *Conus* shells vary continuously (e.g., spire height as a proportion of shell length). To make continuously varying characters easier to use and remember, we have also transformed them to multistate characters, with verbal labels. For example, shell length varies continuously, but we designate shells 25-35 mm long as "moderately small," those 35-55 mm long as "medium-sized," and so on, as indicated in the tabulated material that makes up most of this section.

To simplify the descriptions of species and to keep them free from excessive numbers, the text of each species account includes only the verbal designators. However, each account is accompanied by a box that contains the most important quantitative information. Each box is arranged as shown in the format sample below. The terms used are defined in the character glossary later in this section. The species sample box shows an example of the actual data, presented as the range of measurements, usually of at least 10 specimens. Most of the shells measured are in the collection of the SMNS.

Variation in these characters is often related to geographic distribution, and this is sometimes used to characterize subspecies. In other cases, different morphotypes not related to geography have been recognized. The boxes for these species include this additional information.

The terms used in the boxes are defined in the Glossary of Shell Characters section below.

## Conus Shell Morphometry (Text-fig. 2)

L Shell Length

RW Relative Weight of shell

RD Relative Diameter of last whorl

PMD Position of Maximum Diameter of last whorl

RSH Relative Spire Height, as proportion of shell length

#### Conus marmoreus Shell Morphometry

L New Caledonia RW form suffusus RD form crosseanus PMD	50 -150 mm 40 - 65 mm 0.45 - 1.95 g/mm 0.21 - 0.60 g/mm 0.56 - 0.65 0.60 - 0.67 0.85 - 0.94	
RSH	0.85 - 0.94 0.05 - 0.15	

# Glossary of Shell Characters

#### **Adult Size**

(L = Shell Length in mm)

very small	<15 mm
small	15-25 mm
moderately small	25-35 mm
medium-sized	35-55 mm
moderately large	55-80 mm
large	>80 mm

#### Relative Weight

(RW = absolute weight/L; grams/millimeter of length)

light	<0.06 g/mm
moderately light	0.06-0.10 g/mm
moderately solid	0.10-0.30 g/mm
solid	0.30-0.80 g/mm
moderately heavy	0.80-1.10 g/mm
heavy	>1.10 g/mm

Relative weight is a convenient but only approximate estimate of shell thickness. Relative weight depends on both thickness of the last whorl and shell size. Because shell length and shell thickness are both linear measures, and the rate of weight increase is approximately proportional to the cube of linear dimensions, relative weight increases more rapidly than length or thickness. Values of relative weight will thus be higher for larger shells than for smaller shells of the same species. For this reason, we indicate the shell lengths with all RW values, and we usually present relative weights for a limited range of shell lengths.

## Relative Diameter

(RD = maximum diameter/aperture height)

#### Position of Maximum Diameter

(PMD = height of maximum diameter/aperture height)

## General Shape of Last Whorl

("body whorl")

conical: PMD >0.85; RD 0.50-0.70.

broadly conical: PMD >0.85; RD >0.70.

narrowly conical: PMD >0.85; RD <0.50.

broadly and ventricosely conical:

PMD 0.75-0.85; RD >0.70.

ventricosely conical or conoid-cylindrical:

PMD 0.75-0.85; RD 0.50-0.70.

narrowly conoid-cylindrical:

PMD 0.75-0.85; RD < 0.50.

broadly ovate or broadly cylindrical:

PMD <0.75; RD >0.70.

ovate or cylindrical: PMD <0.75; RD 0.50-0.70.

narrowly ovate or narrowly cylindrical:

PMD <0.75; RD <0.50.

The following definitions apply to terms used to characterize shape of the last whorl:

**cylindrical:** outline with a central parallel-sided region; PMD and RD variable.

ventricosely conical: outline with a straight to slightly convex but not parallel-sided region below PMD.

conoid-cylindrical: outline with a straight to slightly convex and nearly parallel-sided region below PMD.

ovate: outline convex, without a central parallelsided region; PMD low.

**pyriform:** outline concave anteriorly; RD usually high; this term is only applied if both sides of last whorl are concave anteriorly.

These features are illustrated in Text-figure 1, a matrix of last whorl shapes as defined by values of RD and PMD. If the minimum and maximum values of these characters were included, they would indicate the range of shapes or "morphospace" of *Conus* last whorls.

	×		
×L.	PMD > 0.85	0.85 ≥ PMD ≥ 0.75	PMD < 0.75
RD > 0.7	broadly conical	broadly and ventricosely conical	broadly ovate
0.7 ≥ RD 0.5 ≥	conical	or or ventricosely conical conoid-cylindrical	or or ovate cylindrical
RD < 0.5			or or
	narrowly conical	narrowly conoid-cylindrical	narrowly ovate narrowly cylindrica

**Text-fig. 1:** last whorl shapes of *Conus*: a tabular key of terminology.

#### **Outline of Last Whorl**

**convex** (may have modifiers: slightly, distinctly).

straight (sometimes with central waist).

concave (may have modifiers: usually not more

than slightly).

**sigmoid:** convex adapically, concave abapically.

## **Aperture Shape**

If this character is not mentioned, aperture is of nearly uniform width or is somewhat broader at base than near shoulder.

narrow

wider at base than near shoulder

wide

Special characteristics of the **siphonal fasciole** and **siphonal notch**, if any, are also given in this section.

**Shape of Shoulder** 

carinate (may be broadly carinate).

**angulate** (may be sharply angulate).

subangulate

rounded

indistinct

Special characteristics, such as unusually deep **exhalent** (anal) notch, are also given in this section.

### **Sculpture of Shoulder**

If this character is not mentioned, shoulder lacks sculpture.

undulate: outline of shoulder is wavy.

tuberculate:margin of shoulder bears tubercles.

costate: margin of shoulder bears tubercles that ex-

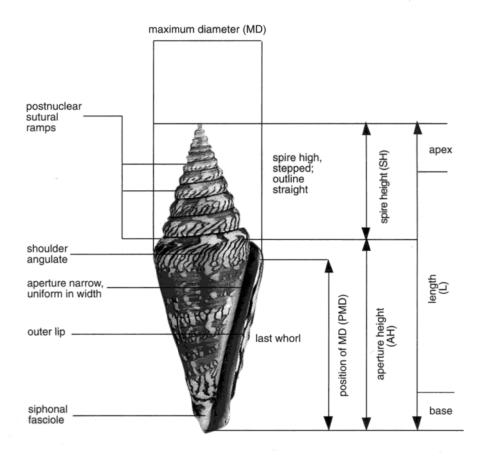
tend axially on last whorl as ridges.

**Relative Height of Spire** (RSH = (Shell Length - Aperture Height)/Shell Length; RSH = (L-AH)/L)

low: <0.12

**moderate:** 0.12 - 0.23

**high:** >0.23



Text-fig. 2: C. excelsus Sowerby III, illustrating terms used in descriptions of shell size and shape.

# **Spire Outline**

concave straight (may have modifiers: slightly, deeply).

sigmoid:

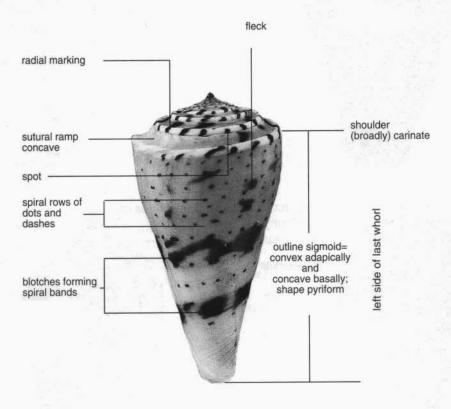
usually early whorls convex, late

whorls concave.

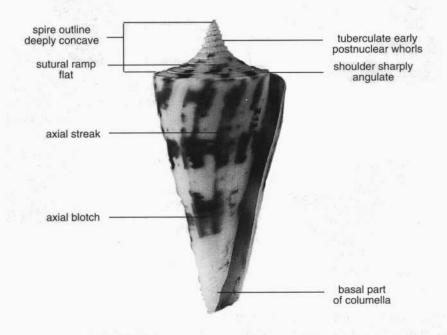
convex

(may have modifiers: slightly, distinctly; distinctly convex spires are sometimes referred to as **domed**).

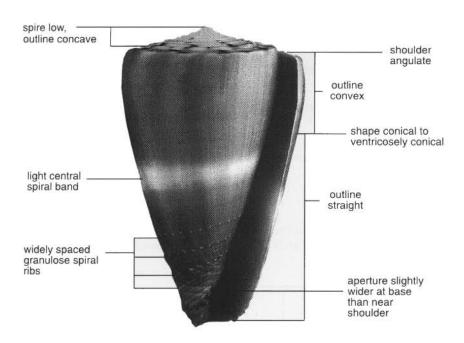
stepped

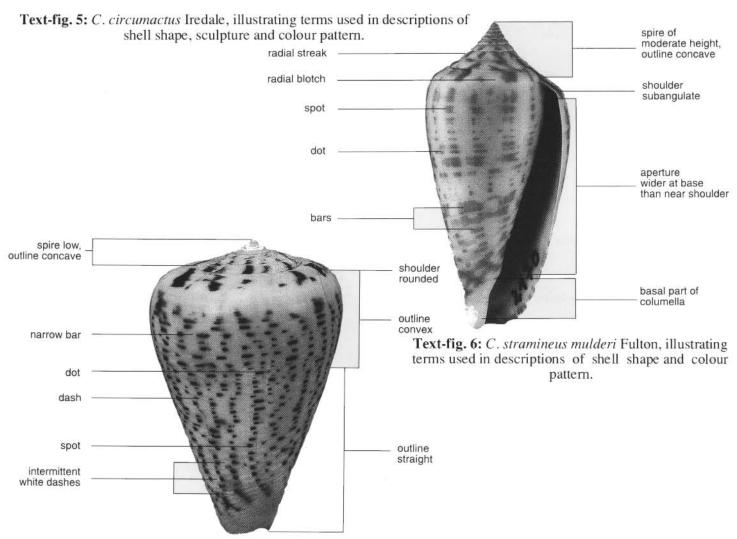


Text-fig. 3: C. ione Fulton, illustrating terms used in descriptions of shell shape and colour pattern.

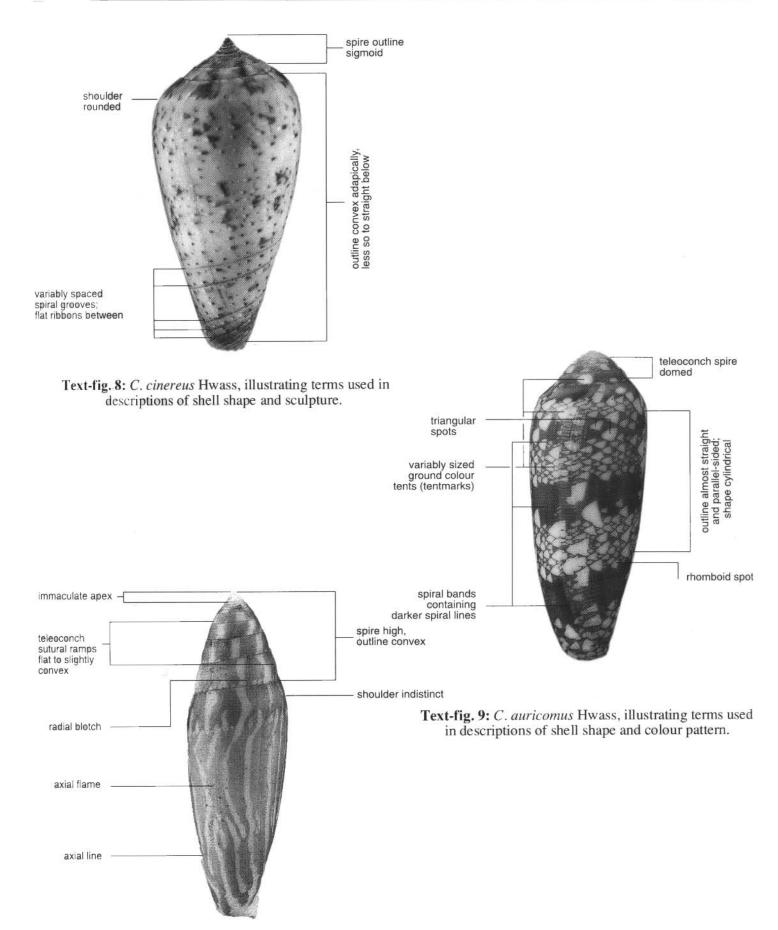


Text-fig. 4: C. bayani Jousseaume, illustrating terms used in descriptions of shell shape and colour pattern.





**Text-fig. 7:** *C. suratensis* Hwass, illustrating terms used in descriptions of shell shape and colour pattern: pattern elements arranged in spiral and axial rows.



Text-fig. 10: C. cylindraceus Broderip & Sowerby I, illustrating terms used in descriptions of shell shape and colour pattern.

# Larval Shell (protoconch) (Text-figs. 11-14)

(= premetamorphic whorls of the shell)

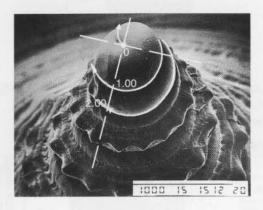
Number of whorls is usually given.

paucispiral (if number is not known): 2 or less.

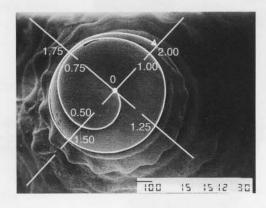
multispiral (if number is not known): more than 2.

## Method of counting whorls (Text-figs. 11, 12)

Whorls are counted from the origin, i.e. the number of revolutions of the suture is counted to the nearest quarter whorl. The count is expressed to the nearest 0.25 whorl.



**Text-fig. 11:** *C. dictator* Melvill: apex (SEM), showing method of counting whorls. Scale bar = 1 mm.



**Text-fig. 12:** *C. dictator* Melvill: larval shell (SEM), showing method of counting whorls. Scale bar = 0.1 mm.

#### Teleoconch Whorls (Postnuclear Whorls)

(= postmetamorphic whorls of the shell; all these whorls are generally called **Teleoconch**)

early teleoconch whorls: First 3-5 whorls of the teleoconch.

**late teleoconch whorls:** Remaining whorls of the teleoconch.

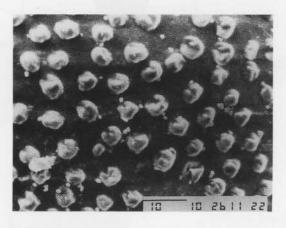
Number of teleoconch whorls is given only when useful in distinguishing similar species. Larval shell and early teleoconch whorls may be referred to as **apex**.

## Sculpture of Larval Shell (Text-figs. 13, 14)

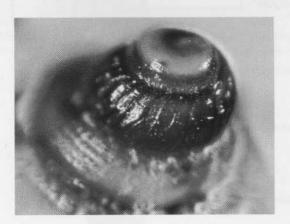
Most known *Conus* larval shells have smooth surfaces under low magnification, although they may have microsculpture visible under high magnification. Some *Conus* species are known to have protoconch surface with macrosculpture visible under low magnification.

#### Size of Larval Shell

Maximum diameter expressed to nearest 0.1 mm.



**Text-fig. 13:** *C. ermineus ermineus* Born: microstructure of larval shell (SEM), showing surface with tubercles (under high magnification). Scale bar = 10 μm.



**Text-fig. 14:** *C. korni* G. Raybaudi Massilia: macro structure of larval shell, showing radial ridges (under low magnification).

# **Sculpture of Postnuclear Whorls** (Text-figs. 15, 17-20)

Early and late whorls may be distinguished.

smooth

undulate (may have modifiers: irregularly, regu-

larly).

tuberculate (may have modifiers: strongly, weak-

ly)

Number of whorls with tubercles is given.

# Outline of Teleoconch Sutural Ramps (Text-figs. 15, 17-20)

Early and late ramps may be distinguished.

concave

flat

convex

# Radial Sculpture of Teleoconch Sutural Ramps (Text-figs. 15, 17-20)

(If this is not mentioned, only very fine growth lines occur)

striae: incised very fine lines.

threads: elevated thin lines.

# **Spiral Sculpture of Teleoconch Sutural Ramps** (Text-figs. 15, 17-20)

striae: very fine, incised.

grooves: pronounced or broad, incised.

threads: fine, elevated; on ribs or ribbons or in

grooves.

ribs: narrow, elevated, with rounded surface.

ribbons: broad, elevated, with flat surface.

**subsutural ridge:** single, narrow to broad elevation just below the suture.

The number of spiral elements on sutural ramps is usually given.

# Spiral Sculpture of Last Whorl (Text-fig. 16)

Surface of the last whorl is assumed to be smooth except for sculptural features mentioned in this section.

**grooves:** incised.

**punctate grooves:** grooves with pointed impressions (= punctations).

threads: fine, elevated.

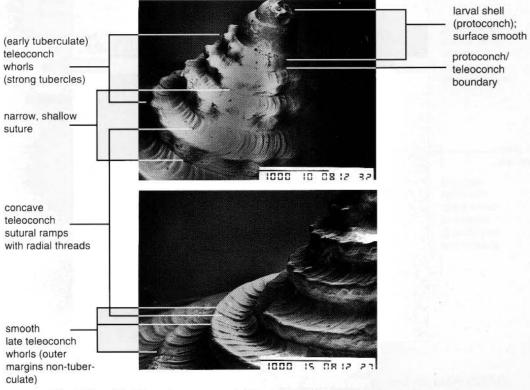
ribs: elevated, narrow, with rounded surface.

ribbons: elevated, wide, with flat surface.

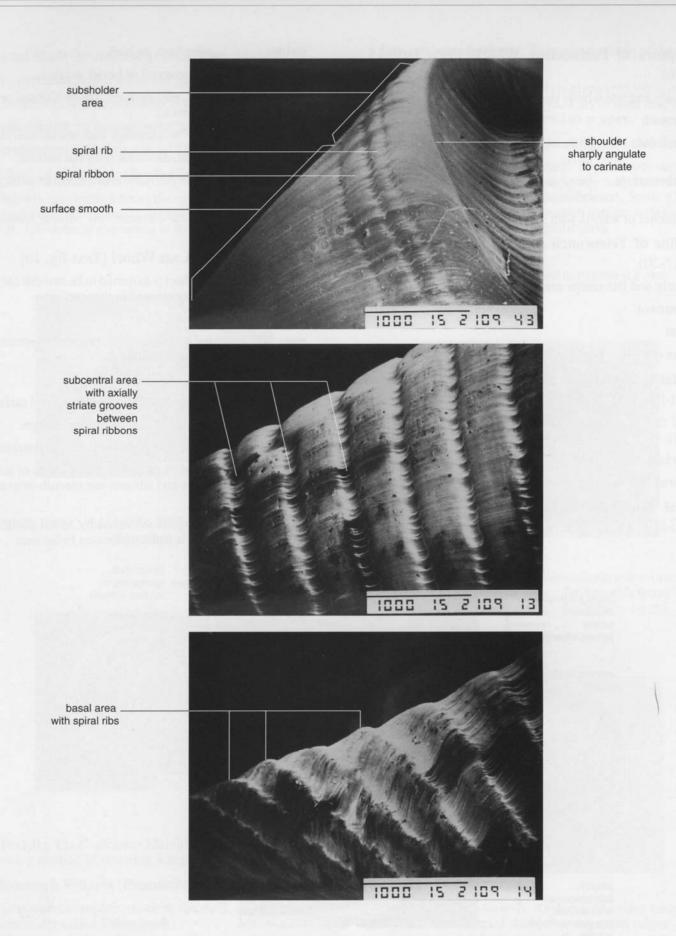
(May include modifiers: e.g. shallow, deep, prominent).

Spacing of sculptural elements, whether entire or interrupted, and whether ribs and ribbons are smooth or granulose are indicated.

Proportion of last whorl occupied by spiral sculpture (e.g. entire, basal third) is indicated.



**Text-fig. 15:** C. wakayamaensis Kuroda: spire (SEM). Scale bars = 1 mm.



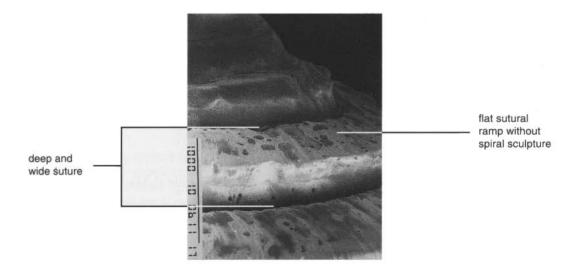
Text-fig. 16: C. wakayamaensis Kuroda: shoulder and last whorl (SEM). Scale bars = 1mm.

# **Axial Sculpture of Last Whorl**

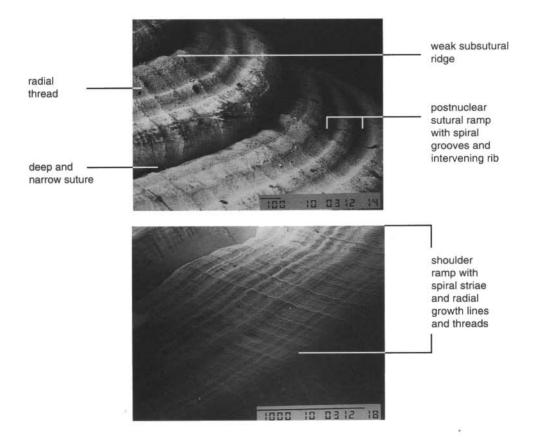
**axially striate spiral grooves:** grooves with axial threads separated by axially elongate cavities between.

axial threads (over entire surface).

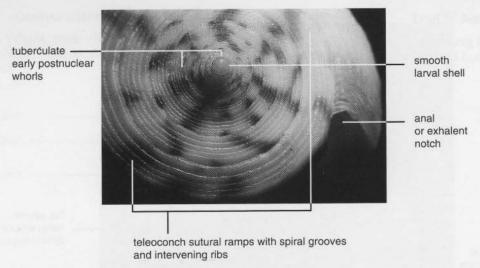
**costae:** strong, usually short, axially oriented elevations below shoulder.



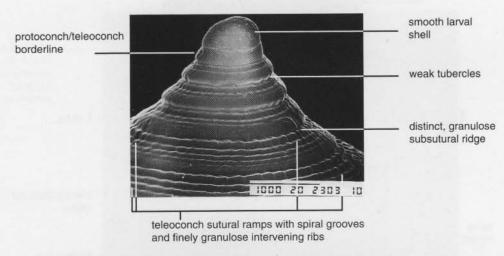
**Text-fig. 17:** *C. melvilli* Sowerby III: spire (SEM). Scale bar = 1 mm.



**Text-fig. 18:** *C. tuticorinensis* Röckel & Korn: sutural ramps and shoulder (SEM). Scale bars = 0.1 mm (top) and 1 mm (bottom).



Text-fig. 19: C. limpusi Röckel & Korn: spire (LM).



Text-fig. 20: C. lizardensis Crosse: apex (SEM). Scale bar = 1 mm.

### **Ground Colour of Last Whorl**

This character is mentioned only if a dominant base colour appears overlaid by other colour pattern; otherwise the less specific term "colour" is used.

#### Colour Pattern Elements (Text-figs. 3-10)

These apply to both last whorl and teleoconch sutural ramps; the term **axial** used for last whorl is replaced by **radial** when applied to spire.

dots: very small points.

dashes: narrow, ± rectangular, spirally or axially oriented.

lines: usually solid; if interrupted, this is indicated (may have modifiers: very fine, fine, broad; very fine lines may be referred to as hairlines); axially or spirally oriented.

spots: round unless other shape is stated.

bars: wide, ± rectangular; usually spirally elongate.

flecks: regularly or irregularly shaped.

**streaks:** ± rectangular, broader than broad lines; orientation variable.

flames: wavy, axially elongate.

**blotches:** irregularly shaped, not elongate, contrasting with ground colour.

**clouds:** irregularly shaped, not elongate; less contrasting with ground colour than blotches.

**bands:** usually spiral, occasionally axial, broader than streaks; usually solid; if interrupted, this is indicated.

Markings increase in size from the beginning to the end of the list above. The following may be of any size.

tents: triangular, with pointed to rounded apices.

reticulate pattern: arranged in net-like form.

Markings may be arranged in spiral or axial groups.

### Colour Pattern of Base

This character is mentioned only if exterior (dorsal side) of base differs in colour from the rest of the last whorl.

#### Colour Pattern of Larval Whorls

In most *Conus* species the larval whorls are of uniform colour, although they may have changed colour after metamorphosis. A few *Conus* species are known to have bicoloured larval shells.

## Colour Pattern of Teleoconch Sutural Ramps

Early and late ramps may be distinguished.

# **Colour of Aperture**

Includes general colour of inner surface of shell; bands at shoulder or centrally; stains at shoulder, deep within aperture, or near base; inner edge of outer lip, if a collabral band there contrasts with rest of aperture. If external pattern is visible through shell in aperture, aperture is described as "translucent."

## Periostracum (Textfigs. 21, 22)

(= Outer shell layer; thin organic layer consisting mainly of sclerotized proteins)

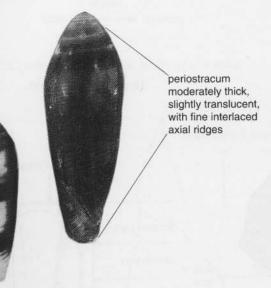
Colour is the first character given.

#### **Thickness**

If not stated, thickness is moderate.

thin

thick



**Text-fig. 21:** *C. violaceus* Gmelin: shells with and without periostracum.

Opacity

opaque

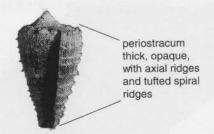
translucent (varying degrees)

#### Surface structure

smooth

axial ridges (may be interlaced; called radial on sutural ramps)

**spiral ridges:** smooth elevations at shoulder and on sutural ramps or on last whorl. If **tufts** are present, these are mentioned.



**Text-fig. 22:** *C. cuneolus* Reeve: sculpture of periostracum.

# Definitions of Other Terms Used in This Book

A list of definitions of technical terms other than those defined in the previous section.

#### **Terms of Orientation of Shells**

(in alphabetical order)

adapical: toward the apex; posterior; above (a

reference point).

abapical: away from the apex; anterior; below (a

reference point); toward the base.

adaxial: toward the axis of coiling; toward the

inner margin of a sutural ramp (used to indicate position of elements of spiral

sculpture on sutural ramps).

abaxial: away from the axis of coiling; toward

the outer margin of a sutural ramp.

basal: see abapical.

collabral: parallel to the outer lip of the aperture

(used to indicate orientation of axial pattern elements on the outer as well as

inner surface of the last whorl).

The following terms are derived from the orientation of the animal (see Anatomical Terms and Figures)

dorsal: side of shell opposite the aperture.

**left/right:** the aperture is on the right side when the

shell is viewed from the ventral side

with the apex up.

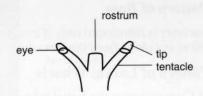
ventral: apertural side of the shell.

# Anatomical Terms and Figures (Text-figs. 23-27)

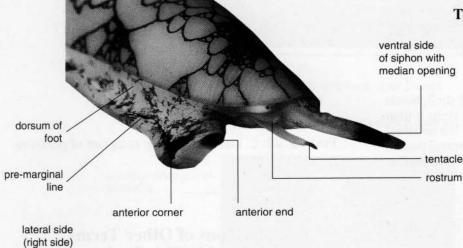
Terms and figures describing external morphology and orientation of the animal.

Body:

Body of the animal; soft parts (do not confuse with "body whorl" = last whorl of the shell).



Text-fig. 25: rostrum and tentacles.



Text-fig. 23: C. omaria Hwass: anterior parts of body.

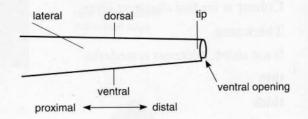
Proboscis: retractable and extendable tubular struc-

ture with the animal's true mouth at its tip.

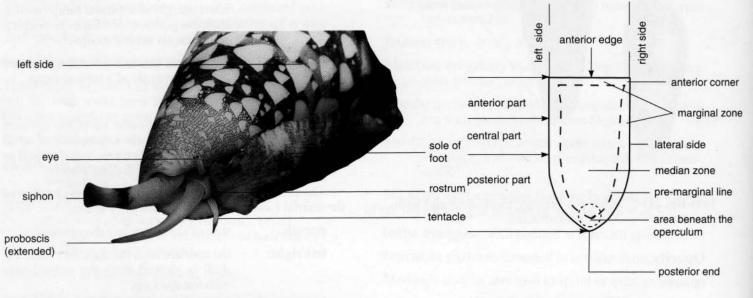
Rostrum: sheath of the proboscis.

Siphon: ventrally open channel directing water into

the mantle cavity (= toward the gill).



Text-fig. 26: siphon.



Text-fig. 24: C. ammiralis Linné: anterior parts of body.

Text-fig. 27: dorsum of foot.

# Terms and Figures describing Radular Teeth

(Text-figs. 28-31)

Apex: apical portion of tooth.

Barb: short or long cutting edge with a termi-

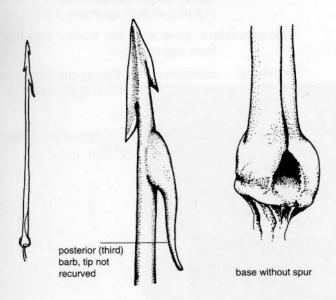
nal hook; part of adaptcal armature.

Base: abapical portion of tooth; often thick-

ened; may have a spur.

Blade: long cutting edge without a terminal

hook; part of adapical armature.



**Text-fig. 31:** *C. ermineus ermineus* Born: piscivorous species.

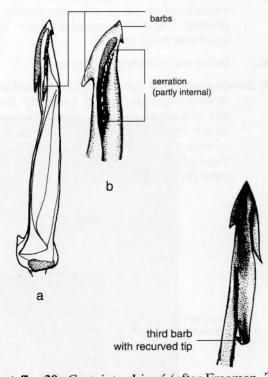
Serration: axial row(s) of denticles, often termi-

nating in a blunt or pointed **cusp**; length of serration and number of denticles per

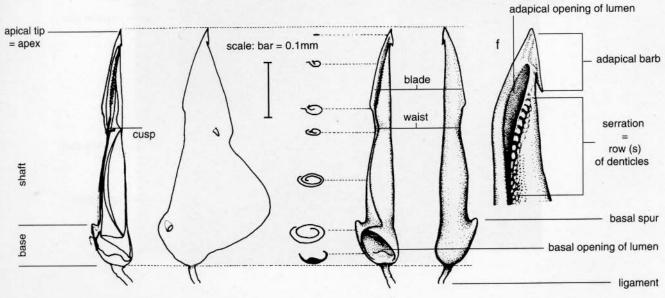
row are variable.

**Shaft:** portion of tooth between apex and base.

**Text-fig. 29:** *C. genuanus* Linné: radular tooth: a) shown as if translucent; b) shown as if opaque.



**Text-fig. 30:** *C. striatus* Linné (after Freeman, Turner & Silva): piscivorous species.



Text-fig. 28: C. ventricosus Gmelin: radular tooth: a) enrolled tubular tooth; b) unrolled sheet; c) cross sections of tooth at various sites; d), e) tooth seen from opposite sides; f) adaptical armature.

## Terms Related to the Study of Conus Venom

intracisternal: into the brain.

intraperitoneal: into the peritoneal cavity.

intravenous: into a vein.

# Terms and Figures Related to Reproduction and Development (Text-figs. 32-39)

basal plate: disk attaching the egg capsule to the sub-

stratum, or to one or more previously deposited capsules; capsules may have

confluent basal plates.

benthic: living on or in the sea bottom.

benthic development: life history without a planktonic

or free-swimming stage; hatchling generally is a crawling stage. *Conus* species in which the hatchling is a veliconcha are considered to have benthic development although the veliconcha may swim for a short period. Species with benthic develop-

ment produce egg capsules with rather few, large eggs that contain much nutrient material, and benthic development is lecithotrophic.

capsule sac: pouch of the egg capsule containing eggs embedded in a viscous matrix.

**capsule stalk:** short shaft rising from the basal plate and bearing the capsule sac.

**crawling stage:** juvenile stage that follows metamorphosis.

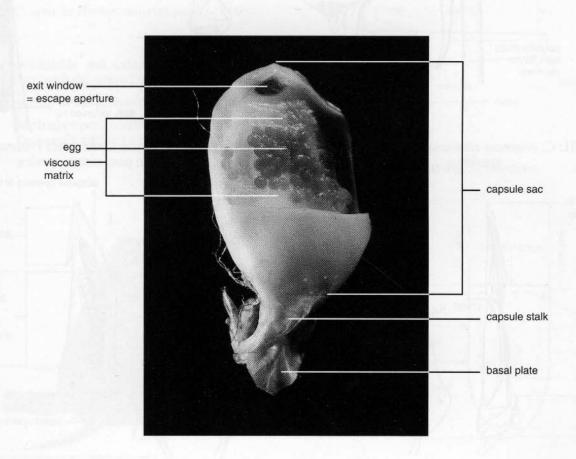
exit window:preformed area of the wall of the capsule sac, by which the hatchlings will leave the capsule; escape aperture is a synonym.

extracapsular: portion of life history after hatching from egg capsule.

**hatching:** emergence from the egg capsule; the hatching stage is often called the hatchling.

hatchling: see hatching.

intracapsular:portion of life history prior to hatching from the egg capsule.



Text-fig. 32: C. nivifer auct.: egg capsule.

larval period: in Conus, portion of life history from veliger to metamorphosis.

lecithotrophic: utilizing yolk for nutrition. Conus species that hatch as veliconcha or crawling stage have lecithotrophic development.

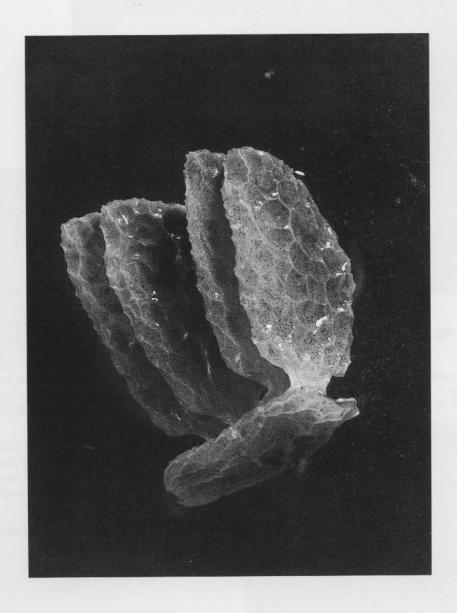
metamorphosis: transformation from larval to juvenile form, involving abrupt and profound morphological and habitat changes; in Conus, it may occur within the egg capsule or after hatching (i.e. intracapsular

or extracapsular).

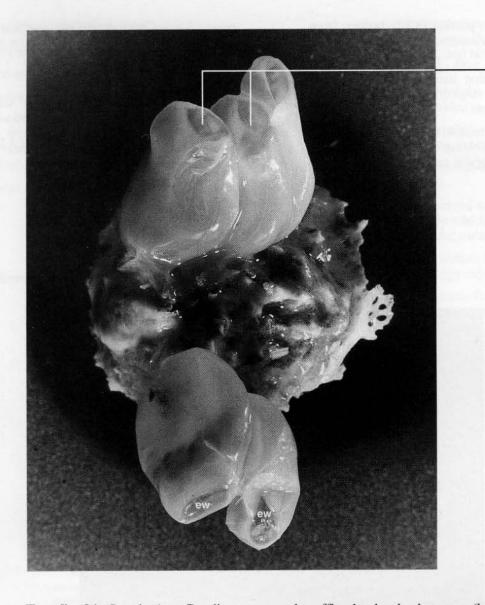
pediveliger: see veliconcha.

floating or swimming weakly in the planktonic: water column; the plankton comprises algae and animals with little or no ability to determine their own move-

ment.



Text-fig. 33: C. figulinus Linné: fragment of spawn: egg capsule attached to previously laid capsules; surface with a rather coarse network of corrugations.



Text-fig. 34: C. achatinus Gmelin: egg capsules affixed to hard substratum (bivalve shell).

planktonic development: life history with a planktonic or free-swimming stage. Conus species in which the hatchling is a veliger are considered to have planktonic development; species with planktonic development produce egg capsules with many small eggs and hence a small amount of yolk and the veligers are planktotrophic.

**planktotrophic:** feeding on plankton; *Conus* species that hatch at the veliger stage are planktotrophic during their larval period.

spawn: mass of egg capsules deposited by a *Conus* female at the same place; often called egg mass.

veliconcha: stage just prior to metamorphosis, may be extra- or intracapsular; the veliconcha is able to crawl and swim; sometimes called

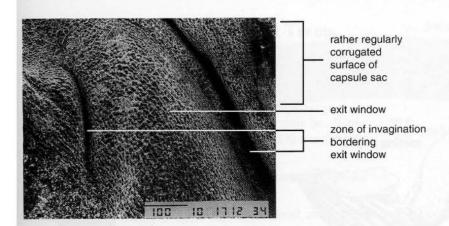
windows (ew)

pediveliger.

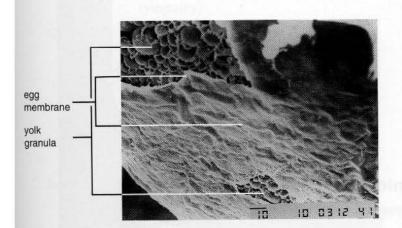
veliger: earliest larval stage in *Conus*; may be an extracapsular, planktonic or free-swimming and planktotrophic stage or a somewhat modified intracapsular stage that feeds on

yolk.

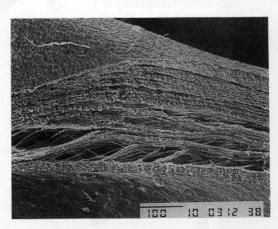
yolk: nutrient material stored in the egg.



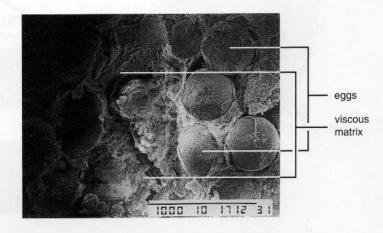
Text-fig. 35: C. nivifer auct.: exit window (SEM).



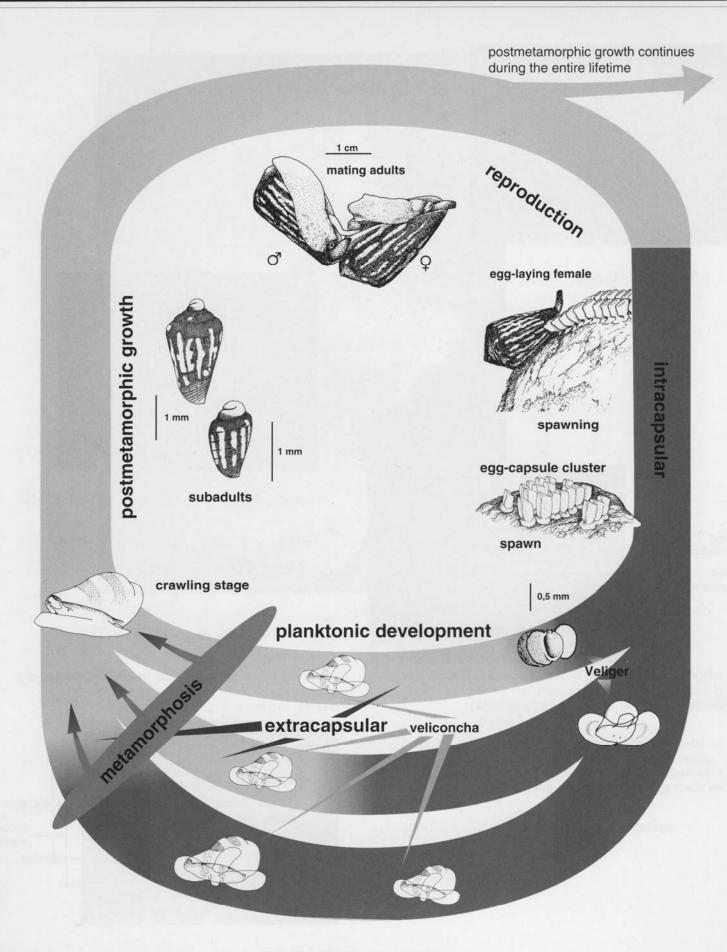
Text-fig. 37: C. nivifer auct.: egg (SEM).



Text-fig. 36: C. nivifer auct.: capsule wall (SEM).



Text-fig. 38: C. nivifer auct.: eggs within capsule (SEM).



Text-fig. 39: life cycles of Conus.

Zoogeographical and Ecological Terms

allopatric: relating to populations or taxa whose

ranges are geographically separate

(noun: allopatry).

geographic subspecies: allopatric or parapatric popula-

tions of a species that can be distinguished by constant and discontinuous

inheritable differences.

infralittoral fringe: transition zone between intertidal

and subtidal zones.

intertidal: shore zone between highest and lowest

tides.

parapatric: relating to populations or taxa with sep-

arate but adjoining ranges (noun:para-

patry).

subtidal: depth zone of the sea-shore extending

from the lower margin of the intertidal zone to about 200 m depth or to the edge

of the continental shelf.

sympatric: relating to populations or taxa that live

in the same geographical area (noun:

sympatry).

syntopic: relating to populations or taxa that live

sympatrically and occupy the same

general habitat.

(For benthic, lecithotrophic, planktonic, and planktotro-

phic see above)

Nomenclatural Terms

holotype: "A single specimen designated as the

name-bearing type of a species or subspecies when it was established, or the single specimen on which such a taxon was based when no type was specified."

(ICZN, 1985).

lectotype: "A syntype designated as the single

name-bearing type specimen subsequent to the establishment of a nominal species or subspecies."(ICZN,

1985).

**neotype:** "The single specimen designated as the

name-bearing type of a nominal species or subspecies for which no holotype, or lectotype, or syntype(s) or prior neotype, is believed to exist." (ICZN,

1985).

paratype: "Each specimen of a type series other

than the holotype." (ICZN, 1985).

species: "(1) The rank next below the genus

group; the basic rank of zoological classification. (2) A taxon at the rank of

species." (ICZN, 1985).

subspecies: "(1) The rank of the species group

below species; the lowest rank at which names are regulated by the Code. (2) A taxon at the rank of subspecies." (ICZN,

1985).

syntype: "Each specimen of a type series from

which neither a holotype nor a lectotype has been designated." (ICZN, 1985).

type series: "The series of specimens, defined in

Articles 72b (i) and 73b, which either constitutes the name-bearing type (syntypes) of a nominal species or subspecies or from which the name-bearing type has been or may be designated.

nated."(ICZN, 1985).

Abbreviations used in this Book

For abbreviations used in boxes, see the Glossary of Shell Characters.

coll. in the collection of ...

**E.** East, or in the eastern part of...

f. form.

ICZN International Commission for Zoological Nomenclature.

Nomenciature

Id. island.

Is. islands; an island group.

LM light microscope.

N. North, or in the northern part of ...

pers. comm. Personal comment, in writing to the

authors.

S. South, or in the southern part of...

SEM scanning electron micrograph

unpubl. observ. unpublished observation, by

authors or others, including photographic rec-

ords.

W. West, or in the western part of...

	<b>Museum Abbreviations</b>	MZUC	Museu Zoologico da Universidade de Coimbra, Portugal
AIM	Auckland Institute and Museum, New Zealand	NM	Natal Museum, Pietermaritzburg, Natal, South Africa
AMNH	American Museum of Natural History, New York, USA	NMC	Natur-Museum Coburg, Germany
AMS	Australian Museum, Sydney, Australia	NMNZ	National Museum of New Zealand, Wellington, New Zealand
ANSP	Academy of Natural Sciences, Philadelphia, USA	NMV	National Museum Victoria, Melbourne, Australia
BMNH	British Museum (Natural History), London, England, Great Britain	NMW	Naturhistorisches Museum, Vienna, Austria
CAS	California Academy of Sciences, San Francisco, USA	NMWC	National Museum of Wales, Cardiff, Wales, Great Britain
CMC	Canterbury Museum at Christchurch, New	NSMT	National Science Museum, Tokyo, Japan
	Zealand Delaware Museum of Natural History,	OUM	Oxford University Museum, England, Great Britain
DMNH	Wilmington, USA	RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
GIUT	Geological Institute, University of Tokyo, Japan	SAM	South Australian Museum, Adelaide, Australia
GIYU	Geological Institute, Yokohama National	SAMC	South Africa Museum, Cape Town, South
OITC	University, Japan	SAME	Africa
HUJ	Zoological Museum, Hebrew University, Jerusalem, Israel	SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
IMT	Institute of Malacology, Tokyo, Japan	SMF	Senckenberg Museum, Frankfurt/M., Germany
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium	TMH	Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia
	[KBIN Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium]	TMT	Taiwan Museum, Taipei, Taiwan
KPM	Kanagawa Prefectural Museum, Japan	USNM	National Museum of Natural History,
KSM	Kikuchi Shell Museum, Hyogo, Japan	WANG	Washington, D.C., USA
LMD	Löbbecke-Museum, Düsseldorf, Germany	WAM	Western Australian Museum, Perth, Australia
LSL	Linnean Collection, Linnean Society, London,	WPMN	Wakayama Prefectural Museum of Natural History, Japan
MCZ	England, Great Britain  Museum of Comparative Zoology, Harvard	ZIUU	Zoological Institute, University of Uppsala, Sweden
MHNB	University, Cambridge, USA Muséum d'Histoire Naturelle de Bordeaux, France	ZMA	Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam, The Netherlands
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland	ZMB	Zoologisches Museum, Humboldt-Universität, Berlin, Germany
MHNN	Muséum d'Histoire Naturelle, Nantes, France	ZMMU	Zoological Museum of Moscow State
MM	Manchester Museum, England		University, Moscow, Russia
MNG	Museum der Natur, Gotha, Germany	ZMUC	Zoologisk Museum, University of
MNHN	Muséum National d'Histoire Naturelle, Paris, France	ZSM	Copenhagen, Denmark Zoologische Staatssammlung, Munich,
MSNP	Museo di Storia Naturale, Universita de Pisa, Italy	ZSI	Germany Zoological Survey of India, Calcutta, India

# **Species Account**

#### 1

### Conus marmoreus LINNÉ, 1758

(Plate 1, Figures 1-9; Plate 74, Figure 1; Plate 77, First row, left; Map 1)

- 1758 Conus marmoreus Linné, Syst. Nat., 10 ed., 1: 712, no. 250
- 1798 Cucullus proarchithalassus Röding, Mus. Bolten., 2: 38, no. 470/5
- 1811 Conus maculatus Perry, Conchology: Pl. 24 fig. 4 (non C. maculatus Bosc, 1801)
- 1839 Conus marmoreus var. granulatus Sowerby I, Conch. Ill.: Pt. 155/156, fig. 120\* (non C. granulatus Linné, 1758)
- 1861 Conus crosseanus Bernardi, J. Conchyl. (Paris), 9: 168-169, pl. 6 figs. 3,4
- 1870 Conus suffusus Sowerby III, Proc. Zool. Soc. London, 1870: 255-256, pl. 22 fig. 9
- 1872 Conus suffusus var. noumeensis Crosse, J. Conchyl. (Paris), 20: 155-156; 20: 350, pl. 16 fig. 2
- 1875 Conus pseudomarmoreus Crosse, J. Conchyl. (Paris), 23: 223-225, pl. 9 fig. 4
- 1878 Conus crosseanus var. lineata Crosse, J. Conchyl. (Paris), 26: 168, pl. 3 figs. 3, 3a (non C. lineatus Solander, 1766)

Types: C. marmoreus: Lectotype (Kohn, 1963, as "holotype", Walls, [1979]) in LSL (51 x 28 mm); C. proarchithalassus: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 62 fig. 686) (56 x 33 mm); C. maculatus: Holotype (Kohn, 1986) figured in Perry (1811: Pl. 24 fig. 4) (76 x 45 mm); C. m. var. granulatus: Lectotype (Kohn, 1992) figured in Sowerby I (1839: Pt. 155/156, fig. 120\*) (30 x 17 mm); C. crosseanus: Lectotype (Coomans et al., 1985a) in BMNH (69 x 39.5 mm); C. suffusus: Holotype in BMNH (55 x 33 mm); C. s. var. noumeensis: Original figure 61 x 34 mm; C. pseudomarmoreus: Holotype in MNHN (50.5 x 30

mm); C. c. var. lineata: Original figure 65 x 37 mm (70 x 36 mm acc. Crosse, 1872).

**Type Localities:** *C. marmoreus*: "Asia"; *C. crosseanus*: "Nova Caledonia"; *C. suffusus*: "New Caledonia"; *C. s.* var. *noumeensis*: "Noumea, Novae Caledoniae"; *C. c.* var. *lineata*: "Nova Caledonia."

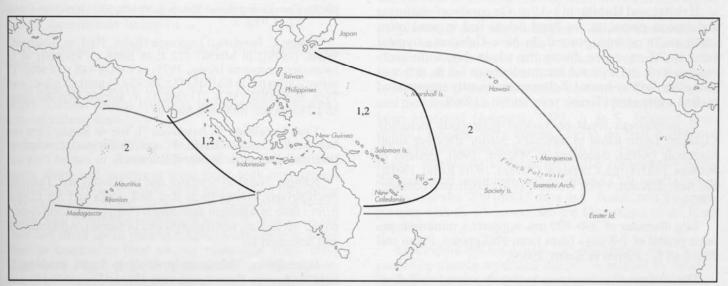
Range: India to Marshall Is. and Fiji.

**Description:** Medium-sized to large, moderately solid to heavy. Shells from New Caledonia consistently smaller than shells from other areas; form *suffusus* (Pl. 1, Fig. 6) also lighter than other forms. Last whorl conical, broadest in form *crosseanus* (Pl. 1, Figs. 7, 8); outline almost straight, somewhat convex adapically. Shoulder angulate, strongly tuberculate to almost smooth. Spire of low to moderate height, outline straight to slightly concave. Postnuclear spire whorls strongly to weakly tuberculate. Teleoconch sutural ramps concave in late whorls, with 2-4 weak spiral grooves and additional spiral striae; spiral sculpture often obsolete. Last whorl with usually weak, regularly spaced spiral ribs on basal fourth to half.

### C. marmoreus Shell Morphometry

L	50 - 150 mm
- New Caledonia	40 - 65 mm
RW	0.45 - 1.95 g/mm (L 50-113 mm)
-form suffusus	0.21 - 0.60 g/mm
RD	0.56 - 0.65
-form crosseanus	0.60 - 0.67
PMD	0.85 - 0.94
RSH	0.05 - 0.15

Map 1



1: C. marmoreus 2: C. bandanus

Ground colour usually white; may be bluish white, pale pink or pale yellow in shells from New Caledonia. Last whorl generally with a regular network of dark brown to black lines and triangular to rhomboid areas, outlining white tents that are often quite uniform in shape and arrangement and usually separate from each other. In New Caledonia, colour of network may grade to orangish red or orangish brown, axial lines may replace network, and pattern may be reduced or absent. Apex purplish red. Postnuclear sutural ramps with a dark brown to black network of lines, streaks and blotches. Aperture white to pinkish orange behind a white marginal zone.

Periostracum yellowish to orangish brown, thin, translucent, smooth.

Dorsum of foot white to tan, mottled with brown, with a black marginal line or band ending in a latero-anterior blotch; a small black triangular blotch at centre either separate from or fusing with lateral blotches. Lateral margins of foot may be flecked with brown; anterior edge of foot occasionally yellow-orange. Sole of foot white to cream, tinged with various shades of brown, with darker brown longitudinal lines. Ventral side of rostrum cream, with tan transverse lines. Tentacles white to light brown; tip white, brown or black; proximal dorsal side often black. Siphon white, sometimes edged with yellow to pale brown; with a black anterior band and a black to brown posterior half-ring or band (Pl. 74, Fig. 1; Pl. 77, First row, left). In subadult specimens from Marshall Is., entire foot with sparse brown mottling on white ground (Walls, [1979]; Chaberman, pers. comm., 1981; Estival, unpubl. observ.; Pearson, unpubl. observ.).

Radular teeth with one barb and a long serration that ends in a cusp at or behind centre of shaft (Bergh, 1895; Peile, 1939; Endean & Rudkin, 1965; Thompson & Bebbington, 1973). Nybakken (1990) reported 2 opposed adapical barbs, the anterior of which is laterally inflated; waist and basal spur are absent. In form *crosseanus*, teeth with an adapical barb opposite a blade, otherwise matching those of typical *C. marmoreus* (Rolán, 1993).

Habitat and Habits: In 1-15 m. On coral reef platforms and lagoon pinnacles, on coral debris and in sand often under rocks or among weed. In New Caledonia, typical form in 1-5 m, active during the whole day; form *crosseanus*, form *suffusus* and intermediates in 1-3 m, active at rising tide; light coloured shells predominantly encountered on fine white sand (Tirard, pers. comm., 1989).

C. marmoreus feeds on various gastropods including Conidae. Toxin lethal to molluscs, hardly affecting small mammals (Kohn, Saunders & Wiener, 1960; Endean & Rudkin, 1963; Cruz, Corpus & Olivera, 1976; Kohn, 1980a; Reichelt & Kohn, 1985; Collins, 1987; Loch, pers. comm., 1987).

Egg diameter of 390-400 µm suggests a minimum pelagic period of 7-8 days (data from Philippines, Palau and Marshall Is.; Perron & Kohn, 1985).

**Discussion:** *C. marmoreus* is closely related to *C. bandanus*. For comparison, see the Discussion of that species.

The New Caledonian populations of *C. marmoreus* (Pl. 1, Figs. 5-9) are often considered to represent a separate subspecies (*C. m. crosseanus*) or species (*C. crosseanus*). However, except for their smaller size, New Caledonian shells intergrade with *C. marmoreus* from other localities in all morphological characters and we consider them as form *crosseanus*, characterized by weakly tuberculate postnuclear whorls and a rather axially lineate dark brown pattern on an often bluish white ground. Specimens with additional spiral ground-colour lines were named var. *lineata*. Form *suffusus* (Pl. 1, Fig. 6) has distinct spire tubercles, lacks any pattern elements on its white, pale pink or pale yellow background, and its aperture is pink to orange. Immaculate white shells with a white aperture were described as *C. suffusus* var. *noumeensis*.

Form *pseudomarmoreus* (Pl. 1, Fig. 4) is characterized by an almost smooth shoulder. Shells with a typically arranged reddish to brownish orange pattern are known from the Isle of Pines (New Caledonia).

# 2 Conus bandanus HWASS in BRUGUIÈRE, 1792

(Plate 1, Figures 10-23; Plate 2, Figures 1-4; Plate 77, First row, right, Second row, left; Map 1)

- 1792 Conus bandanus Hwass in Bruguière, Encycl. Méth., 1: 611, no. 5
- 1798 Cucullus equestris Röding, Mus. Bolten., 2: 38, no. 474/6 (non C. equestris Röding, Mus. Bolten., 2: 46)
- 1798 Cucullus torquatus Röding, Mus. Bolten., 2: 38, no. 475/7 (non C. torquatus Röding, 2: 45).
- 1843 Conus vidua Reeve, Proc. Zool. Soc. London, 11: 169; Conch. Icon., 1, Conus: Pl. 8 sp. 45
- 1859 Conus nigrescens Sowerby II, Proc. Zool. Soc. London, 1859: 429, pl. 49 fig. 2
- 1980 Conus vidua mozoii Melvin & Melvin, 1000 World Sea Shells: 27, pl. 9 fig. 2

**Types:** *C. bandanus*: Lectotype (Kohn, 1964, as "holotype", Walls, [1979]) in MHNG (77 x 45 mm); *C. equestris & C. torquatus*: Lectotype (Kohn, 1975) in ZMUC (48 x 25 mm); *C. vidua*: 2 syntypes in BMNH (47 x 26; 72 x 41 mm); *C. nigrescens*: Type in BMNH (37 x 21 mm); *C. v. mozoii*: Original figure 56 x 28 mm acc. Melvin & Melvin.

**Type Localities:** *C. bandanus*: "L'Isle de Banda, l'une des Moluques"; *C. vidua*: "Island of Capul, Philippines"; *C. v. mozoii*: "in Honda Bay, Arricife Island, Palawan."

Range: Natal to Somalia and to Hawaii and Tuamotu Archipelago, absent from Red Sea, India and Sri Lanka; form *vidua* in southern and central Philippines; form *equestris* in Moluccas; form *nigrescens* in Samoa, Admiralty Is. and Solomon Is.

**Description:** Moderately small to large, moderately light to heavy. Forms *equestris* (Pl. 1, Figs. 14, 15) and *vidua* (Pl. 1, Figs. 16-23) smaller than other forms; form

nigrescens moderately small to medium-sized and moderately light to moderately solid. Last whorl conical to ventricosely conical; outline nearly straight, variably convex adapically. Shoulder angulate, moderately to strongly tuberculate. Spire of low to moderate height, consistently low in forms vidua, nigrescens (Pl. 2, Figs. 1-4) and equestris; outline straight to moderately concave. Larval shell of about 2.25 whorls. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps concave in late whorls, with 2-4 weak spiral grooves and additional spiral striae; spiral sculpture often obsolete. Last whorl with weak spiral grooves on basal third to three-fourths.

C. banda	anus Shell Morphometry
L	50 - 150 mm
- form vidua	45 - 80 mm
- form nigrescens	25 - 65 mm
- form equestris	45 - 60 mm
RW	0.08 - 1.90 g/mm (L 25-123 mm)
RD	0.53 - 0.66
- form vidua	0.57 - 0.63
- form <i>nigrescens</i>	0.58 - 0.66
PMD	0.82 - 0.94
RSH	0.03 - 0.20
- form vidua	0.03 - 0.10
- form nigrescens	0.07 - 0.11
- form equestris	0.07 - 0.10

Ground colour white to pale violet or pale pink. Last whorl with a blackish brown network of lines, triangular areas and rhomboid blotches clustered in a spiral band on either side of central area; bands often with an orange to brown background. Base may be tinged with bluish grey. Apex white to light purple; larval whorls light yellow in Hawaiian shells (Perron, 1981a). Postnuclear sutural ramps with a blackish brown network of lines and streaks. Aperture white, occasionally tinged with violet, pink or yellow; base of aperture may be brown.

Periostracum yellow to orange, thin, translucent, smooth.

In form *equestris* (Pl. 1, Figs. 14, 15), colour bands with larger blackish brown blotches, interspersed with white tents of various sizes.

In form *vidua* (Pl. 1, Figs. 16-23), last whorl with a broad blackish brown or occasionally bright orange spiral band above centre and another at basal third, both interspersed with small white to brownish white tents. Lower band often extends to base. White zones below shoulder and below centre with a variably incomplete network of fine zigzag lines and small spots; pattern ranging from obsolete wavy lines to continuous lines edging coalescent tents. Base tinged with bluish grey. Anterior end of aperture violetbrown or orange-brown; rest of aperture white, suffused with blue or orange.

In form *nigrescens* (Pl. 2, Figs. 1-4), colour pattern ranging from typically patterned to almost solid black shells. Aperture white to bluish white.

Dorsum of foot white to cream, heavily mottled with brown, lighter in transition zone from anterior to central part; marginal zone with a relatively broad black band ending in latero-anterior blotch; a black central spot at anterior end and a white fleck beneath the operculum. Sole of foot cream, transversely and longitudinally mottled with brown. Rostrum cream, mottled with brown on dorsal side. Tentacles white to brown, with a dark tip, dorsally mottled with brown. Siphon white, with or without a yellow edge and with a red, brown or black anterior ring as well as a posterior band or half-ring shading from tan to blackish brown (Kohn, 1959a; Kohn & Weaver, 1962; Pearson, unpubl. observ.; Kohn, unpubl. observ.; Pl. 77, First row, right, Second row, left).

In form *vidua*, radular teeth with an adapical barb opposite a blade; serration about twice as long as blade, ending in a prominent cusp; base with a spur (Nybakken, 1990).

Habitat and Habits: Shallow subtidal to 90 m (Hawaii: Kohn & Weaver, 1962), mostly encountered in 5-20 m. On coral reef and in reef lagoons, in sand, on weedy sand, rocks, and rubble. Animals active at night (New Caledonia; Tirard, pers. comm., 1989).

*C. bandanus* feeds on gastropods, including congeners (Hawaii; Kohn, 1959b). In form *vidua*, radular tooth structure suggests vermivory (Nybakken, 1990).

Egg diameter varies from 299  $\mu$ m (Palau) to 355  $\mu$ m (Hawaii) suggesting a minimum pelagic period of 15-10 days (Perron, 1981a,b,c; Perron & Kohn, 1985).

Discussion: C. bandanus is a close relative of C. marmoreus, and some authors have included it in the latter species. The conchological differences are comparatively slight, consisting of more pronounced spire tubercles and a less regular pattern with 2 distinct dark colour bands in C. bandanus, while the pattern of C. marmoreus is generally uniform and lacks bands. Ecological differences also favour separation at the species level: C. bandanus usually lives in deeper water and often occupies a different microhabitat where both occur in sympatry. In Kwajalein, Marshall Is., C. marmoreus is found on inter-island coral reef and at the east side of the lagoon on sand bottom, while C. bandanus is restricted to rock and rubble bottoms of the ocean-side and the lagoon-side of the west reef; co-occurrence has not been observed (Johnson, 1977; J. & S. Johnson, pers. comm.; Pearson, pers. comm., 1991). In New Caledonia, the bathymetric ranges differ (1-5 m in C. marmoreus; 5-18 m in C. bandanus). In Palau, they differ considerably in egg diameter and minimum pelagic period (393 µm/8 days in C. marmoreus; 299 µm/15 days in C. bandanus). For comparison with C. nocturnus, see the Discussion of the latter species.

Specimens agreeing with the description of *C. vidua* cannot be clearly separated from *C. bandanus* by conchological characters. In the western part of the central Philippines, they intergrade with *C. bandanus*. Their co-

occurrence, with intermediate shells, favours the ranking of *C. vidua* as a form of *C. bandanus*.

Specimens agreeing with the description of *C. nigrescens* show a gradual transition from the typical *C. bandanus* pattern to almost black shells. In Western Samoa, 6% of the population have nearly black shells, while in American Samoa, the pattern is like that of *C. bandanus* elsewhere. Shell size is similar in American Samoa and Western Samoa. The habitat is very similar in American Samoa and Hawaii (Purtymun, 1977). We provisionally consider *C. nigrescens* a form, occurring in Samoa, Solomon Is. and Admiralty Is.

3

## Conus nocturnus [LIGHTFOOT], 1786

(Plate 2, Figures 5-8; Map 2)

- 1786 Conus nocturnus [Lightfoot], Cat. Portland Mus.: 156, no. 3411
- 1792 Conus nocturnus Hwass in Bruguière, Encycl. Méth., 1: 611-612, no. 6
- 1857 Conus deburghiae Sowerby II, Thes. Conch., 3: 2, no. 7, pl. 1 figs. 6, 7

**Types:** *C. nocturnus* [Lightfoot]: Lectotype (Kohn, 1964) figured in Martini (1773: Pl. 62 fig. 687) (49 x 24 mm); *C. nocturnus* Hwass: Lectotype (Kohn, 1968) in MHNG (63 x 32 mm); *C. deburghiae*: Lectotype (Coomans et al., 1985b) figured in Sowerby II (1857: Pl. 1 fig. 6) (58 x 31 mm, see Coomans et al., 1985b).

**Type Localities:** C. nocturnus [Lightfoot]: "China"; C. nocturnus Hwass: "aux Moluques"; C. deburghiae: "Moluccas."

Range: Moluccas and N.W. New Guinea.

**Description:** Medium-sized to moderately large, moderately solid to solid. Last whorl slightly ventricosely conical to conoid-cylindrical, outline convex; left side concave abapically. Shoulder angulate, strongly tuberculate. Spire of low to moderate height, outline straight to slightly concave. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps concave in late whorls, with 2-3 distinct to obsolete spiral grooves. Last whorl with weak spiral ribs on basal fourth; ribs often granulose and extending up to shoulder (form *deburghiae*).

C. n	octurnus Shell Morphometry
- nometal-	45 - 86 mm
RW	0.19 - 0.40 g/mm (L 43-61 mm)
RD	0.55 - 0.60
PMD	0.80 - 0.93
RSH	0.09 - 0.20

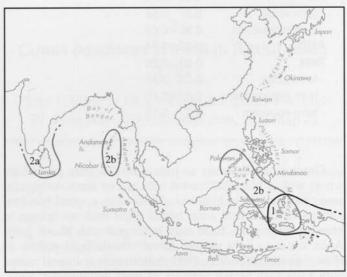
Ground colour white. Last whorl with 2 broad blackish brown spiral bands, above and below centre. White zones with dark brown reticulate lines. Teleoconch sutural ramps with irregularly spaced brown reticulate lines. Aperture white.

**Habitat and Habits:** In 1.5-2 m, on coral sand under rocks and on dead coral (Ormas, pers. comm., 1993).

**Discussion:** C. nocturnus is most similar to C. bandanus. We accept the conclusion of Coomans et al. (1985b) that it is a distinct species. C. bandanus attains larger maximum size (to 150 mm) and has a more conical last whorl with straighter outline. The banding pattern of C. nocturnus is most similar to C. bandanus form equestris from the Moluccas, which is also similar in size. However, the latter differs in shape as mentioned above, has a more pronounced tent-marked pattern, and has a lower spire (RSH 0.07-0.10). C. nocturnus has recently been found living together with C. bandanus and C. marmoreus in Seram, Indonesia (Ormas, pers. comm., 1993).

C. deburghiae represents a granulated form (Coomans et al., 1985b), C. nocturnus Hwass is a homonym and synonym of C. nocturnus [Lightfoot].

Map 2



1: C. nocturnus 2a: C. araneosus araneosus 2b: C. araneosus nicobaricus

### 4

# Conus araneosus [LIGHTFOOT], 1786

(Plate 2, Figures 9-15; Map 2)

- 1786 Conus araneosus [Lightfoot], Cat. Portland Mus.: 76, no. 1714; 106, no. 2328
- 1791 Conus arachnoideus Gmelin, Syst. Nat., 13 ed., 1: 3388, no. 34
- 1792 Conus nicobaricus Hwass in Bruguière, Encycl. Méth., 1: 612, no. 7
- 1792 Conus araneosus Hwass in Bruguière, Encycl. Méth., 1: 612-613, no. 8
- 1811 Conus reticulatus Perry, Conchology: Pl. 24 no. 2
- 1838 Conus monstrosus "Chemnitz" Küster, Syst. Conch. Cab. Martini Chemnitz, 4 (2), 1, Conus: 77, pl. 12 figs. 5, 6
- 1857 Conus peplum Sowerby II, Thes. Conch., 3: 3, no. 11, pl. 1 fig. 13; pl. 17 fig. 408

Types: C. araneosus [Lightfoot]: Lectotype (Kohn, 1964), figured in Martini (1773: Pl. 61 fig. 676) (64 x 39 mm); C. arachnoides: Lectotype (Kohn, 1966), figured in Knorr (1772: Pl. 4 fig. 4) (49 x 27 mm); C. nicobaricus: Lectotype (Kohn, 1968) figured in Tableau (1798: Pl. 318 fig. 9) (63 x 36 mm); C. araneosus Hwass: Lectotype (Kohn, 1968) in MNHG (94 x 55 mm); C. reticulatus: Holotype figured in Perry (1811: Pl. 24, no. 2) (61 x 37 mm); C. monstrosus: Holotype figured in Küster (1838: Pl.12 fig.6) (50 x 32 mm); C. peplum: Original figure (fig. 13) 30 x 18 mm.

**Type Localities:** *C. araneosus* [Lightfoot]: "China, Coromandel"; *C. nicobaricus*: "des grandes Indes"; *C. araneosus* Hwass: "isles Moluques"; *C. monstrosus*: "Indischer Ozean"; *C. peplum*: "Red Sea."

Range: C. a. araneosus: Sri Lanka and S.E. India. C. a. nicobaricus: Moluccas to Philippines; Nicobar and Andaman Is.

**Description:** Moderately large to large, solid to heavy. Last whorl conical, generally broader in *C.a. araneosus* (Pl. 2, Figs. 9-12); outline straight to slightly convex. Shoulder angulate, weakly to strongly tuberculate. Spire of low to moderate height, consistently low in *C. a. nicobaricus* (Pl. 2, Figs. 13-15); outline straight. Postnuclear spire whorls tuberculate. Late teleoconch sutural ramps concave and nearly smooth. Last whorl with weak spiral ribs above base.

## C. araneosus Shell Morphometry

L	55 - 100 mm	
RW	0.40 - 1.50 g/mm	
RD		
- C. a. araneosus	0.61 - 0.70	
- C. a. nicobaricus	0.54 - 0.63	
PMD	0.86 - 0.94	
RSH		
- C. a. araneosus	0.09 - 0.15	
- C. a. nicobaricus	0.04 - 0.09	

C. a. araneosus: Ground colour white, tinged with violet in shells from India. Last whorl with a fine network of reddish brown lines outlining small white tents, usually with a dark brown spiral band on each side of centre. Bands interrupted by bluish ground-colour tents and a few brown tents. Teleoconch sutural ramps with fine reddish brown zigzag lines and bluish brown marginal blotches between tubercles. Aperture nearly white (shells from Sri Lanka) or outer part pale violet, interior deep yellow (shells from S.E. India, Pl. 2 Fig. 12).

Periostracum yellow, thin, translucent, smooth.

Foot buff; sides and dorsum mottled with brown and with a black longitudinal line continued as a broad band around the anterior dorsum; anterior edge of sole yellow. Rostrum buff. Tentacles buff, anterior margins grey. Tip of

siphon orange, followed proximally by a narrow white stripe, broad grey stripe and broad stripe of buff heavily mottled with reddish brown (Kohn, 1978a).

Radular teeth matching those of *C. a. nicobaricus* in shape and armature; differences stated by Nybakken in 1990, were in error (Nybakken, pers. comm., 1993).

C. a. nicobaricus: Ground colour white, occasionally with a tinge of red or violet. Last whorl with a network of reddish brown to blackish brown lines outlining variously sized white tents that often coalesce. Usually with 3 discontinuous bluish or blackish brown spiral bands, on both sides of centre and below shoulder; central band more pronounced than other bands. Spire and shoulder with fine, dark brown zigzag lines and blue-tinged brown blotches between tubercles. Aperture white to light violet, yellow deeper within.

Periostracum cream to brown, thin, translucent, smooth.

Foot buff, paler and with a bilobate black blotch on anterior part of dorsum; sole with irregular transverse and longitudinal brown lines, posterior half darker and anterior edge yellow. Siphon tipped with yellow, then banded with white, black, yellow and dark brown (Kohn, unpubl. observ.).

Radular teeth long and narrow, with one barb and a long, fine serration terminating in a distinct backward-pointing cusp at centre of shaft or somewhat posterior to it (Bergh, 1895). According to Nybakken (1990), radular teeth less elongate, serration shorter, shaft with a waist and base with a spur; adaptical armature consisting of a barb opposite a blade.

Habitat and Habits: C. a. araneosus: Intertidal to 20 m, on limestone and sandy substrata. C. a. araneosus appears to feed on gastropods (Kohn, 1978a). The egg mass consists of several layers of capsules, each containing 63-214 eggs about 490 μm in diameter. The larvae hatch at a stage that "swims and crawls" (=veliconcha; Natarajan, 1957). C. a. nicobaricus: Shallow water, on sand substrate under corals and in coral rubble on subtidal reef platforms. Radular tooth structure as given by Nybakken (1990; pers. comm., 1993) indicates vermivory, while that given by Bergh (1895) rather suggests molluscivory.

**Discussion:** C. araneosus resembles C. bandanus in shape, but the latter species attains larger size (to 150 mm); its last whorl colour pattern is a much coarser network forming fewer white tents.

We consider *C. a. araneosus* and *C. a. nicobaricus* as subspecies, because they are nearly indistinguishable in shell characters and colouration of the animal. *C. a. nicobaricus* usually has a relatively narrower last whorl and larger shoulder tubercles, and it tends to have a slightly lower spire and coarser colour pattern.

5

## Conus distans HWASS in BRUGUIÈRE, 1792

(Plate 2, Figures 16-19; Plate 74, Figure 2; Map 3)

- 1792 Conus distans Hwass in Bruguière, Encycl. Méth., 1: 634, no. 32
- 1896 Conus waterhouseae Brazier, Proc. Linn. Soc. New South Wales, 10: 471
- 1896 Conus kenyonae Brazier, Proc. Linn. Soc. New South Wales, 21: 346
- 1896 Conus kenyonae var. arrowsmithensis Brazier, Proc. Linn. Soc. New South Wales, 21: 346
- 1970 Conus (Rhizoconus?) chinoi Shikama, Venus, 29: 115-116, figs. 1-4

**Types:** *C. distans*: Lectotype (Kohn, 1964, as "holotype", Coomans et al., 1985b) in MHNG (100 x 51 mm); *C. waterhouseae*: Holotype in SAM (28.5 x 16 mm); *C. kenyonae*: Holotype in SAM (42 x 23.5 mm); *C. k.* var. *arrowsmithensis*: Holotype in SAM (35.5 x 20.5 mm); *C. chinoi*: Holotype in NSMT (32 x 17.5 mm).

Type Localities: C. distans: "les côtes de la nouvelle Zélande"; corrected in "Moluccas" (Coomans et al., 1985b); C. waterhouseae: "Solomon Islands"; C. kenyonae: "Shark's Bay, W. A."; C. k. var. arrowsmithensis: "Arrowsmith Isl., Marshall Islands"; C. chinoi: "Ogokuda, Shiono-misaki; Wakayama Prefecture, Japan."

Range: Southern Natal to Red Sea and to Hawaii and French Polynesia. No reports from the Arabian Sea and India.

Description: Moderately large to large, solid to heavy. Last whorl conical; outline convex to strongly convex near shoulder, straight below. Shoulder variably angulate, tuberculate in smaller adults (up to 75-85 mm in length). Spire of low to moderate height, outline concave to convex. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps concave, with 2-3 weak spiral grooves on middle ramps, and finer spiral striation on later ramps. In subadults,

last whorl with broad spiral ribs at base, followed by about 5 widely set spiral grooves almost to adapical third with ribbons between. In large adults, surface smooth except for broad but weak spiral ribs at base.

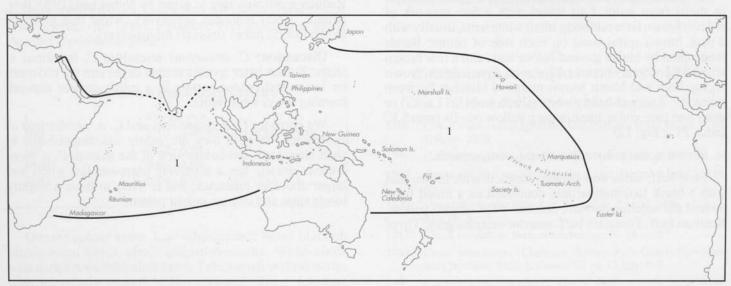
C. distans Shell Morphometry	
L	65 - 137 mm
RW	0.60 - 2.00 g/mm
RD	0.54 - 0.64
PMD	0.85 - 0.95
RSH	0.04 - 0.18

Ground colour white. In smaller subadults (Pl. 2, Fig. 19), last whorl with olive brown clouds, base dark brown. During growth, clouded pattern changing to a band on each side of centre; bands either progressively occupying entire last whorl (Pacific populations) or secondarily reduced (Indian Ocean populations). Bands usually become less olive and base slightly lighter during growth. Teleoconch spire with blackish brown radial markings between tubercles (including large Indian Ocean shells without colour bands on last whorl).

Periostracum blackish brown, thick, opaque, and rough in large adults from Philippines (L 130 mm) and lighter brown, thinner, with widely set spiral rows of strong tufts on last whorl and spire in subadults from Madagascar. A thick, olive-green or brown periostracum with tufted ridges around last whorl is reported from Hawaii (Kohn, 1959a) and Fiji (Cernohorsky, 1964).

Dorsum of foot with orange-brown marginal zone, except for anterior end; a line of blackish brown spots setting off marginal zone from pale orange median and anterior areas, with tan spots centrally and dark brown spots anteriorly. Foot often largely brown (Hawaii). Rostrum whitish

Map 3



1: C. distans

tan (N. Papua New Guinea) to dark brown (Hawaii); tipped with yellow in Hawaii. Tentacles light brown (Hawaii) to greyish white with white tip (N. Papua New Guinea). Siphon light tan mottled with brown (Hawaii) or white, mottled with orange and brown except tip (N. Papua New Guinea) (Kohn, 1959a; Chaberman, pers. comm., 1981) (Pl. 74, Fig. 2).

Radular teeth relatively small and stout, with a fold near apex and an adapical barb opposite a blade; neither serration nor basal spur present (Peile, 1939; James, 1980). Nybakken (1990) described the teeth as similar to those of predators of amphinomid polychaetes (e.g. *C. zonatus, C. imperialis*).

Habitat and Habits: Intertidal and upper subtidal; juveniles in greater depths. In Hawaii, C. distans inhabits intertidal benches and subtidal coral reef platforms, more frequently in the latter habitat, where it occurs epifaunally in outer areas exposed to surf action (Kohn, 1959b; Kay, 1979). In Fiji, on patches of sand among weed (Cernohorsky, 1964). Tirard (pers. comm., 1989) reports C. distans from New Caledonia in 2-6 m on coral reef being active during the whole day. In E. New Britain, subtidally under rocks, wedged inside holes and crevices of the deeper reef and boulders, or on the shallow reef covered by epiflora (Richards, pers. comm., 1989). On subtidal reef flats in Indonesia and Thailand (Kohn & Nybakken, 1975), and more frequent on intertidal benches than subtidal reefs in the Maldive and Chagos Archipelagoes (Kohn, 1968b). In Mocambique, on outer areas of reef platforms (Grosch, pers. comm., 1989).

C. distans feeds on polychaetes (Eunicidae) in Hawaii (Kohn, 1959b). However, armature of radular teeth differs from that of congeners with a similar diet (Nybakken, 1990). Egg capsules large, containing numerous eggs. Egg diameter of about 148 μm in Palau suggests a minimum pelagic period of about 28 days (Perron & Kohn, 1985; Loch, pers. comm., 1987).

**Discussion:** The shells of *C. distans* are quite distinctive and are unlikely to be confused with those of any of its congeners.

## 6 Conus imperialis LINNÉ, 1758

(Plate 3, Figures 1-13; Plate 74, Figure 3; Plate 77, Second row, right; Third row, left; Map 4)

- 1758 Conus imperialis Linné, Syst. Nat., 10 ed., 1: 712, no. 251
- 1778 *Conus fuscatus* Born, Index Mus. Vindob., 1: 126-127; 1780, Test. Mus. Vindob.: 148
- 1798 Cucullus coronaducalis Röding, Mus. Bolten., 2: 38, no. 464/2\*
- 1798 Cucullus regius Röding, Mus. Bolten., 2: 38, no. 465/2 (non C. regius Gmelin, 1791)
- 1810 Conus viridulus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 31, no. 9

- 1906 Conus queketti E. A. Smith, Ann. Natal Govt. Mus., 1 (1): 22, pl. 7 fig. 1
- 1933 Conus imperialis nigrescens Barros e Cunha, Mem. Est. Mus. Zool. Univ. Coimbra (1) 71: 17, no. 9 (non C. nigrescens Sowerby II, 1859)
- 1933 Conus imperialis flavescens Barros e Cunha, Mem. Est. Mus. Zool. Univ. Coimbra, (1) 71: 18, no. 10 (non C. flavescens Sowerby I, 1834)
- 1942 Conus dautzenbergi Fenaux, Bull. Inst. Océan., (Monaco), 814: 2, fig. 2
- 1942 Conus douvillei Fenaux, Bull. Inst. Océan, (Monaco), 814: 2-3, fig. 5 (non Hemiconus douvillei Cossmann & Pissarro, 1901, a fossil)
- 1970 Conus imperialis compactus Wils, Fam. Conidae: 8, 12, pl. 2 fig. 7

Types: C. imperialis: Lectotype (Kohn, 1963, as "holotype", Walls, [1979]) in LSL (65 x 37 mm); C. fuscatus: Lectotype (Kohn, 1964, Walls, [1979]) in NMW (53 x 31 mm); C. coronaducalis: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 62 fig. 693) (41 x 26 mm); C. regius: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 139 fig. 1289) (44 x 25 mm); C. viridulus: A specimen of Lamarck's collection (no type) figured by Kiener (1845: Pl. 7 fig. 1) in MHNG (65 x 36 mm); C. queketti: Holotype in BMNH (27 x 14 mm); C. i. flavescens: 2 syntypes in MZUC (42 x 25; 39 x 20.5 mm); C. i. nigrescens: Holotype in MZUC (66 x 39 mm); C. dautzenbergi: Original figure 41 x 18 mm; C. douvillei: Original figure 54 x 26 mm; C. i. compactus: Lectotype (Coomans et al., 1985a) in ZMA (71 x 43 mm).

**Type Localities:** *C. fuscatus*: "Mauritius"; *C. viridulus*: "Océan austral."; *C. queketti*: "Isezela, Natal"; *C. dautzenbergi*: "Madagascar;" *C. douvillei*: "Madagascar"; *C. i. compactus*: "Nosy Bé, Madagascar."

Range: Entire Indo-Pacific except for Red Sea.

Description: Moderately large to large, solid to heavy. Last whorl conical; outline largely straight, variably convex adapically; in form *fuscatus*, outline often slightly concave at upper two-thirds and straight below. Shoulder angulate, strongly to sometimes weakly tuberculate. Spire usually low; outline slightly concave to slightly sigmoid, often with domed early postnuclear whorls and a projecting larval shell surmounting an otherwise flat spire. Postnuclear spire whorls distinctly tuberculate. Teleoconch sutural ramps flat to variably concave; 4 increasing to about 10 spiral striae on late ramps. Last whorl with weak to obsolete spiral ribs at base.

### C. imperialis Shell Morphometry

L	50 - 110 mm
RW	
-Pacific shells	0.50 - 1.60 g/mm (L 50-100 mm)
-Indian Ocean shells	0.30 - 1.35 g/mm (L 50-85 mm)
RD	
-Pacific shells	0.53 - 0.64
-Indian Ocean shells	0.50 - 0.68
PMD	0.84 - 0.97
RSH	0.01 - 0.14

Ground colour white to bluish grey (blue tint more common in form *fuscatus*). Colour pattern of last whorl maximally variable in the Indian Ocean.

Pacific shells (Pl. 3, Figs. 1-3): Last whorl encircled with 2 brown or olive bands. Bands variable in width, usually distinct, occasionally split into axial streaks and blotches. Adapical band occasionally divided in two. Spiral rows of alternating blackish brown and white dashes extending from base to shoulder; rows variable in number and arrangement. Variably numerous spiral rows of fine to minute brown dots, partially alternating with white markings in irregular sequence, also extending over entire last whorl. Base, siphonal fasciole and basal part of columella dark bluish grey, occasionally suffused with brown.

Indian Ocean shells (Pl. 3, Figs. 4-13): Some specimens have a pattern typical of Pacific shells; others vary widely. Spiral bands vary from brown to blackish olive or almost black. They may either be very wide, covering entire last whorl, or be reduced to sparse flecks. Bands often split into fused or separate patches and axial flames or blotches.

Teleoconch spire immaculate white to bluish grey in early whorls; late ramps with orange to nearly black radial streaks and blotches. Pattern elements variable. Aperture white to violet, except for a dark violet to brown base, rarely extending to shoulder along outer margin.

Periostracum olive to orange, thin, translucent, smooth (Hawaii; Marshall Is.; Fiji; Philippines; Madagascar).

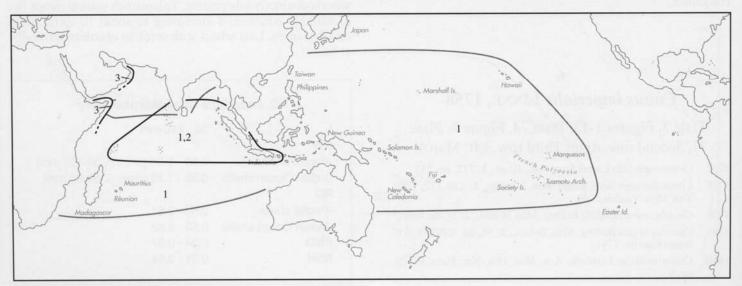
Animal (Pl. 74, Fig. 3; Pl. 77, Second row, right, Third row, left) dominated by various shades of red: In the Marshall Is., anterior part of dorsum of foot purple and red; central part white, mottled with brown, with white dots. In N. Papua New Guinea, dorsum of foot white to light pink, dotted with white and radially mottled with shades of red or purple; pale blackish brown dots set off a narrow solid red marginal zone; anterior half of dorsum solid red toward front and with black dots arranged in 2 medio-lateral lines.

Sole of foot pink, washed or mottled with red and brown, darker red anteriorly. Rostrum, tentacles and siphon violet, streaked and mottled with reddish brown, with white dots; rostrum and tentacles may also be solid dark pink (Garrett, 1878; Kohn, 1959a; Chaberman, pers. comm.,1981; Pearson, unpubl. observ.).

Radular teeth stout, with a short adapical barb opposite a second large barb, both perpendicular to a complex row of serration; serration consists of a double (to triple) row of denticles and terminates in an internal barb slightly posterior to the second barb; base with a distinct spur (Bergh, 1895; Peile, 1939; Kohn, 1965; Nybakken, 1970; Kohn, Nybakken & van Mol, 1972). Radular teeth of form *fuscatus* identical to those of typical form (Ramalho, pers. comm., 1989).

**Habitat and Habits:** Intertidal to 75 m; in Philippines, dredged to 240 m. In Hawaii, C. imperialis on subtidal coral reef platforms, on fine to coarse sand, reef limestone with or without algal turf, and on coral rubble as well as dead coral. In Fiji, in sand under coral and in sand pockets of coral reefs (Cernohorsky, 1964); in New Caledonia, in 1-25 m inside the lagoon, on coarse sand bottom and dead coral of platforms exposed to waves (Richer de Forges & Estival, 1986; Tirard, pers. comm., 1989); on the Great Barrier Reef, subtidally in lagoons (Huish, 1978); in Indonesia, subtidally on lagoon reef platforms and seaward reef platforms (Kohn & Nybakken, 1975; Kengalu, 1980) and also reported from coral rubble at low tide level. In Mozambique (Grosch, pers. comm., 1989), typical C. imperialis intertidally close to the infralittoral fringe on pure sand bottoms; form fuscatus in depressions, holes and crevices of rocky ledges and seldom on coral sand. Although both forms live syntopically in Mozambique, they do not share the same microhabitat. The rocky bottoms, on which form fuscatus occurs, are covered with crustose coralline algae, as are the shells of the living animals, whereas more typical C. imperialis exhibits hardly any encrustation. However, in Pacific localities C. im-

Map 4



1: C. imperialis 2: C. zonatus 3: C. biraghii

*perialis* often has heavy encrustations of coralline algae on its shells. In Réunion, form *fuscatus* ranges from slightly subtidal habitats to 50 m.

C. imperialis is known to feed almost exclusively on polychaetes of the family Amphinomidae ("fireworms"); Eunicidae are rarely consumed; the radular teeth share characteristics with those of other *Conus* species that prey on amphinomids (Nybakken, 1970).

In Hawaii, the species has been observed ovipositing in a depression in 0.3 m. Capsules are skewed to one side and are 18-20 x 12-13 mm. Each capsule contains about 6,000 eggs of 225  $\mu$ m diameter, suggesting a minimum pelagic period of 21 days. In Palau, egg diameter is 265  $\mu$ m, indicating a minimum pelagic period of about 18 days. In the Seychelles, dense clusters of capsules are deposited in shallow water. Capsules are affixed to the substratum by confluent basal plates and to other previously laid capsules. Number of eggs per capsule varies from 2,300 to 4,300, and capsules measure 18-19 x 11-12 mm. Egg diameter of 220  $\mu$ m indicates a minimum pelagic period of 22 days (Kohn, 1961a, b; Perron & Kohn, 1985).

**Discussion:** *C. imperialis* is most similar to *C. zonatus* but cannot be confused with any congener.

Typically patterned shells from the Indian Ocean tend to have weaker shoulder tubercles and sometimes have relatively broader last whorls than shells from the Pacific. Wils (1970) and Coomans et al. (1985a) considered the latter populations as a separate subspecies, *C. i. compactus* (Pl. 3 Fig. 11), but this form occurs sympatrically with specimens agreeing with the description of *C. fuscatus*.

The name *C. fuscatus* applies to shells from the W. Indian Ocean having a narrower last whorl, usually darker colouration, and irregular pattern with mainly axial orientation (Pl. 3, Figs. 4-13). This form occurs sympatrically with the typical form in Kenya and Zanzibar (in slighly greater depths) as well as Mozambique (in different microhabitats). The two forms intergrade in colour pattern and shape (RD 0.50-0.63 in form *fuscatus* and 0.57-0.68 in sympatric typical shells; PMD 0.87-0.97 and 0.84-0.92). We therefore regard *C. fuscatus* as a form of *C. imperialis* and not as a sibling species or geographic subspecies. Synonyms include *C. viridulus* (Pl. 3, Fig. 12 illustrates Lamarck's specimen), *C. coronaducalis*, *C. queketti* (a subadult specimen), *C. i. flavescens*, *C. i. nigrescens*, *C. douvillei*, and *C. dautzenbergi*.

#### 7

# Conus zonatus HWASS in BRUGUIÈRE, 1792

(Plate 3, Figures 14-17; Map 4)

1792 Conus zonatus Hwass in Bruguière, Encycl. Méth., 1: 613-614, no. 9

1798 Cucullus turritus Röding, Mus. Bolten., 2: 38, no. 477/8

1802 Conus lapideus Holten, Enum. Syst. Conch.: 35, no. 464

1908 Conus edwardi Preston, Rec. Indian Mus., 2: 190, pl. 15 fig. 28

**Types:** *C. zonatus*: Lectotype (Kohn, 1968, as "holotype"; Walls, [1979]) figured in Tableau (1798: Pl. 318 fig. 4) (59 x 34 mm); *C. turritus*: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 139 fig. 1286) (73 x 44 mm); *C. lapideus*: Lectotype (Kohn, 1981) same as lectotype of *C. turritus*; *C. edwardi*: Holotype in ZSI (58 x 28 mm).

Type Localities: C. zonatus: "l'Océan Asiatique"; C. edwardi: "Andaman Islands."

Range: Seychelles to Strait of Malacca and Indonesia (Bali).

**Description:** Medium-sized to large, solid to moderately heavy. Last whorl conical, outline almost straight, slightly convex adapically. Shoulder angulate to subangulate, strongly to weakly tuberculate. Spire of low to moderate height; outline variably sigmoid, with convex apex. Postnuclear spire whorls tuberculate to strongly tuberculate. Late teleoconch sutural ramps concave, with often obsolete spiral striation. Last whorl with weak spiral ribs at base.

### Conus zonatus Shell Morphometry

L	50 - 85 mm
RW	0.40 - 0.90 g/mm (L 50-70 mm)
RD	0.55 - 0.64
PMD	0.85 - 0.94
RSH	0.06 - 0.14

Ground colour white. Last whorl with 3 usually continuous bluish grey spiral bands, below shoulder and on both sides of centre; posterior bands may be variably fused. Rather evenly spaced orange-brown spiral lines extending from base to shoulder. Base and basal part of columella dark bluish brown. Teleoconch sutural ramps with brown to bluish brown radial markings. Aperture white, bluish brown at base.

Foot, rostrum and siphon rose or pink. Dorsum of foot and rostrum heavily mottled with dark brown. Sole of foot lightly mottled with dark brown or black. Siphon with a darker tip. Tentacles white, mottled with pink. Penis pale pink (Maldives, Thailand; Kohn, unpubl. observ.).

Radular teeth large, with a small adapical barb followed by a large second barb; adapical portion of the inner fold with a double row of denticles ending in an internal barb; large base with 2 protruding pointed spurs (Peile, 1939; Nybakken, 1970).

**Habitat and Habits:** Shallow water to about 30 m, on hard substrata of coral reefs. *C. zonatus* feeds on Amphinomidae (Kohn, 1968b; Kohn & Nybakken, 1975; Nybakken, 1970).

**Discussion:** *C. zonatus* is similar to *C. imperialis* in size, shape of shell, colouration of the animal, shape and armature of the radular teeth and in the diet of the animal. However, the latter species differs in the colour pattern of

its last whorl, exhibiting variably arranged spiral rows of alternating black/brown and white dashes and numerous spiral rows of minute brown dots, in contrast to the evenly spaced solid lines of *C. zonatus*. In addition, *C. imperialis* usually has only 2 instead of 3 colour bands around the last whorl. For comparison with *C. biraghii*, see the Discussion of the latter species.

# 8 Conus biraghii (G. RAYBAUDI MASSILIA, 1992)

(Plate 3, Figures 18, 19, 21, 22; Plate 73, Figures 22-24; Map 4)

- 1991 Leptoconus (Thoraconus) biraghii G. Raybaudi Massilia, Acta Conchyl., 3: 31-32, pl. 3 figs. 16-22
- 1993 Conus biraghii omanensis Moolenbeek & Coomans, Apex, 8 (1-2): 21-25, figs. 11-16, 18
- 1993 Conus (Leptoconus) biraghii congruens Korn & G. Raybaudi Massilia, La Conchiglia, 25 (268): 32-36

**Types:** *L. biraghii:* Holotype in SMNS (10.5 x 6.5 mm); *C. b. omanensis:* Holotype in ZMA (7.5 x 3.5 mm); *C. b. congruens:* Holotype in SMNS (11 x 6 mm).

Type Localities: L. biraghii: "Obja, 600 km North of Mogadishu, Somalia, W. Indian Ocean"; C. b. omanensis: "Sultanate of Oman, Masirah Island, Sur/Umm Rasas"; C. b. congruens: "Off northern Somalia, Gulf of Aden."

Range: C. b. biraghii: Somalia, from Mogadishu to Obya; C. b. congruens: Djibouti area to Cape Guardafui; C. b. omanensis: Oman, from Masirah Id. to Kuria Muria Is.

Description: C. b. biraghii (Pl. 3, Figs. 18, 19, 21, 22) very small and light. Last whorl broadly and ventricosely conical to broadly conical, sometimes ventricosely conical to conical in form A; outline convex adapically, less so to straight below; left side usually slightly concave at base. Shoulder angulate to carinate, smooth to usually undulate due to axial costae on subshoulder area, consistently smooth in form B. Spire usually of moderate height, stepped; outline almost straight. Postnuclear spire whorls weakly tuberculate to undulate due to axial subshoulder costae (form A) or consistently smooth (form B). Teleoconch sutural ramps slightly concave, with obsolete spiral striae. Last whorl with spiral grooves on basal fourth and 1-2 weak spiral grooves just below shoulder.

#### C. biraghii Shell Morphometry

	C. b. biraghii	C. b. congruens	C. b. omanensis
L	9 - 11.5 mm	9 - 11 mm	7 - 11 mm
RW	0.01 - 0.04 g/mm	0.01 - 0.02 g/mm<	0.01 g (L 7.5 mm)
RD	0.68 - 0.80	0.68 - 0.78	0.61 - 0.74
PMD	0.77 - 0.91	0.82 - 0.94	0.80 - 0.95
RSH	0.12 - 0.19	0.24 - 0.30	0.23 - 0.30

- C. b. congruens (Pl. 73, Fig. 24) with an often less ventricose last whorl. Shoulder often irregularly undulate due to weak axial subshoulder costae. Spire high, stepped; outline straight to slightly concave. Larval shell of 2-2.25 whorls, with widely spaced fine radial ridges; maximum diameter about 0.8 mm. Postnuclear spire whorls usually smooth, sometimes irregularly undulate due to very weak axial subshoulder costae. Teleoconch sutural ramps concave, often with 1 increasing to 2-3 weak or distinct spiral grooves in early whorls; spiral sculpture obsolete on late ramps. Last whorl with spiral ribs basally and 1-2 distinct spiral grooves just below shoulder; subshoulder grooves may be visible in stepped preceding spire whorls.
- C. b. omanensis (Pl. 73, Figs. 22, 23) with an often narrower, ventricosely conical last whorl. Shoulder angulate. Larval shell of about 2 whorls, with fine radial ridges on final part. Teleoconch sutural ramps flat, with 1 increasing to 3 distinct spiral grooves pronounced also in late whorls. Spiral subshoulder grooves consistently visible in stepped spire whorls. C. b. omanensis otherwise matching C. b. congruens in morphology. Some shells of C. b. omanensis closer to C. b. biraghii due to concave teleoconch sutural ramps and prominent axial subshoulder costae.
- In C. b. biraghii form A, ground colour white to grey. Last whorl with a broad dark grey to olive grey spiral band within adapical third and at base, edged with brown to blackish brown spots and interspersed with scattered to regularly arranged ground-colour spots. Ground-colour band below centre usually with an indistinct meshwork of white spots. Sparse spiral rows of brown dots between subshoulder area and base. Specimens of form B with lighter, bluish to brownish grey spiral colour bands, more prominently edged and overlain with dark brown spots; ground-colour band below shoulder narrower than in shells of form A, subcentral ground-colour band with a more indistinct pattern of white background spots. Spiral rows of brown dots and dashes often more prominent, sometimes extending to shoulder. Final part of larval shell white to pale beige, initial part eroded. Postnuclear sutural ramps with brown radial markings crossing outer margins. Aperture showing exterior pattern.
- C.b. congruens similar in colour pattern to C.b. biraghii. Spiral colour bands more solid and olive-brown. Prominent dashed brown spiral lines extending from base to subshoulder area, articulated with bright white dashes. Larval shell bicoloured: Initial part white to grey, with brown sutural areas; remaining part grading to solid dark brown. Dark brown radial streaks extending from shoulder ramp to adapical spiral colour band.
- C. b. omanensis similar to C. b. congruens in the colouration of the larval shell, in colour pattern matching C. b. biraghii.
- In C. b. omanensis, radular teeth with unique armature resembling that of C. californicus, consisting of 2 opposed adapical barbs, followed by a third barb perpendicular to the anterior two, a fourth barb about 1/3 the length down the shaft, and an internal double-barb between third and fourth

barb.; with a slight waist at the height of the posterior barb; serration and basal spur absent (Rolán & G. Raybaudi Massilia, in press).

**Habitat and Habits:** No reliable data on the shells from Somalia; *C. b. omanensis:* In 0.1-8m below low tide level.

**Discussion:** The colour pattern of *C. biraghii* suggests a "miniature" *C. zonatus* (G. Raybaudi Massilia, 1992). However, *C. zonatus* differs in its narrower last whorl (RD 0.55-0.64, likely lower in juveniles) and its third spiral colour band below shoulder. *C. zonatus* has prominently tuberculate postnuclear whorls without axial subshoulder costae. The holotype of *C. traillii* (Plate 71, Figs. 10, 11) is similar in size and last whorl pattern. It can be distinguished by the more convex outline of its last whorl, its convex and immaculate postnuclear sutural ramps, rounded shoulder, and by the absence of axial subshoulder costae. The relationship between *C. locumtenens* and *C. biraghii* awaits further studies, when juvenile specimens of the former species become known. For comparison with *C. korni* and *C. boschorum*, see the Discussions of those species.

The differences between *C.b. biraghii* form A and form B do not justify separation at the species level. *C.b. omanensis* was provisionally described as a geographical subspecies. This status seems to be justified by intermediate specimens occasionally occurring within the population from Masirah Id. *C.b. congruens* is conchologically more similar to *C.b. omanensis* than to *C.b. biraghii*.

#### 9

## Conus lividus HWASS in BRUGUIÈRE, 1792

(Plate 4, Figures 1-5; Plate 74, Figure 4; Plate 77, Third row, right; Map 5)

- 1792 Conus lividus Hwass in Bruguière, Encycl. Méth., 1: 630-632, no. 28
- 1792 Cucullus monachos Röding, Mus. Bolten., 2: 39, no. 490/16
- 1807 Conus plebejus Link, Beschr. Nat. Samml. Univ. Rostock, 3: 106
- 1849 Conus primula Reeve, Conch. Icon., 1, Conus suppl.: Pl. 6 sp. 259

Types: *C. lividus*: Lectotype (Kohn, 1968) in MHNG (43 x 26 mm); *C. monachos*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 63 fig. 694) (47 x 28 mm); *C. plebejus*: Lectotype (Kohn, 1981) same as lectotype of *C. monachos*; *C. primula*: Type in BMNH (31 x 18 mm).

Type Localities: C. lividus: "isles Antilles."

Range: Entire Indo-Pacific.

Description: Moderately small to moderately large, moderately solid to moderately heavy. Last whorl conical to broadly conical; outline almost straight, somewhat convex at adapical fourth. Shoulder angulate, strongly to weakly tuberculate; tubercles occasionally obsolete. Spire of low to moderate height, outline straight to slightly concave. Larval shell of about 4 whorls. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat, with 2

increasing to 4 spiral grooves. Last whorl with often variably granulose spiral ribs above base, sometimes to centre.

C.	lividus Shell Morphometry
L	30 - 81 mm
RW	0.20 - 0.94 g/mm (L 30-70 mm)
RD	0.59 - 0.73
PMD	0.87 - 0.93
RSH	0.06 - 0.20

Last whorl light olive or yellowish brown with narrow white spiral bands at centre and below shoulder that may be suffused with bluish grey or rose. Base dark purple. Apex usually pink; larval shell yellow (Hawaii; Perron, 1981a). Late spire whorls and shoulder white, occasionally suffused with bluish grey or pale orangish violet. Aperture deep purple-violet behind a narrow orange-brown margin, with pale bands at centre and below shoulder.

Periostracum yellow-olive to greyish brown, moderately thick, translucent to opaque, with fine axial ridges and sometimes also with close-set spiral rows of tufts on last whorl.

Foot violet to brownish red, sometimes dark olive; mottled with dark brown to black and dotted with white; a darker sole may contrast with a light dorsum. White dots occasionally absent; black mottling may be so dense to produce a completely black appearance. On dorsum, black spots sometimes concentrated in a broad pre-marginal band, setting off an immaculate median zone from a narrow immaculate marginal zone; sole occasionally also with immaculate margins. Rostrum and tentacles red to dark purple, often mottled with black and dotted with white; white dots may be closely set at tip of tentacles. Siphon purple to dark red or dark olive, variably spotted or mottled with black, dotted with white; white dots variable in number, sometimes absent; black mottling often so dense as to produce a solid black siphon narrowly edged with red (Kohn, 1959a; Kohn, unpubl. observ.; Marsh, 1971; Chaberman, pers. comm., 1981; Fainzilber, pers. comm., 1987; Pearson, unpubl. observ.) (Pl. 74, Fig. 4; Pl. 77, Third row, right).

Radular teeth slender, with an adapical barb opposite a very weak blade; a group of small cusps just behind the barb and one prominent cusp 2/3 the length down the shaft; base with a distinct spur (James, 1980; Kohn, unpubl. observ.).

Habitat and Habits: Infrequently intertidal, common on subtidal coral reef platforms. *C. lividus* occupies diverse microhabitats: sand patches and pockets, coral rubble with and without sand, reef limestone with algal turf, bare reef limestone, dead coral heads, and beach rock (Kohn, 1959b, 1960, 1968b; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Cernohorsky, 1964; Kilburn & Rippey, 1982; Tirard, pers. comm., 1989).

C. lividus feeds on polychaetes of the sedentary families
Terebellidae and Maldanidae and the errant Nereidae and

Eunicidae as well as on enteropneusts (Kohn, 1959b, 1960, 1968b; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985).

Egg capsules flat, short-stalked, with crenulate margins, 6-17 x 6-12 mm (Kohn, 1961b; Perron 1981a; Kilburn & Rippey, 1982). Capsules fixed in rows by confluent basal plates to the underside of coral rocks or on bare limestone pavement. Each capsule contains about 2.000-3.300 eggs of 135-150 μm diameter, suggesting a pelagic period of at least 28-29 days (50 days in Hawaii, based on in vitro observations; Kohn, 1961b; Perron, 1981a; Perron & Kohn, 1985).

**Discussion:** *C. lividus* is very similar to *C. sanguinolentus*. They have often been synonymized, and their relationship remains somewhat uncertain. For comparison of *C. lividus* with *C. sanguinolentus* and *C. moreleti*, see the Discussions of those species.

### 10

# Conus sanguinolentus QUOY & GAIMARD, 1834

(Plate 4, Figures 6-13; Plate 74, Figure 5; Plate 77, Fourth row, left; Map 5)

1834 Conus sanguinolentus Quoy & Gaimard, Voy. l'Astrolabe, Zool., 3: 99-100, pl. 53 fig. 18

**Type:** Lectotype (Kohn, 1992) figured in Quoy & Gaimard (1834: Pl. 53 fig. 18) (22 x 10.5 mm).

Type Locality: "le havre Carteret, la Nouvelle-Guinée."

Range: Indo-Pacific; except for Hawaii and Central Indian Ocean.

**Description:** Moderately small to moderately large, moderately solid to solid. Last whorl conical to slightly

Map 5

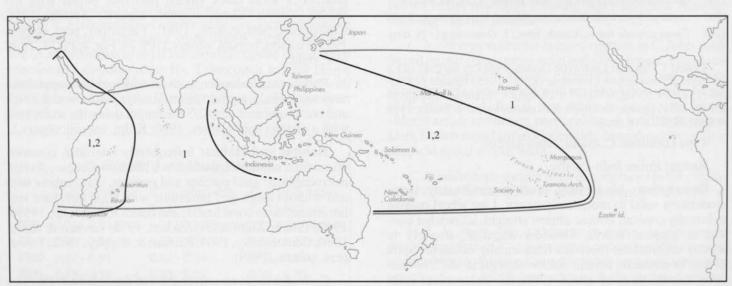
pyriform, consistently conical in shells from Marquesas and Tahiti; outline variably convex at adapical third or half, straight to slightly concave below. Shoulder angulate, weakly to strongly tuberculate. Spire of low to moderate height, outline straight to slightly concave. Postnuclear spire whorls strongly tuberculate. Teleoconch sutural ramps almost flat, with 1 increasing to 3-5 spiral grooves. Last whorl with variably granulose spiral ribs on basal half, sometimes to subshoulder area.

C. san	guinolentus Shell Morphometry
L	25 - 65 mm
RW	0.18 - 0.70 g/mm (L 30-60 mm)
RD	0.60 - 0.71
PMD	0.82 - 0.95
RSH	0.06 - 0.16

Last whorl olive to orange brown, except for whitish granules on spiral ribs. Some specimens with a slightly lighter central spiral band. Often evenly spaced brown spiral lines from base to subshoulder area, abapically following granulated spiral ribs. Base and basal part of columella purplish brown. Apex pale yellow to orange. Late postnuclear sutural ramps matching colouration of last whorl except for nearly white tubercles. Aperture bright bluish violet behind a orange-brown marginal zone; pale violet deeper within.

Periostracum yellow to olive-brown, moderate in thickness, translucent, with very fine axial ridges.

A more uniformly coloured form is known from the Marquesas and Tahiti (Pl. 4, Figs. 11-13). Last whorl olive brown to dark brown without the spiral lines. Entire shell tinged with violet; base and basal part of columella not



1: C. lividus 2: C. sanguinolentus

contrastingly darker in colour. Aperture violet, often darker at base and lighter deeper within.

Colour of animal variable: red, purple or brown, uniform or patterned. In N. Papua New Guinea, dorsum of foot reddish brown, edged with red; a red pre-marginal line parallels latero-posterior margins; a few black spots scattered at each end of median zone. In Marshall Is., dorsum of foot uniformly light purple, mottled with black and dotted with white. In other localities, dense black markings may produce solid areas. Sole of foot either immaculate or mottled with brown or black. In Marshall Is., sole red with brown mottling and white dots; with brick red edge anteriorly and grey medial strip posteriorly. In N. Papua New Guinea, siphon with a red tip, followed by black and brick red bands; base red or black. Animals from the Great Barrier Reef and Marshall Is. with a brick red or purple siphon, mottled with black, sometimes solid black distally, with white dots. Marshall Is. juveniles orange-red, more sparsely flecked with black than adults. (Cernohorsky, 1964; Fainzilber, pers. comm., 1987; Fainzilber et al., 1992; Marsh, 1971; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.; Kohn, unpubl. observ.) (Pl. 74, Fig. 5; Pl. 77, Fourth row, left).

Radular teeth with an adaptical barb opposite a weak blade; base with a spur (Bandel, 1984).

Habitat and Habits: Usually in 0.5-3 m. On sand and reef rock under coral boulders (Fiji); under rocks on reef flats and at the reef crest (Great Barrier Reef); in the N. Red Sea, reported from bare reef flats, usually toward the outer edge of the reef (Cernohorsky, 1964; Fainzilber et al., 1985, 1992; Loch, pers. comm., 1988). The form from the Marquesas and Tahiti is reported from reefs and rocky ledges in 5-30 m. *C. sanguinolentus* is known to feed on polychaetes (Reichelt & Kohn, 1985).

**Discussion:** C. sanguinolentus is very similar to C. lividus, and the relationship of the two taxa is not fully resolved. Cernohorsky (1964) redescribed C. sanguinolentus; the name clearly applies to the species described here. C. lividus differs in its somewhat larger maximum size, strictly conical last whorl, and immaculate late sutural ramps. The pale central band on the last whorl and within the aperture characteristic of C. lividus is weak or totally absent in C. sanguinolentus (see Marsh, 1971). In areas where both species occur sympatrically, they are either clearly separable by the colouration of the animal (N. Papua New Guinea; Fiji; Kenya, fide Cernohorsky, 1964) or identical in this character (Red Sea; Queensland). Across their entire ranges, the colour pattern of the animal thus is not a reliable character for distinguishing the two species. Conchological intergrades between C. lividus and C. sanguinolentus have not been found where both co-occur, and in such situations they occupy slightly different microhabitats (Kohn, unpubl. observ.). We thus regard these taxa as distinct species. For comparison with C. moreleti, see the Discussion of that species.

The conchological differences between *C. sangui-nolentus* and the variant from the Marquesas and Tahiti are too slight to justify separation at the species level. The latter

form is sometimes erroneously referred to as *C. unicolor* Sowerby (a nomen dubium). We assign it as a form of *C. sanguinolentus* rather than of *C. lividus*, because of the rare presence of a pale central band on the last whorl and the consistent presence of dark markings between the shoulder tubercles.

## 11 Conus moreleti CROSSE, 1858

(Plate 4, Figures 14-18; Map 6)

- 1843 Conus elongatus Reeve, Conch. Icon., 1, Conus: Pl. 27 sp. 157 (non C. elongatus Dillwyn, 1817)
- 1849 Conus oblitus Reeve, Conch. Icon., 1, Conus suppl.:1 (nom. nov. for C. elongatus Reeve, 1843; non C. oblitus Michelotti, 1847, a fossil)
- 1858 Conus moreleti Crosse, Rev. Mag. Zool., (2) 10: 122 (nom. nov. for C. elongatus Reeve, 1843)

Type: Original figure 26 x 13 mm.

Type Locality: Not stated.

Range: E. Africa and Maldives to French Polynesia and Hawaii.

**Description:** Moderately small to moderately large, moderately solid to solid. Last whorl conical; outline slightly to moderately convex adapically and straight below, occasionally slightly concave at centre. Shoulder angulate, tuberculate to strongly tuberculate. Spire low, outline nearly straight; apex convex. Postnuclear spire whorls with closely spaced tubercles. Teleoconch sutural ramps flat to slightly concave, with 2-3 distinct or inconspicuous spiral grooves. Last whorl with weak, smooth or granulose spiral ribs near base.

# C. moreleti Shell Morphometry L 30 - 61 mm RW 0.15 - 0.40 g/mm (L 35-48 mm) RD 0.52 - 0.60 PMD 0.85 - 0.98 RSH 0.03 - 0.13

Last whorl almost completely yellowish to dark brown or olive, sometimes with a lighter central spiral band. Background tinged with greyish blue or violet. Base and basal part of columella dark violet. Tip of apex usually purplish blue; Reeve reports a rose-tinted apex. Postnuclear sutural ramps either immaculate bluish grey to white or radially maculated with colour of last whorl; tubercles mostly immaculate. Aperture dark violet behind an orange-brown margin.

Periostracum yellowish brown, thin, translucent, minutely tufted on the shoulder tubercles (Kohn, 1959a; Cernohorsky, 1964).

Dorsum of foot brownish red, mottled with brown and tipped with red. Rest of foot and rostrum yellowish brown, mottled with darker brown. Sole of foot may be orange-brown, edged with orange. Tentacles white or pale yellow. Tip of siphon dark orange or yellow, followed proximally by black and pink, yellow or red bands; rest of siphon yellow mottled with black (Hawaii: Kohn & Weaver, 1962; Seychelles: Kohn, unpubl. observ.).

Habitat and Habits: In 1-50 m, mainly encountered in 8-20 m on reef substrata.

Egg capsules of about  $10.5 \times 8$  mm are attached to the underside of coral rocks. Basal plates remain separated. Capsules contain 2,300-2,400 eggs of about 150  $\mu$ m diameter, suggesting a minimum pelagic period of about 28 days (Kohn, 1961b; Perron & Kohn, 1985).

**Discussion:** C. moreleti can only be mistaken for C. lividus or C. sanguinolentus. These species both differ considerably in their broader last whorl (RD: C. lividus 0.59-0.73; C. sanguinolentus 0.60-0.71) and often have a relatively higher spire (RSH: C. lividus up to 0.20; C. sanguinolentus up to 0.16). The tubercles of the spire whorls are more widely spaced in the two latter species. The colour pattern of the body described above occurs neither in C. lividus nor in C. sanguinolentus. C. lividus has a weaker tuberculation of the postnuclear whorls, and C. sanguinolentus often differs in having a slightly pyriform last whorl.

# 12 Conus caillaudii KIENER, 1845

(Plate 4, Figures 19-25; Map 6)

1845 Conus caillaudii Kiener, Coq. Vivant., 2: Pl. 55, fig. 5; 1849-1850: 285

Type: Holotype in MNHN (51.5 x 25 mm).

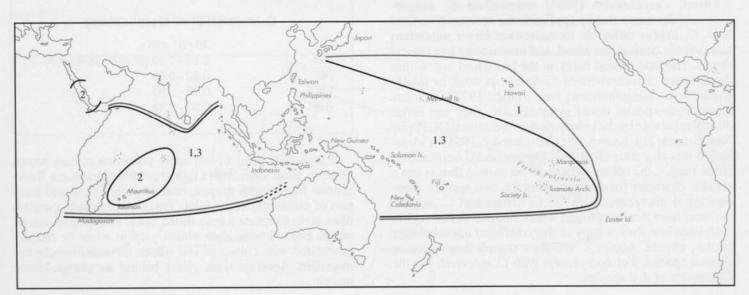
Type Locality: "Cargados Carajos Islands" (Coomans et al., 1983).

Range: W. Indian Ocean: Mascarene Is., Mascarene Plateau, Chagos Archipelago and Red Sea.

**Description:** Moderately small to medium-sized, usually moderately solid. Last whorl narrowly conical to conical, broadest in shells from the Red Sea; outline straight, slightly convex adapically. Shoulder angulate to subangulate, tuberculate to undulate. Spire of low to moderate height; outline variably concave, sometimes slightly sigmoid (Réunion). Postnuclear spire whorls tuberculate to undulate. Teleoconch sutural ramps flat, with 2 increasing to 3-4 spiral grooves; Red Sea shells with 4-6 weak spiral grooves on last 2 ramps. Last whorl with weak spiral grooves at base, occasionally followed adapically by widely spaced pairs of weak spiral ribs.

Ground colour yellowish tan to brown. Last whorl with fine, evenly spaced reddish brown spiral lines; adjacent lines often differing in width. Base and basal part of columella either white or somewhat darker than rest of last whorl. Apex cream or violet. Teleoconch sutural ramps with reddish brown radial markings. Aperture white or pale violet.

Map 6



1: C. moreleti 2: C. caillaudi 3: C. varius

### C. caillaudii Shell Morphometry 29 - 51.5 mm RW ca. 0.20 g/mm (L 40-45 mm) RD 0.47 - 0.54 (Cargados Carajos) 0.57 - 0.58 (Saya de Malha) 0.54 - 0.56 (Réunion) 0.58 - 0.62 (Red Sea) 0.55 (unknown locality) **PMD** 0.84 - 0.940.08 - 0.12 (Cargados Carajos) **RSH** 0.12 - 0.13 (Saya de Malha) 0.13 - 0.16 (Réunion) 0.13 - 0.14 (Red Sea) 0.12 (unknown locality)

Specimens from Réunion (Pl. 4, Figs. 22, 23) differ in having broader reddish brown spiral lines on last whorl; the abapical lines narrower but variable in width. Base and basal part of columella creamy white.

Specimen from Banka Saya de Malha (Pl. 4, Fig. 21) lacks any pattern elements.

In specimens from Red Sea (Pl. 4, Figs. 24, 25), last whorl with a variably broad white spiral band at centre, flanked by a broad tan band on each side; additional narrow white zone below shoulder interspersed with widely spaced brown axial dashes. Base and basal part of columella dark brown.

Periostracum tan, thin, translucent, smooth.

Habitat and Habits: Subtidal. Specimen from Banka Saya de Malha dredged in 160 m.

**Discussion:** This poorly known species is unmistakable within the genus because of its combination of spirally lineate colour pattern and undulate to tuberculate shoulder.

Whether the specimens of Banka Saya de Malha and Red Sea belong to this species or not, is not fully resolved, because they have broader last whorls lacking a spirally lineate pattern.

# 13 Conus varius LINNÉ, 1758

(Plate 4, Figures 26-28; Plate 74, Figure 6; Plate 77, Fourth row, right; Map 6)

- 1758 Conus varius, Linné, Syst. Nat., 10 ed., 1: 715, no.270
- 1798 Cucullus granulosus Röding, Mus. Bolten., 2: 40, no. 498/24
- 1798 Cucullus annularis Röding, Mus. Bolten., 2: 40, no. 499/24\*
- 1798 Cucullus radula Röding, Mus. Bolten., 2: 40, no. 500/25
- 1834 Conus pulchellus Sowerby I, Conch. Ill.: Pt. 54, fig. 61 (non C. pulchellus Röding, 1798, non C. pulchellus Swainson, 1822)

- 1854 Conus hevassii A. Adams, Proc. Zool. Soc. London, 1853: 118 (nom. nov. for C. pulchellus Sowerby I, 1834)
- 1874 Conus hwassi "A.Adams" Weinkauff, Syst. Conch. Cab. Martini Chemnitz, 4: 252-253, pl. 42 figs. 6a-b (emendation for C. hevassii)

**Types:** *C. varius*: Lectotype (Kohn, 1963, as "holotype") in LSL (33.5 x 16 mm); *C. granulosus*: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 138 fig. 1284) (38 x 19 mm); *C. annularis*: no type; *C. radula*: no type; *C. pulchellus*: Lectotype (Kohn, 1992) figured in Sowerby I (1834: Pt. 54, Fig. 61) (36 x 19 mm); *C. hwassi*: Original figure 50 x 27 mm.

**Type Localities:** *C. pulchellus*: "Freemantle" (Sowerby, 1834a); *C. hwassi*: "Molukken."

Range: S. and E. Africa to Marshall Is. and Tuamotu Archipelago; absent from Red Sea, India and Sri Lanka.

Description: Medium-sized to moderately large, moderately solid to solid. Last whorl conical to conoid-cylindrical, sometimes slightly ovate in Pacific shells; outline almost straight to evenly convex. Shoulder angulate to subangulate, moderately to strongly tuberculate. Spire of moderate height, outline slightly concave to slightly convex. Larval shell of 4 or more whorls, maximum diameter 0.80-0.85 mm. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat to slightly concave, with 1 increasing to 6 spiral grooves; grooves finer and sometimes obsolete in late whorls. Specimens with heavily granulose evenly spaced ribs around entire last whorl intergrade with specimens with widely set, weak granulose ribs around basal fourth of last whorl.

### C. varius Shell Morphometry

O. varias	Official Morphometry
Learning	35 - 61 mm
RW	
- Indian Ocean Shells	0.20 - 0.48 g/mm
- Pacific Shells	0.14 - 0.34 g/mm (L 35-54 mm)
RD	
- Indian Ocean Shells	0.57 - 0.67
- Pacific Shells	0.54 - 0.62
PMD	
- Indian Ocean Shells	0.82 - 0.91
- Pacific Shells	0.73 - 0.91
RSH	0.12 - 0.23

Ground colour white. Last whorl often tinged with pale pink or violet, with dark brown, irregularly shaped or axial blotches within adapical and abapical third. Blotches variable in size and number, sometimes fusing into 2 spiral bands. Closely spaced spiral rows of dark brown dashes and dots extend from base to shoulder. Larval whorls white. Teleoconch sutural ramps with sparse brown dots. Aperture nearly white or pale yellow to orange behind a white marginal zone. Periostracum yellowish brown, thin, translucent, almost smooth.

Dorsum of foot white to pale yellow, often with a dotted black or dark brown pre-marginal line; anterior part with brown or black markings laterally and centrally; a small black fleck beneath operculum. Sole of foot white to yellow. Rostrum yellow. Tentacles yellow, tipped with darker yellow or brown. Siphon pale yellow with a light brown to black ring somewhat back from the tip; distal end sometimes darker and sparse mottling may replace transverse ring laterally (Chaberman, pers. comm., 1981; Pearson, unpubl. observ.; Kohn, unpubl. observ.) (Pl. 74, Fig. 6; Pl. 77, Fourth row, right).

Radular teeth with an adaptical barb opposite a long second barb (or blade?); serration terminating in a cusp; central waist and small basal spur present (Nybakken, 1990).

**Habitat and Habits:** Intertidal to about 30 m; in Philippines, dredged to 240 m. On coral reef platforms and fore-reefs, in or under dead coral, on limestone bench and in sand often beneath coral rocks.

Egg capsules are deposited in parallel rows on the underside of coral rocks and affixed to the substratum by confluent basal plates. Capsules 8-11 x 6-8 mm, each containing 1,700-2,700 eggs; number of eggs per spawn 63,000-81,000. Egg diameter of 160-166 µm predicts a minimum pelagic period of 26-27 days (Kohn, 1961b; Cernohorsky, 1964; Perron & Kohn, 1985).

**Discussion:** The shells of *C. varius* are very distinctive and cannot be confused with any Indo-Pacific congeners. The lectotype of *C. varius* is of the more slender conoid-cylindrical form occurring more frequently in Pacific populations, while the more conical form is commoner in Indian Ocean populations.

# 14 Conus biliosus (RÖDING, 1798)

(Plate 5, Figures 1-13; Plate 74, Figure 7; Map 7)

- 1792 Conus punctatus Hwass in Bruguière, Encycl. Méth., 1: 628, no. 23 (non *C. punctatus* Gmelin, 1791)
- 1798 Cucullus biliosus Röding, Mus. Bolten., 2: 39, no. 489/15\*
- 1807 Conus parvulus Link, Beschr. Nat. Samml. Univ. Rostock, 3: 106
- 1810 Conus roseus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 37, no. 32 (non C. roseus Fischer, 1807)
- 1817 Conus piperatus Dillwyn, Descr. Catal. Rec. Shells, 1: 401, no. 86
- 1866 Conus concinnus Sowerby II, Thes. Conch., 3 suppl.: 329, no. 438, pl. 28 fig. 646 (non C. concinnus Sowerby I, 1821, a fossil)
- 1874 Conus sapphirostoma Weinkauff, Jahrb. deutsch. malak. Ges., 1: 268 (nom. nov. for C. concinnus Sowerby II; spelt C. sapphyrostoma in Syst. Conch. Cab., 1875: 368)
- 1956 Virroconus imperator Woolacott, Proc. Roy. Zool. Soc. New South Wales, 1954-1955: 72, fig. 3
- 1979 Conus biliosus meyeri Walls, The Pariah, 5: 3
- 1993 Conus neoroseus da Motta, La Conchiglia, 24 (265): 29-30 (nom. nov. for C. roseus Lamarck, 1810)

**Types:** *C. punctatus*: Lectotype (Kohn, 1968 as "holotype", Walls, [1979] in MHNG (54 x 33 mm); *C. biliosus*: Lectotype

(Kohn, 1975) figured in Chemnitz (1788: Pl. 139 fig. 1294) (42 x 25 mm); *C. parvulus*: Lectotype (Kohn, 1981) figured in Martini (1773: Pl. 63 fig. 707) (20 x 12 mm); *C. roseus*: Lectotype (Kohn, 1981) in MHNG (30 x 21 mm); *C. piperatus*: Lectotype (Walls, [1979]; Kohn, 1984) same as lectotype of *C. biliosus*; *C. concinnus*: Original figure 25 x 19 mm; *V. imperator*: Holotype in AMS (42 x 23.5 mm); *C. b. meyeri*: Holotype in DMNH (44 x 24.5 mm).

**Type Localities:** *C. punctatus*: "l'Océan Africain"; *C. biliosus*: "Gulf of Mannar, between India and Ceylon" (Coomans et al., 1982); *C. roseus*: "Antilles"; *V. imperator*: "Trinity Bay, Queensland, Australia"; *C. b. meyeri*: "South Africa, Natal, Genezzano; *C. neoroseus*: "Tabayas Bay, Luzon, P. I."

Range: S. Africa to Somalia and to India and Sri Lanka, absent from Red Sea and Persian Gulf; Indonesia to Philippines and to Papua New Guinea, Solomon Is. and Queensland.

Description: Moderately small to moderately large, moderately light to solid. Last whorl conical, ventricosely conical or broadly and ventricosely conical, occasionally pyriform; outline variably convex at adapical fourth to half and straight to moderately concave below; left side often sigmoid. In Indian populations, last whorl most conical, RD most variable. Shoulder angulate to subangulate, distinctly tuberculate to irregularly edged. Spire of low to moderate height, outline slightly concave to slightly convex. Postnuclear spire whorls variably tuberculate. Teleoconch sutural ramps almost flat, with 1 increasing to 4-7 spiral grooves; spiral sculpture may be weak in last whorls. Entire last whorl with rather evenly spaced, wrinkled spiral ribs and alternating wrinkled threads; spiral sculpture may be weaker toward shoulder, and some specimens are quite smooth.

Ground colour pale greyish blue or pale pink. Last whorl spirally banded with tan to olive brown or orangish brown, usually with variably broad ground-colour bands at centre and shoulder. In Indian Ocean populations (Pl. 5, Figs. 1-8), last whorl often maculated with bluish brown axial streaks; overlying spiral rows of brown dots sparsely to heavily developed on ribs. Basal part of last whorl and columella dark brown; in Indian shells (Pl. 5, Figs. 1, 3, 4), basal part mostly orange or tan, often similar to adjacent parts. Apex light brown or pink. Teleoconch sutural ramps radially maculated with orange to blackish brown, varying from sparse spots between marginal tubercles to solid dark brown colouration. In small adults, aperture bluish violet, edged with brownish violet, with a pale central band and a translucent marginal zone; aperture white in large adults.

In Indian shells, periostracum brown or yellowish brown, variably thick, slightly translucent to opaque, with about 20 variously arranged tufted spiral ridges.

Dorsum of foot brown or black anteriorly, with a red distal edge; sides of foot reddish brown, flecked with white dorsally; sole and ventro-lateral edges of foot red. Rostrum reddish brown, red distally. Tentacles light brown to red. Siphon reddish brown dorsally, edged with pale red distally (Indian animals, Kohn, 1978a & unpubl. observ.). In Indonesian and W. Pacific animals, foot and siphon brownish red dotted with black; with sparse white dots on siphon. Sole

of foot and siphon may also be light red, with thin transverse brown lines on the dorsal side of siphon. Rostrum and tentacles dark red to brown (Chaberman, pers. comm., 1981; Kohn, unpubl. observ.) (Pl. 74, Fig. 7).

C. biliosus Shell Morphometry		
	25 - 64 mm	
South Africa, Mo	zambique, Madagascar	
RW	0.15 - 0.29 g/mm (L 30 - 45 mm)	
RD	0.65 - 0.72	
PMD	0.77 - 0.91	
RSH	0.13 - 0.17	
Pakistan		
RW	0.21 - 0.45 g/mm (L 33 - 38 mm)	
RD	0.65 - 0.67	
PMD	0.86 - 0.89	
RSH	0.10 - 0.12	
India and Sri Lar	nka	
RW	0.14 - 0.46 g/mm (L 30 - 64 mm)	
RD	0.58 - 0.78	
PMD	0.82 - 0.92	
RSH	0.10 - 0.19	
Indonesia		
RW	0.18 - 0.34 g/mm (L 30 - 43 mm)	
RD	0.65 - 0.76	
PMD	0.82 - 0.90	
RSH	0.10 - 0.15	
Philippines		
RW	0.14 - 0.25 g/mm (L 32 - 36 mm)	
RD	0.64 - 0.74	
PMD	0.85 - 0.92	
RSH	0.11 - 0.14	
Solomon Is.		
RW	0.08 - 0.13 g/mm (L 25 - 31 mm)	
RD	0.62 - 0.74	
PMD	0.79 - 0.88	
RSH	0.09 - 0.16	
Queensland		
RW	0.10 - 0.33 g/mm (L 32 - 49 mm)	
RD	0.62 - 0.76	
PMD	0.78 - 0.90	
RSH	0.09 - 0.19	

In specimens from India and Sri Lanka, radular teeth with an indistinct adapical barb opposite a weak blade; short

serration, slight central waist and prominent basal spur present (Bandel, 1984).

Habitat and Habits: Intertidal and slightly subtidal. In Mozambique and South Africa, at and below low-tide level in sandy crevices and caverns (Kilburn & Rippey, 1982; Grosch, pers. comm., 1989). Some Indian populations occupy small caves and associated tidal pools on terraced intertidal limestone benches (Kohn, 1978a). In Indonesia, on intertidal to slightly subtidal benches of truncated reef limestone, on varied hard and soft substrata (Kohn & Nybakken, 1975). In N. Papua New Guinea, common on exposed shallow reefs (Chaberman, pers. comm., 1981); more frequently found on extensive mud flats of mainland habitats than on coral reef in E. Australia (Huish, 1978).

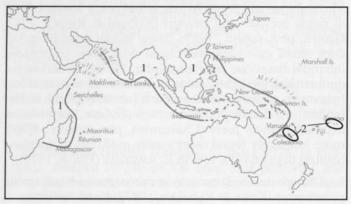
The species is known to prey on eunicid and nereid polychaetes (Kohn & Nybakken, 1975; Kohn, 1978a).

In Queensland, *C. biliosus* deposits small, stocky egg capsules underneath rocks near the reef crest (Loch, pers. comm., 1987). In Pakistan, number of eggs per capsule is 100-1,410; egg diameter of 160-180 μm, predicts a miminum pelagic period of 27-25 days (Zehra, 1990; Perron & Kohn, 1985; Zehra & Perveen, 1991).

**Discussion:** *C. biliosus* is most similar to *C. hyaena*. For the distinctions between them, see the Discussion of the latter species.

Most authors regard C. parvulus as a distinct, valid species. Coomans et al. (1982) provisionally separated C. biliosus, C. imperator, and C. parvulus at the species level, while da Motta (1993) did so with C. biliosus, C. parvulus (C. imperator as synonym), and C. neoroseus (shells from Philippines and Indonesia). Here, all these nominal taxa are considered conspecific and even not conclusively separable at the subspecies level. The South Indian population is distinctive in its size and colour, but shows no clear differences in other shell characters. Walls ([1979]) described populations from South Africa and Mozambique (Pl. 5, Figs. 5, 6) as a separate subspecies (C. b. meyeri). These shells tend to be smaller than Indian shells and have a more convex outline of the last whorl, and more often weak tubercles. However, they intergrade with shells from southern India and the differences in shell morphometry are minimal. Our results suggest a clinal variation, in agreement with Kilburn (1982).

C. biliosus refers to a specimen from the Gulf of Mannar, India, C. punctatus and C. piperatus seem to be synonyms. C. neoroseus is based on a specimen assumed to be from Philippines (da Motta, 1993); we know of similar shells from Indonesian populations. Specimens matching the lectotype of C. parvulus are known from Philippines and the W. Indian Ocean. C. imperator represents the Queensland population. The original figure of C. concinnus (= C. sapphirostoma) shows a small shell with smooth last whorl as occurring in Queensland and S. Africa (see Coomans et al., 1985a).



1: C. biliosus 2: C. exiguus

# 15 Conus exiguus LAMARCK, 1810

(Plate 5, Figures 14-31; Plate 72, Figures 14,15; Map 7)

- 1810 Conus exiguus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 39, no. 43
- 1843 Conus plumbeus Reeve, Proc. Zool. Soc. London, 11: 178; Conch. Icon., 1, Conus: Pl. 46 sp. 253
- 1858 Conus cabritii Bernardi, J. Conchyl. (Paris), 7: 377-378, pl. 13, figs. 2, 2a
- 1872 Conus vayssetianus Crosse, J. Conchyl. (Paris), 20: 154-155, pl. 16 fig. 1
- 1880 Conus taylorianus E. A. Smith, Proc. Zool. Soc. London, 1880: 32, pl. 48 fig. 3
- 1907 Conus bougei Sowerby III, Proc. Malac. Soc. London, 7: 299, pl. 25 figs. 1, 2
- 1913 Conus optimus Sowerby III, Ann. Mag. Nat. Hist., 12: 235, pl. 3 fig. 7
- 1985 Conus bougei var. poumensis Prigent, Rossiniana, 29: 22-23 figs. 5, 6

Types: C. exiguus: Holotype in MHNG (18.5 x 9.5 mm); C. plumbeus: 3 syntypes in BMNH (27 x 14.5; 25 x 12.5; 25 x 13 mm); C. cabritii: Holotype in MNHG (20 x 12 mm); C. vayssetianus: Original figure 14 x 7.5 mm; C. taylorianus: Holotype in BMNH (20 x 12 mm); C. bougei: 2 syntypes in BMNH (21 x 11; 22.5 x 12 mm); C. optimus: Holotype in BMNH (23 x 13 mm); C. bougei var. poumensis: 4 "syntypes" in coll. Prigent (L 24.5; 24.7; 25.2; 25.5 mm).

Type Localities: C. exiguus: "les mers de l'Asie", restricted to "New Caledonia" (Coomans et al., 1986); C. cabritii: "Nouvelle-Calédonie"; C. vayssetianus: "Nova Caledonia"; C. taylorianus: "Australia?"; C. bougei: Monac Island, New Caledonia"; C. optimus: "New Caledonia"; C. b. var. poumensis: "presqu'île de Poum, côte Ouest, Nord de la Nouvelle Calédonie."

Range: New Caledonia area; probably also Samoa.

Description: Small to medium-sized, light to moderately solid. Last whorl conical, sometimes conoid-cylindri-

cal in populations from very shallow water; outline convex, or slightly convex adapically and less convex to straight toward base. Shoulder angulate and tuberculate, subangulate and weakly tuberculate in populations from very shallow water. Spire of low to moderate height; outline concave to convex. In southern New Caledonia, larval shell of 2-2.25 whorls; maximum diameter 0.7 mm in northern New Caledonia to 1 mm in the south. Shells from Samoa match those from New Caledonia in the characters of the larval shell. Postnuclear spire whorls tuberculate to weakly tuberculate. Teleoconch sutural ramps flat, with 1 increasing to 4-7 spiral grooves. Last whorl with variably spaced, shallow, punctate spiral grooves, sometimes from base to shoulder; spiral ribs usually granulose and restricted to abapical area or extending to centre or shoulder (form plumbeus) (Pl. 5, Fig. 31). Largely smooth specimens often with distinct non-granulose spiral ribs at shoulder.

C.	exiguus Shell Morphometry
L	16 - 54 mm
RW	0.05 - 0.26 g/mm (L 19-45 mm
RD	0.57 - 0.67
PMD	0.83 - 0.95
RSH	0.09 - 0.20

Last whorl of various shades of brown, leaving variously shaped and sized white dots, spots or blotches, mostly located near shoulder and at centre, sometimes also at base. Brownish tones ranging from yellowish, orangish and olivebrown to dark reddish and blackish brown. Small individuals in northern New Caledonia (Pl. 5, Figs. 24, 25, 30) with small spirally arrayed white markings either extending across entire last whorl or restricted to central area. The medium-sized individuals in southern New Caledonia lighter in colour, with small to large white markings often fusing into 2-3 spiral bands or reduced to a few scattered dots or spots. Shells from very shallow water darkest in colour, with large, partially white markings, axially or spirally arranged. Base sometimes light violet. Larval shell white to pale yellow, pink in medium-sized shells from the south. Postnuclear sutural ramps matching last whorl in colouration (including number and size of white markings). Aperture of various shades of violet (southern population) or bluish violet to brown (other populations).

Periostracum thin and translucent.

In S. New Caledonia, animal red, dotted with white; siphon with sparse white dots at distal end. In the northern population, animal red, dotted with cream. In populations from very shallow water, animal red (Estival, 1981 & unpubl. observ.).

Habitat and Habits: In S. New Caledonia, *C. exiguus* known from coral, rubble, and coarse sand with algae in 13-53 m, often in channels of the barrier reef with strong water currents. In N. New Caledonia, a population with small shells is reported from similar habitats in 15-32 m. Moderately small, heavily flecked brownish black and

white shells are more widely distributed in New Caledonia and more common in the north; on coastal flats in 0.5-15 m, on dead coral and coarse sand bottoms (Estival, 1981; Tirard, pers. comm., 1989).

**Discussion:** *C. exiguus* as presented in this book may be a composite or complex of more than one species, but the common characters of its members are so distinctive that confusion with Indo-Pacific congeners is unlikely.

Previous authors (e.g. Estival, 1981; Richard, 1990) suggested 2 to 5 (mostly 3) morphological species in this complex: 1, a southern form (cited as C. optimus by Estival) with strictly conical shells (RD 0.57-0.63; PMD 0.86-0.95) of medium size (35-45 mm); 2, a relatively widely distributed form (C. cabritii of Estival) with moderately small (22-33 mm), conical to conoid-cylindrical shells (RD 0.57-0.67; PMD 0.83-0.92); 3, a northern form (C. bougei of Estival), of small shells (16-25 mm) with a conical last whorl (RD 0.60-0.65; PMD 0.85-0.90). Although we find that the shell characters of all intergrade, they may represent partially geographically differentiated populations. C. plumbeus (Pl. 5, Fig. 31) refers to completely granulose shells of this species. The type specimens of C. vayssetianus, C. taylorianus (Pl. 5, Fig. 29) and C. optimus (Pl. 5, Fig. 28) cannot be conclusively assigned to any of these forms, but all are within the range of variation of C. exiguus.

Specimens recently found in Western Samoa (Pl. 72, Figs. 14, 15) are similar to form *bougei*.

# 16 Conus boeticus REEVE, 1843

(Plate 6, Figures 1-18; Plate 70, Figures 1-3; Map 8)

- 1843 Conus boeticus Reeve, Proc. Zool. Soc. London, 11: 174; 1844: Conch. Icon., 1, Conus: Pl. 42 sp. 226
- 1843 Conus nitidus Reeve, Proc. Zool. Soc. London, 11: 180; 1844: Conch. Icon., 1, Conus: Pl. 47 sp. 266
- 1848 Conus ruppellii Reeve, Conch. Icon., 1, Conus suppl.: Pl. 2 sp. 273
- 1848 Conus cerinus Reeve, Conch. Icon., 1, Conus suppl.: Pl. 3 sp. 283a-b
- 1849 Conus lachrymosus Reeve, Conch. Icon., 1, Conus suppl.: Pl. 6 sp. 258
- 1849 Conus rivularis Reeve, Conch. Icon., 1, Conus suppl.: Pl. 6 sp.
- 1887 Conus fultoni Sowerby III, Thes. Conch., 5 suppl.: 273, no. 512, pl. 36 fig. 758
- 1913 Conus meleus Sowerby III, Ann. Mag. Nat. Hist., 11: 588, pl. 9 fig. 3

Types: *C. boeticus*: Type in BMNH (38 x 19 mm); *C. nitidus*: Original figure 19 x 9.5 mm; *C. ruppellii*: Type in BMNH (24.5 x 14 mm); *C. cerinus*: Type in BMNH (29 x 15 mm); *C. lachrymosus*: Type in BMNH (30 x 15 mm); *C. rivularis*: Syntype in BMNH (23 x 14 mm); *C. fultoni*: Holotype in BMNH (23 x 14 mm); *C. meleus*: Holotype in BMNH (29 x 15 mm); *C. ruppellii*: "Red Sea".

**Type Localities:** *C. boeticus*: "Philippine Islands"; *C. ruppelii*: "Red Sea"; "Red Sea"; *C. cerinus*: "Island of Mindanao, Philippines"; *C. rivularis*: "Moluccas"; *C. fultoni*: "Singapore"; *C. meleus*: "Kii, Japan."

Range: Mozambique, Mascarenes and Seychelles; Indonesia to Japan and to Fiji.

**Description:** Small to medium-sized, light to moderately solid. Last whorl conical to ventricosely conical, broadly conical in form *ruppellii*; outline variably convex adapically, slightly convex to almost straight below. Shoulder angulate to subangulate, smooth to weakly tuberculate. Spire of low to moderate height, variably concave in outline. Larval shell of about 2 whorls; maximum diameter 0.7-0.8 mm, 0.95 mm in shells from Mozambique. Postnuclear spire whorls weakly tuberculate to nearly smooth. Teleoconch sutural ramps flat, with 1-2 increasing to 3-5 spiral grooves. Last whorl with weak or strong, mostly granulose ribs around basal fourth to half; sometimes granulose ribs to shoulder (form *rivularis*) (Pl. 6, Fig. 16).

# C. boeticus Shell Morphometry

L	20 - 40 mm
RW	0.03 - 0.15 g/mm (L 20-33 mm)
RD	
- form ruppellii	0.61 - 0.72
- other forms	0.54 - 0.68
PMD	0.78 - 0.90
RSH	0.09 - 0.18

Ground colour white. Last whorl with large, irregularly shaped, yellowish to blackish brown markings above and below centre, often fusing into 2 spiral bands and sometimes coalescing axially. Spiral rows of fine brown to blackish brown dots extend from base to shoulder; dotted lines may be variably reduced or replaced by dashed lines. Base usually white ventrally. Larval shell and a variable number of adjacent sutural ramps light red or white. Late sutural ramps radially maculated with brown; usually same colour as last whorl; maculation variable. Sutural zone sometimes solid brown. Aperture white to light violet or pink.

In form *ruppellii* (Pl. 6, Figs. 11-13), last whorl usually reddish to blackish brown except for narrow white spiral bands at centre and at shoulder, both crossed by brown axial markings. Spiral rows of larger brown dots and dashes than in other forms, from base to shoulder, often with intermittent white dots and dashes within dark areas. Larval shell white. Aperture white.

Shells from Mozambique with bluish grey ground colour and olive-tan to dark olive spiral bands. Larval whorls white (Pl. 6, Figs. 9-10).

Periostracum olive to orange, thin, translucent to opaque, with fine axial and tufted spiral ridges (Cernohorsky, 1964; Chaberman, pers. comm., 1981).

At Hansa Bay (N. New Guinea), dorsum of foot cream to brown, with a dotted brown pre-marginal line ending anteriorly in a blotch on each side; lateral marginal zone and median zone dotted with brown. Sole of foot beige. Rostrum cream. Tentacles cream with white tips. Siphon tan to reddish brown, paler ventrally, with 2 weak brown rings back from the tip (Chaberman, pers. comm., 1981).

Habitat and Habits: Reported from lower reef slopes in Papua New Guinea and on sand and weed beneath coral in Fiji (Cernohorsky, 1964; Chaberman, pers. comm., 1981).

**Discussion:** For comparison to *C. pauperculus* and *C. montillai*, see the Discussions of those species.

The nominal species listed above in synonymy represent intraspecific variability of *C. boeticus*, as follows:

- C. cerinus (Pl. 6, Fig. 17) is a form of C. boeticus with a relatively stout shell (RD 0.66-0.68), with few spiral rows of dots.
- C. lachrymosus (Pl. 6, Fig. 18) is a form of C. boeticus with the shell largely overlaid with tan to reddish brown axial markings and dashed to dotted spiral lines.
- *C. meleus*, represented only by its holotype (Pl. 70, Figs. 1, 2), has a white shell with yellow axial blotches on both sides of centre; its morphological characters do not justify taxonomic separation from *C. boeticus*. Similar shells from Augustus Is., N.W. Australia (Pl. 70, Fig. 3) may be attached to this form.
- *C. nitidus* (Pl. 6, Fig. 14) seems to be a juvenile specimen, described and depicted by Reeve as "light orange-brown . . and encircled . . with interrupted brown lines, apex . . pink."
- C. rivularis (Pl. 6, Fig. 16) refers to entirely granulose shells of C. boeticus, known from Indonesia and Philippines.
- *C. ruppellii* (syn. *C. fultoni*) (Pl. 6, Figs. 11-13), known from Philippines and Indonesia, is assigned as a form of *C. boeticus*, because both occur sympatrically and the conchological differences do not justify separation at the species level. They can be separated neither by the characters of their larval shell nor by the morphometry and the sculpture Map 8

Adadives Sri Lanka Merchall Is.

Maldives Sri Lanka New Object School Is.

Mauritius Réunian Madagascur

Madagascur

1: C. boeticus 2: C. montillai 3: C. pauperculus

of the teleoconch, and shells with an intermediate colour pattern occur.

## 17 Conus montillai RÖCKEL, 1985

(Plate 6, Figures 19, 20; Map 8)

1985 Conus montillai Röckel, Heldia 1 (2): 61-62, pl. 9

Type: Holotype in SMF (19 x 11 mm).

Type Locality: "Coron, Palawan, Philippinen."

Range: Palawan, Philippines.

**Description:** Small, light to moderately light. Last whorl conical or ventricosely conical to broadly or broadly and ventricosely conical; outline variably convex, left side often sigmoid. Shoulder angulate, moderately to weakly tuberculate. Spire of moderate height, outline concave. Larval shell of about 1.75 whorls, maximum diameter 1 mm. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat, with 1 increasing to 4-6 spiral grooves. Specimens with granulose spiral ribs from base to shoulder intergrade with specimens with granulose ribs restricted to basal third of last whorl; ribs stronger abapically.

# C. montillai Shell Morphometry L 17 - 23 mm RW 0.04 - 0.09 g/mm RD 0.66 - 0.76 PMD 0.78 - 0.89 RSH 0.16 - 0.22

Ground colour white. Last whorl with variably sized brown axial blotches, often fusing into 2 smeary spiral bands within adapical and abapical third. Usually with sparse spiral rows of brown dots and dashes, rarely extending from base to shoulder. Larval shell and a few adjacent sutural ramps pink. Late spire whorls crossed by brown streaks, often partially reduced to brown spots between marginal tubercles. Aperture white.

Habitat and Habits: Reported from shallow coastal waters.

**Discussion:** *C. montillai* is closely related to *C. boeticus*; however, the latter species attains larger size (20-40 mm). Philippine specimens of *C. boeticus* have generally narrower last whorls (RD 0.54-0.68 vs. 0.66-0.76), smoother, often subangulate shoulders, and pronounced dots around the last whorl. Form *ruppellii* of *C. boeticus* is also narrower (RD 0.72 is maximum value in form *ruppellii* but mean value in *C. montillai*), has a white larval shell and a largely black-brown, heavily dotted last whorl with a straighter outline. *C. boeticus* has a somewhat narrower larval shell (max. diameter usually 0.8 mm) with 2 whorls. More de-

tailed information may support the status of *C. montillai* as either a valid species or a geographic subspecies of *C. boeticus. C. montillai* has been confused with *C. sphacelatus* Sowerby, but the latter is a Caribbean species.

# 18 Conus pauperculus SOWERBY I, 1834

(Plate 6, Figures 21-23; Map 8)

1834 Conus pauperculus Sowerby I, Conch. Ill.: Pt. 56, fig. 78

Type: Holotype figured in Sowerby I (1834: Pt. 56, fig. 78) (26 x 12 mm)

Type Locality: "Cape of Good Hope" (Sowerby II, 1858).

Range: Japan.

Description: Moderately small to medium-sized, light to moderately light. Last whorl conical to ventricosely conical; outline slightly convex, left side sometimes sigmoid. Shoulder angulate to subangulate, occasionally weakly undulate. Spire of moderate height, variably concave in outline. Postnuclear spire whorls weakly tuberculate to almost smooth. Teleoconch sutural ramps flat, with 2 increasing to 4-6 spiral grooves. Last whorl with a few weak, widely spaced spiral ribs above base.

# C. pauperculus Shell Morphometry L 25 - 40 mm RW 0.04 - 0.10 g/mm (L 24-38 mm) RD 0.57 - 0.61 PMD 0.83 - 0.88 RSH 0.13 - 0.16

Ground colour mixed bluish grey and tan. Last whorl encircled with brownish violet, leaving a ground-colour band at centre and at base. About 10-20 rather evenly spaced dotted brown spiral lines extending from base to shoulder. Apex pink. Late sutural ramps crossed by brown streaks or blotches. Aperture pale violet, darker above centre.

Habitat and Habits: Shallow water.

**Discussion:** *C. pauperculus* seems related to *C. boeticus*, from which it differs in its lighter weight, its smoother outer edges of the late sutural ramps, and the weak spiral sculpture as well as the dull brownish violet colouration of the last whorl.

Specimens from Philippines (see Appendix 2, no. 30, Pl. 73, Figs. 10-12) with a brown colour pattern with coarse, brown spiral lines, may belong to *C. pauperculus*, but differ in conical last whorl, white ground colour, light brown apex, and higher relative weight (RW more than 0.13 g/mm).

### 19

## Conus balteatus SOWERBY I, 1833

(Plate 6, Figures 24-36; Map 9)

- 1833 Conus balteatus Sowerby I, Conch. Ill.: Pt. 37, fig. 58
- 1848 Conus pigmentatus A. Adams & Reeve, Zool. Voy. Samarang, Moll., 1: 18, pl. 5 figs. 11 a-b
- 1865 Conus moussoni Crosse, J. Conchyl. (Paris), 13: 299, pl. 10 fig.3
- 1869 Conus (Coronaxis) cernicus "Barcl. MS" H. Adams, Proc. Zool. Soc. London, 1869: 272, pl. 19 fig. 1
- 1873 Conus tenuisulcatus Sowerby III, Proc. Zool. Soc. London, 1873: 145-146, pl. 15 fig. 2 (non C. tenuisulcatus Sowerby III, 1870)
- 1877 Conus propinquus E. A. Smith, Ann. Mag. Nat. Hist., 19: 223 (nom. nov. for C. tenuisulcatus Sowerby, 1873)
- 1933 Conus pigmentatus concolor Barros e Cunha, Mem. Est. Zool. Univ. Coimbra, (1) 71: 52-53, no. 43 (non C. concolor Sowerby I, 1834)
- 1942 Conus circumclausus Fenaux, Bull. Inst. Océan. (Monaco), 814: 3, fig. 8

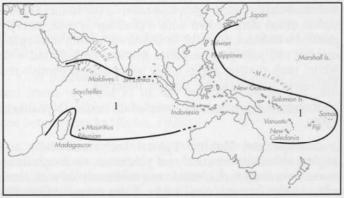
**Types:** *C. balteatus*: Lectotype (Kohn, 1992) figured in Sowerby (1833: Pt. 37, fig. 58) (32 x 20 mm); *C. pigmentatus*: Type in BMNH (28 x 14 mm); *C. moussoni*: Holotype in BMNH (28 x 13 mm); *C. cernicus*: Original figure 25 x 12 mm; *C. tenuisulcatus*: Original figure 25 x 16 mm; *C. p. concolor*: Holotype in MZUC (23 x 15 mm); *C. circumclausus*: Original figure 18 x 9.5 mm.

**Type Localities:** *C. balteatus*: "the Mascarenes" (Coomans et al., 1982); *C. cernicus*: "Barkly Island, Mauritius"; *C. tenuisulcatus*: "Mauritius;" *C. moussoni*: "in archipelago Seychellarum"; *C. p. concolor*: "Mares orientais"; *C. circumclausus*: "I. Maurice."

Range: Indian Ocean: Mozambique to N. Somalia, Mascarenes, Maldives and Indonesia; Pacific: Japan to W. Australia and Queensland and to Fiji and Samoa.

**Description:** Small to medium-sized, moderately light to moderately solid; shells of form *cernicus* (Pl. 6, Figs. 29-32) smaller than shells of typical form. Last whorl conical or ventricosely conical to broadly conical or pyriform, narrower in form *cernicus*; outline slightly to distinctly convex adapically, less so, straight or somewhat concave below. Shoulder usually angulate, strongly to weakly tuberculate. Spire of low to moderate height, outline

Map 9



1: C. balteatus

straight to concave. Larval shell of 1.75-2 whorls, maximum diameter about 0.7 mm. Postnuclear spire whorls tuberculate to weakly tuberculate. Teleoconch sutural ramps flat, with 1-2 increasing to 4-7 spiral grooves. Entire last whorl with closely spaced spiral ribs, weak in some populations.

C. balte	
L	
- typical form	25 - 47 mm
- form cernicus	18 - 30 mm
RW	
- typical form	0.09 - 0.30 g/mm (L 23-35 mm)
- form cernicus	0.05 - 0.14 g/mm (L 17-29 mm)
RD	
- typical form	0.60 - 0.77
- form cernicus	0.56 - 0.65
PMD	0.78 - 0.90
RSH	0.07 - 0.18

Ground colour white, sometimes bluish violet. Last whorl encircled with a band of various shades of brown to brownish red or olive, on each side of centre. Specimens with separate colour bands and ground-colour zones at centre, shoulder and base intergrade with specimens having only shoulder tubercles partially with ground colour. Dark zones of last whorl often speckled with white dots or dashes arranged in spiral rows, either scattered or regularly arrayed. Larval whorls and a few adjacent sutural ramps reddish violet. Late sutural ramps often of immaculate ground colour, sometimes with markings matching spiral bands of last whorl in colour. Aperture translucent in small shells, violet to brown in larger shells.

Periostracum yellow-olive, thin, translucent, and smooth in shells from Japan, darker olive, thicker and opaque in shells from Somalia.

Foot dull red; sides may be mottled with black and sole may have scattered white dots. In the Indian Ocean, rostrum evenly reddish brown or dark brown with a pink tip. In specimens from Okinawa, rostrum pink, with white dots and dark brownish red transverse streaks longitudinally arrayed near tip; tentacles pale grey, mottled with white dots and short dark reddish brown streaks. In the Indian Ocean, siphon either dark brown with a pink tip or rose, heavily mottled with black dorsally. In Okinawa, siphon with a pink anterior and pale grey posterior portion, both dotted with white; pink portion additionally with dark brownish red transverse streaks (Kohn, unpubl. observ.).

Radular teeth matching those of *C. varius* (Nybakken, 1990).

Habitat and Habits: Typical form intertidally and slightly subtidally on coral reef platforms, on rough limestone, dead coral rocks, rubble and rubble mixed with sand, often hidden beneath coral rocks. Form *cernicus* from the Mascarenes and from Somalia is reported in 20-30 m (Cer-

nohorsky, 1964; Kohn & Nybakken, 1975; Huish, 1978; Reichelt & Kohn, 1985; Loch, pers. comm., 1987).

C. balteatus is known to feed on errant polychaetes (Kohn & Nybakken, 1975; Reichelt & Kohn, 1985).

In the E. Indian Ocean, egg diameter of  $310 \, \mu m$  predicts a minimum pelagic period of about 14 days (Perron & Kohn, 1985).

**Discussion:** *C. balteatus* is similar to *C. rattus*. For distinction, see the Discussion of the latter species. *C. lividus* and *C. sanguinolentus* may be similar in shape, sculpture and colouration but typically attain larger size. Both differ in the more widely spaced, weaker and usually granulose ribs around the last whorl, the apex is not reddish violet and the aperture is bluish to purple violet behind a orange-brown margin. Both have more larval whorls and a differently coloured animal.

The intraspecific variability of C. balteatus has resulted in a number of synonyms that refer to individual variants or ecological forms. C. pigmentatus (Pl. 6, Fig. 35) is a typically patterned form with a tuberculate shoulder and the last whorl quite straight in outline. Such shells occur across the entire range of the species, although they are more common in eastern populations. C. p. concolor differs only in its violet colouration. C. tenuisulcatus Sowerby III, 1873, corresponds with the original figure of C. balteatus except for a slightly different colour pattern. C. moussoni (Pl. 6, Fig. 36) may represent a comparatively slender (RD 0.61) colour variant with a largely yellowish cream last whorl. The name C. cernicus applies to an ecological variant co-occurring with the typical form in the Mascarenes (Pl. 6, Figs. 29-32). Shells from this deep subtidal population closely resemble the original figure of C. circumclausus. If the high spire seen in the original figure of C. cernicus is considered to be somewhat aberrant, C. circumclausus can be synonymized with C. cernicus and hence with C. balteatus. Shells of this form differ only slightly from the typical form in their morphometry, less pronounced sculpture and often subangulate shoulder, and they intergrade in all characters with typical C. balteatus. A separation of the western and the eastern populations at the subspecies level (Coomans et al., 1982, 1983) is not justified, because the differences indicated by those authors are not geographically restricted.

### 20

## Conus miliaris HWASS in BRUGUIÈRE, 1792

(Plate 7, Figures 1-14; Plate 74, Figure 8; Map 10)

- 1792 Conus miliaris Hwass in Bruguière, Encycl. Méth., 1: 629-630, no. 26
- 1792 Conus barbadensis Hwass in Bruguière, Encycl. Méth., 1: 632, no. 29
- 1834 Conus minimus var. granulatus Sowerby I, Conch. Ill.: Pt. 56, fig. 81 (non C. granulatus Linné, 1758)
- 1834 Conus fulgetrum Sowerby I, Conch. Ill.: Pt. 56, fig. 82

1845 Conus scaber Kiener, Coq. Vivant., 2: Pl. 100 fig. 1; 1849-1850: 351-352 (non C. scaber Link, 1807)

1980 Conus miliaris pascuensis Rehder, Smithsonian Contrib. Zool., 289: 91-92, 147, figs. 21, 22

Types: C. miliaris: Lectotype (Kohn, 1968) in MHNG (43 x 27 mm); C. barbadensis: Lectotype (Kohn, 1968) in MHNG (22 x 14 mm); C. minimus var. granulatus: Lectotype (Kohn, 1992) in NMWC (24 x 16 mm); C. fulgetrum: Lectotype (Wils, 1986; Kohn, 1992) in NMWC (22 x 14 mm); C. scaber: Original figure 28 x 18 mm; C. miliaris pascuensis: Holotype in USNM (26 x 15 mm).

Type Localities: C. miliaris: "les mers de la Chine"; C. barbadensis: "l'isle de Barbade"; C. fulgetrum: "Red Sea" (Sowerby II, 1857); C. scaber: "les mers de l'Océanie"; C. miliaris pascuensis: "Easter Island."

Range: Indo-Pacific, except for Marquesas Is. and Hawaii. *C. m. miliaris*: S. Africa to Red Sea and to French Polynesia and Marshall Is.; *C. m. pascuensis*: restricted to Isla de Pascua (Easter Id.) and Sala y Gomez (Chile).

Description: Small to medium-sized, usually moderately light to solid. Last whorl broadly or broadly and ventricosely conical, sometimes conical to ventricosely conical in Indian Ocean shells; outline slightly to distinctly convex. In large specimens, aperture often with a distinct median pad and an oblique abapical ridge. Shoulder variably tuberculate, angulate (C. m. miliaris) or subangulate to rounded (C. m. pascuensis). Spire of low to moderate height, outline straight to convex (C. m. miliaris) or domeshaped (C. m. pascuensis). Maximum diameter of larval shell about 0.7 mm. Postnuclear spire whorls weakly to strongly tuberculate. Teleoconch sutural ramps flat or faintly concave, with 2 increasing to 4-5 spiral grooves. Last whorl with widely spaced granulose spiral ribs basally, smooth or with ribbons separated by grooves adapically. In form fulgetrum, widely set, fine, punctate grooves encircling a variable adaptical portion of last whorl.

	C. miliaris Shell Morp	onometry
	C. m. miliaris	C. m. pascuensis
L	22 - 43 mm	15 - 30 mm
RW	0.12 - 0.48 g/mm	0.05 - 0.17 g/mm
RD	0.67 - 0.83	0.71 - 0.75
	0.70 - 0.79 (Pacific C	Ocean)
PMD	0.79 - 0.92	0.78 - 0.84
RSH	0.06 - 0.20	0.11 - 0.22

Ground colour white. Last whorl heavily shaded with pink or grey and rose leaving only blotches, broad axial zigzag lines, and broad arrow-shaped markings. White blotches fusing into a spiral band at centre and a pale band below shoulder. Variously spaced spiral rows of alternating brown and white dots and dashes from base to shoulder. Larval whorls white, beige, pink or violet-red. Postnuclear sutural ramps with broad orange to red-brown dashes composed of collabral lines between tubercles. Aperture pink to brownish violet, with paler bands at centre and below shoulder.

Periostracum yellowish grey, thin, translucent, smooth.

Form fulgetrum (Pl. 7, Figs. 9-11) differs from typical C. m. miliaris (Pl. 7, Figs. 1-8) in the dark orange-brown colouration of its last whorl, with fine brown reticulate lines and narrow crosshatchings, small spots and axial zigzag flames of white. Spiral rows of brown and white dots or dashes are absent. Aperture grey to brown, edged with violet-brown.

C. m. pascuensis (Pl. 7, Figs. 12-14) may be tinged with various shades of olive-brown and has a pronounced light coloured band without dots and dashes below edge of shoulder.

Foot and siphon narrow. In typical C. m. miliaris (Pl. 74, Fig. 8), foot white to pale buff mottled with pink to brown, usually lighter and with sparser mottling on sole; dorsum of foot often pink to light orange anteriorly; with a dotted black marginal line, broader posteriorly and ending in a large cluster of black dots anteriorly. Rostrum pale red. Tentacles white to buff. Siphon red at tip, grading to pale pink or brown, white or grey behind; distal part with or without black or white dots; rest of siphon mottled with brown to black, more heavy at base (Chaberman, pers. comm., 1981; Pearson, unpubl. observ.; Fainzilber et al., 1992; Kohn, unpubl. observ.). In C. m. pascuensis, sole of foot buff, mottled with brown; rostrum pale orange; tentacles grey, with a few brown and white spots at their distal end. Tip of siphon rose, with a few white spots; posterior to the tip, dorsum of siphon buff, with a transverse pattern of dark brown streaks extending to the ventro-lateral edge and becoming paler there; anterior third of dorsum often with a lighter mottling of transverse or longitudinal dashes or spots; in some specimens, rose tip separated from darkly mottled portion by a pale immaculate ring (Kohn, unpubl. observ.).

Radular teeth with an adapical barb opposite a weak blade; serration no longer than blade; shaft with a central waist and base with a spur. *C. m. pascuensis* with smaller teeth in proportion to shell length than *C. m. miliaris* (Peile, 1939; Bandel 1984; Kohn, 1978b).

Habitat and Habits: Intertidal to about 10 m. Typical form of *C. m. miliaris* is more common on intertidal benches of beachrock or truncated reef limestone than on slightly subtidal reef platforms. It can be found at protected or exposed sites, in or on sand, coral rubble or rocks, and algal turf, infrequently also on large patches of sand and on bare reef limestone (Kohn, 1961b, 1968b, 1978b; Kohn & Nybakken, 1975; Kohn & Leviten, 1976; Leviten & Kohn, 1980; Tirard, pers. comm., 1989; Fainzilber et al., 1992).

*C.m. pascuensis* on marine benches and among boulders and corals to about 12 m. On intertidal benches, in sand bound by algal turf and chaetopterid tubes, in sand pockets and between rocks (Kohn, 1978b).

C. m. miliaris feeds exclusively on errant polychaetes, primarily Eunicidae. C. m. pascuensis also preys on eunicids and infrequently on nereids, but its diet composition differs from that of C. m. miliaris in including a member of the family Onuphidae as most common prey species

(Kohn, 1968b & 1978b; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985).

 $C.\ m.\ miliaris$  deposits egg masses on the underside of coral rocks. Capsules of 5.5 x 6.0 mm contain about 1,000 eggs each. Egg diameter of about 160  $\mu$ m predicts a minimum pelagic period of about 27 days (Kohn, 1961b; Perron & Kohn, 1985).

**Discussion:** C. miliaris is closely related to C. abbreviatus, C. encaustus and C. tiaratus (the latter species in Vol. 2). For comparison with C. abbreviatus, C. encaustus and C. coronatus, see the Discussions of those species.

C. m. pascuensis differs from C. m. miliaris in morphometry of the shell and radular teeth, in some ecological characters, and to some extent in colour pattern of both shell and animal (Kohn & Riggs, 1975; Kohn, 1978b). These differences may be explained by geographic separation, perhaps over a period of 1-2.5 my, and by adaptation to different environmental conditions. The differences are balanced by striking morphological and ecological similarities, which strongly suggest subspecies status for the population from Easter Island (Rehder, 1980).

The name *C. fulgetrum* (syn. *C. scaber*) appears to apply to populations from Japan southward to the Solomon Is. We tentatively consider this nominal species a form of *C. m. miliaris*. It is not distinct from typical *C. m. miliaris* in shell morphometry but differs constantly in the colour pattern of the shell without intergrading. More data on additional aspects of morphology, ecology and zoogeography are needed for a conclusive determination of these populations as a valid species or as a form of *C. m. miliaris*.

A form from the Indian Ocean often referred to as *C. fulgetrum* (e.g. Sharabati, 1984; Bandel, 1984) is actually fairly typical of *C. m. miliaris* and not intermediate between form *fulgetrum* from the W Pacific, as described above, and the typical Indo-West Pacific form.

Map 10

# 21 Conus abbreviatus REEVE, 1843

(Plate 7, Figures 15-17; Map 10)

1843 Conus abbreviatus Reeve, Conch. Icon., 1, Conus: Pl. 16 sp. 86

**Type:** Lectotype (Coomans et al., 1979) in BMNH (34 x 22 mm).

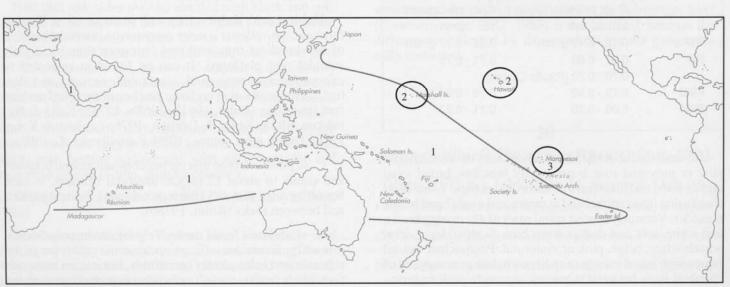
Type Locality: "Wahoo, Sandwich Islands."

Range: Hawaii; probably Fanning Is. and Enewetak, Marshall Is.

**Description:** Small to medium-sized, moderately solid to solid. Last whorl usually broadly conical, outline variably convex. Shoulder angulate to rounded, tuberculate. Spire of low to moderate height, outline straight to convex. Larval shell of about 4 whorls. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat to slightly concave, with 2 increasing to 3-5 spiral grooves. Last whorl with weak to obsolete spiral ribs on basal third; in smaller specimens, followed by well-separated punctate grooves up to shoulder.

O. u.	obreviatus Shell Morphometry
L	20 - 58 mm
RW	0.10 - 0.50 g/mm (L 18-45 mm)
RD	0.70 - 0.83
PMD	0.83 - 0.92
RSH	0.09 - 0.22

Ground colour bluish grey. Last whorl with 2-3 paler spiral bands, at shoulder, below centre and often within adapical third. Very fine brown or olive axial lines usually forming spiral bands above base, centrally and below pale



1: C. miliaris 2: C. abbreviatus 3: C. encaustus

subshoulder band. Variably spaced spiral rows of dark brown dots extending from base to shoulder. Teleoconch sutural ramps with inconspicuous brown dots or fine axial lines between tubercles. Aperture brownish violet, with pale bands below shoulder and at centre.

Periostracum yellow, thin, and translucent.

Foot pale brown; siphon pale brown, tinged with pink (Kohn, 1959a).

Radular teeth with an adaptical barb opposite a long narrow blade extending halfway down the shaft; serration occurs on the inner margin close to the apex; base with a spur (James, 1980).

Habitat and Habits: Abundant on intertidal benches and common on subtidal reef platforms, where size is larger; mainly to 15 m, a few specimens have been dredged in 100 m (Kohn & Weaver, 1962). *C. abbreviatus* mainly in sand and algal turf on reef limestone (Kohn, 1959b).

*C. abbreviatus* feeds exclusively on polychaetes, mainly Eunicidae and Nereidae.

Egg capsules 9-10 x 7-9 mm, deposited in rows and attached to the substratum by their basal plates; about 1,300 eggs per capsule and about 44,000 eggs per egg mass. Egg diameter is 160-180 μm. The planktotrophic veliger has an observed pelagic period of 32 days (Perron 1981c; Perron & Kohn, 1985).

**Discussion:** The endemic Hawaiian species *C. abbreviatus* is closely related to *C. miliaris*, which is not known from Hawaii and differs in its smaller maximum size (ca. 40 mm), variously granulose surface and intermittent white dashes usually present within the dotted brown lines around the last whorl, and in the colour pattern of its animal. In spite of a 30-day pelagic period observed both in *C. miliaris* and *C. abbreviatus*, and occasional dispersal of *C. abbreviatus* to the Marshall and Line Is., no intermediates between these two species are known.

# 22 Conus encaustus Kiener, 1845

(Plate 7, Figures 18-21; Map 10)

1845 Conus encaustus Kiener, Coq. Vivant., 2: Pl. 14 fig. 2; 1846: 54-55

1848 Conus praetextus Reeve, Conch. Icon., 1, Conus suppl.: Pl. 2 sp. 277

Types: C. encaustus: Original figure 26 x 15 mm; C. praetextus: 3 syntypes in BMNH (33 x 21; 33 x 21; 28 x 19 mm).

Type Localities: C. encaustus: "Marquesas Islands" (Coomans et al., 1986); C. praetextus: "Marquesas Islands."

Range: Marquesas.

**Description:** Moderately small, usually moderately solid. Last whorl generally conical to broadly conical, straight to slightly convex in outline. Shoulder angulate,

prominently tuberculate. Spire of low to moderate height, somewhat convex to concave in outline. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps nearly flat, with 2 increasing to 4-5 spiral grooves. Basal half of last whorl with well-separated spiral ribs and adjacent punctate grooves, occasionally extending to shoulder.

C. e	ncaustus Shell Morphometry
	25 - 35 mm
RW	0.15 - 0.37 g/mm
RD	0.68 - 0.74
PMD	0.83 - 0.94
RSH	0.07 - 0.16

Ground colour bluish white. Last whorl with 2 interrupted to solid, olive brown or reddish brown spiral bands, leaving ground-colour bands at shoulder edge and well above as well as just below centre. Shoulder band usually narrow and suffused with pale red. Numerous closely spaced spiral rows of alternating white and brown dashes or dots from base to subshoulder area or shoulder. Teleoconch sutural ramps with fine brown axial lines and with dark brown dashes along the outer edge between tubercles. Aperture violet-brown, with pale bands centrally and below shoulder.

**Habitat and Habits:** In 0.5-6 m; on reefs, sand, boulders and beneath rocks.

**Discussion:** *C. encaustus* is closely allied to the allopatric species *C. abbreviatus* and *C. miliaris. C. abbreviatus* may attain larger size (up to 58 mm) and tends to have a higher spire and a broader last whorl; it is more convex in outline and lacks the pronounced, olive or brown spiral banding, the intermittent white dashes or dots within the lines around last whorl and the brown lining at the shoulder edges of *C. encaustus. C. miliaris* has a generally broader, often ventricosely conical last whorl, lacks the pronounced brown lining of the shoulder edges, and has the white and brown elements less regularly arranged within the spiral rows. The colour of typical *C. miliaris* lacks grey, blue and olive tones.

# 23 Conus coronatus GMELIN, 1791

(Plate 7, Figures 22-31; Plate 74, Figure 9; Map 11)

- 1791 Conus coronatus Gmelin, Syst. Nat., 13 ed., 1: 3389, no. 39
- 1798 Cucullus coronalis Röding, Mus. Bolten., 2: 38, no. 478/9
- 1802 Conus parvus Gebauer, Syst. Verz. Seest., Seeig., Conch., Pflanzent.: 7, no. 55 (non C. parvus (Röding), 1798)
- 1857 Conus aristophanes "Duclos" Sowerby II, Thes. Conch., 3: 9, sp. 63, pl. 4 figs. 81, 82

1864 Conus minimus Linné var. condoriana Crosse & Fischer, J. Conchyl. (Paris), 12: 334

Types: C. coronatus: Neotype (Kohn, 1966) in BMNH (27.5 x 16.5 mm); C. coronalis: Refers to the original figure of C. coronatus Gmelin; C. parvus: Lectotype (Kohn, 1981) figured in Martini (1773: Pl. 63 fig. 704) (30 x 18 mm); C. aristophanes: Lectotype (Coomans et al., 1981) in BMNH (35.5 x 23 mm); C. m. var. condoriana: Holotype 21 x 12 mm acc. Crosse & Fischer.

**Type Localities:** *C. coronatus*: "Australia"; *C. aristophanes*: "Philippine and Sandwich Islands"; *C. m.* var. *condoriana*: "Poulo-Condor, in the South China Sea, off Saigon."

Range: Entire Indo-Pacific.

Description: Small to medium-sized, moderately light to solid. Last whorl usually broadly to broadly and ventricosely conical or even ovate; outline slightly to pronouncedly convex; left side straight to concave at base. Shoulder subangulate to angulate, tuberculate. Spire of low to moderate height, outline concave to convex. Larval shell multispiral. Postnuclear spire whorls tuberculate to strongly tuberculate. Teleoconch sutural ramps flat to concave, with 1-7 spiral grooves in late whorls; last ramp may have additional spiral striae. Last whorl variable in surface sculpture; largely smooth shells with well separated weak spiral ribs at base intergrade with shells with distinct granulose ribs from base to adapical third.

Ground colour pale grey, beige to pink; often with several shades merging together. Last whorl with pale, occasionally obsolete spiral bands below shoulder and centre. Variously sized markings of brown, black or olive, spirally aligned on either side of subcentral band, either separate or fusing into 2 solid colour bands. Variably spaced spiral rows of alternating white and dark dots or dashes from base to shoulder; occasionally, with additional diagonal or zigzag-shaped white markings. Larval whorls grey or light violet to red. Teleoconch spire radially maculated with varying brown to black blotches or bundles of fine lines.

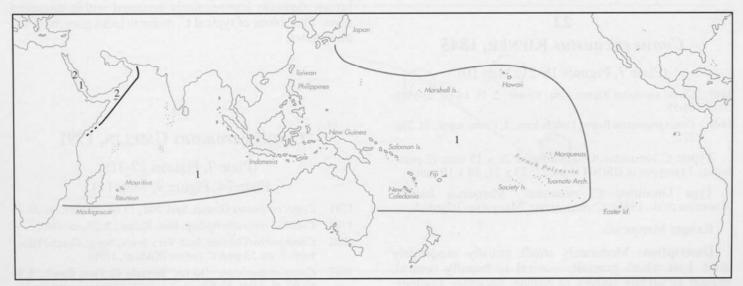
Aperture bluish to brownish grey, with pale bands below shoulder and centre.

C. c	oronatus Shell Morphometry
L	20 - 47 mm
RW	0.08 - 0.45 g/mm
RD	0.68 - 0.84
PMD	0.69 - 0.89
RSH	0.10 - 0.23

Periostracum yellow to yellowish grey, thin, variously translucent, smooth.

Colour pattern of animal (Pl. 74, Fig. 9) variable within local populations and between populations from different areas: Foot white to brown or brownish green (form aristophanes from Marshall Is.). Dorsum of foot sometimes spotted with purple or black, sometimes with orange or red anterior edge, and often a dotted black marginal line joining a large, brown or black, trilobate blotch anteriorly. Sides of foot may be lighter in colour posteriorly, with or without a reddish tinge. Sole of foot often edged with red anteriorly or at both ends, with or without purple and black mottling. Rostrum uniformly brown, pink, or brown tipped with orange, sometimes finely mottled with black. Tentacles beige with darker tips, brown or solid white. Siphon white to dark reddish brown, variously dotted with brown to black, usually with a variably wide red tip; black mottling either on entire siphon or only behind the distal red zone; occasionally also densely dotted with white dots or with heavy black streaks (Kohn, 1978a, unpubl. observ.; Lewis, 1979; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.).

Map 11



1: C. coronatus 2: C. taeniatus

In the N. Red Sea, animals rather uniformly coloured: scattered brown spots on a greyish white ground (Fainzilber et al., 1992).

Radular teeth small and stout, with an adapical barb opposite a long blade; serration short, ending anterior to the central constriction of the shaft; base with a distinct spur (James, 1980; Bandel, 1984; Kohn, unpubl. observ.).

Habitat and Habits: Intertidal to about 10 m, at protected or exposed sites. In southern Africa, usually in the mid-intertidal zone, in or on sand pockets, sand-filled crevices and in sand along edges of rocks as well as among sea-weeds and oysters; it favours semi-sheltered or sheltered habitats (Kilburn & Rippey, 1982; Grosch, pers. comm., 1989). In the Red Sea, living on the entire inner reef flat among rocks and boulders (Sharabati, 1984; Fainzilber et al., 1992). In India, intertidally on rough limestone benches and in or on rubble or coarse sand beneath or near coral rocks (Kohn, 1978a); in Sri Lanka, both intertidally and slightly subtidally on reef flats inhabiting the same microhabitats as in India and additionally bare coral rocks with or without algal turf (Kohn, 1960). On intertidal reef flats in Thailand and Indonesia, in sand-filled depressions, larger areas of sand, and on bare limestone pavement (Kohn & Nybakken, 1975). Data from intertidal reef rock benches of the Seychelles, E. Australia and Micronesia indicate a similar selection of microhabitats as in the areas mentioned above (Leviten & Kohn, 1980). In New Caledonia, coral in 1-3 m is the main microhabitat (Tirard, pers. comm., 1989). In the Maldive and Chagos Archipelagoes, on intertidal limestone benches as well as on subtidal reef flats (Kohn, 1968b; Leviten & Kohn, 1980). According to Lewis (1979), the typical form of C. coronatus in Fiji on moderately coarse sand near the edge of the reef; form aristophanes (see below) usually farther inshore on finer sand and mudflats. The two forms overlap only slightly in habitat. Findings from Philippines indicate a similar conchological and ecological separation.

C. coronatus feeds mainly on errant polychaetes (Eunicidae, Glyceridae, Nereidae), rarely consuming sedentary species (Capitellidae).

Egg capsules deposited singly or in short rows of 3-10 on the underside of coral or limestone rocks. Collective clusters may be made by several females. Capsules more or less quadrangular with a short stalk and a small basal plate, measuring 4.5-12.5 x 4.0-11.0 mm. Number of capsules per capsule mass is 14-83, number of eggs per capsule mass 25,000-52,000 and number of eggs per capsule 330-3,000. Egg diameter of 150-180 μm predicts a minimum pelagic period of about 28-25 days (Kohn, 1961b; Perron & Kohn, 1985).

**Discussion:** *C. coronatus* resembles the typical form of *C. miliaris miliaris* in shell characters and often also in the colouration of the animal. Typical *C. m. miliaris* can be distinguished by its generally less ventricose last whorl, consistently angulate shoulder with generally more prominent tubercles and in the presence of a central pad as well as an abapical ridge within the aperture. *C. miliaris* lacks the variously sized brown or olive markings on the last

whorl, the spiral rows of dots and dashes are finer, and white instead of dark markings are the dominant pattern element. In addition, the aperture of *C. m. miliaris* is paler brown, pink and violet, rather than blue, grey and darker brown. Where both species occur sympatrically, differences can usually be observed in the distribution pattern across the habitat, the diet composition and the microhabitats chosen. Some specimens of *C. coronatus* are similar to *C. abbreviatus* in shell shape and colouration but differ in the colour of animals and apertures (bluish to brownish grey vs. brownish violet); the intermittent white markings are absent from the dotted spiral lines on the last whorl of *C. abbreviatus*.

In Tahiti, Fiji and Philippines, typical C. coronatus and a form corresponding with C. aristophanes as redescribed by Cernohorsky (1964), differ in a number of shell characters as well as in habitat. Form aristophanes (Pl. 7, Figs. 29, 31) has a narrower, less ventricose last whorl with a straighter outline, and fewer spiral grooves on the late sutural ramps. It more often has a bluish or greyish last whorl with more pronounced pale spiral bands. In other regions (e.g. Solomon Is., Japan, Maldives, Oman and Zanzibar), the two forms intergrade. In the type locality of C. aristophanes, "Philippines Is.," they are separable. Based on data from such areas, Cernohorsky (1964) and Lewis (1979) considered C. aristophanes a valid species. However, data from the entire range favour ranking C. aristophanes as a form of C. coronatus. Coomans et al. (1981) reached the same conclusion.

# 24 Conus taeniatus HWASS in BRUGUIÈRE, 1792

(Plate 7, Figures 32-35; Map 11)

1792 Conus taeniatus Hwass in Bruguière, Encycl. Méth., 1: 628-629, no. 24

1798 Cucullus fernambucinus Röding, Mus. Bolten., 2: 39, no. 492/18

1798 Cucullus genuinus Röding, Mus. Bolten., 2: 42, no. 523/45

**Types:** *C. taeniatus*: Lectotype (Kohn, 1968, as "holotype", Walls, [1979]) in MHNG (42.5 x 29 mm); *C. fernambucinus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 57 fig. 632) (35 x 23 mm); *C. genuinus*: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 144 A figs. m, n) (29 x 19 mm).

Type Localities: C. taeniatus: "les mers de la Chine"; corrected to "Sharm el Sheik, Sinai, Rode Zee" (Wils, 1986).

Range: Red Sea to Oman and Strait of Hormuz, probably also Kenya.

**Description:** Moderately small to medium-sized, moderately solid to solid. Last whorl broadly to broadly and ventricosely conical or pyriform; outline convex adapically, straight to concave below. Shoulder angulate, smooth or weakly tuberculate. Spire of low to moderate height, outline straight to convex. Teleoconch sutural ramps flat to con-

cave, with 2 spiral grooves in early whorls, obsolete in late whorls. Last whorl smooth with weak spiral ribs at base.

C. 1	taeniatus Shell Morphometry
L	25 - 50 mm
RW	0.13 - 0.56 g/mm (L 25-43 mm)
RD	0.72 - 0.85
PMD	0.75 - 0.89
RSH	0.10 - 0.20

Ground colour white. Last whorl with numerous narrow, grey spiral bands, partially fusing into broader bands. Spiral rows of alternating black and white spots and dashes from base to shoulder. Teleoconch sutural ramps with black radial streaks between tubercles. Aperture reddish brown, external ground colour bands visible within, bluish white and opaque in larger specimens.

Periostracum yellow to green, thin, translucent to nearly opaque, smooth.

Animal yellow, mottled with brown flecks on foot and siphon (Ehrenberg, 1828; Bergh, 1895). Foot dirty brown, spotted with red and black. Tentacles greyish white. Siphon rust red, spotted with black (Fainzilber et al., 1992).

Radular teeth with a very small adapical barb opposite a blade; serration extends nearly to the central waist of the shaft; base with a spur (Bergh, 1895). Bandel (1984) depicted a very short serration ending well above the central waist.

**Habitat and Habits:** Intertidally, on algal turf on rocks, in sand bound by algal turf, and in sand among rocks (Bosch & Bosch, 1982; Sharabati, 1984). *C. taeniatus* feeds on polychaetes (Dance & von Cosel, 1977; Fainzilber et al., 1992).

**Discussion:** *C. taeniatus* appears most closely related to *C. coronatus*, but its shell is very distinctive in comparison to other Indo-Pacific *Conus* species.

# 25 Conus sponsalis HWASS in BRUGUIÈRE, 1792

(Plate 8, Figures 1-8; Plate 74, Figure 12; Plate 78, First row, right; Map 12)

- 1792 Conus sponsalis Hwass in Bruguière, Encycl. Méth., 1: 635, no. 34
- 1792 Conus puncturatus Hwass in Bruguière, Encycl. Méth., 1: 635-636, no. 35
- 1801 Conus maculatus Bosc, Hist. Nat. Coq., 5: 124, pl. 40 fig. 5
- 1833 Conus nanus Sowerby I, Conch. Ill.: Pt. 24, fig. 6

**Types:** *C. sponsalis*: Lectotype (Kohn, 1968, as "holotype") figured in Tableau (1798: Pl. 322 fig. 1) (29 x 20 mm); *C. puncturatus*: Lectotype (Kohn, 1968, as "holotype") figured in Tableau (1798: Pl. 322 fig. 9) (20 x 11 mm); *C. maculatus*: Holotype figured in Bosc (1801: Pl. 40 fig. 5; same shell as lectotype of *C. sponsalis*) (27 x 20 mm); *C. nanus*: Lectotype (Kohn, 1992) in BMNH (22 x 13 mm).

**Type Localities:** *C. sponsalis*: "aux îles Saint-George"; *C. puncturatus*: "la Nouvelle-Hollande, sur les côtes de la baie Botanique"; *C. nanus*: "Lord Hood's Island."

Range: Entire Indo-Pacific.

**Description:** Small to moderately small, moderately light to moderately solid. Last whorl conical to broadly and ventricosely conical, rarely slightly pyriform; outline convex at adapical half and usually straight below. In large specimens, aperture often with a distinct spiral ridge at centre. Shoulder rounded to angulate, weakly to distinctly tuberculate. Spire of low to moderate height, outline concave to convex. Larval shell of 4-5 whorls (Taylor, 1975), maximum diameter about 0.7 mm. Postnuclear spire whorls finely tuberculate. Teleoconch sutural ramps flat to slightly concave, with 1-4 spiral grooves, obsolete on late ramps. Last whorl with fine, granulose spiral ribs on basal half.

C. spoi	nsalis Shell Morphometry
L	15 - 34 mm
RW	0.08 - 0.26 g/mm (L 15-30 mm)
RD	
- typical form	0.63 - 0.84
- form <i>nanus</i>	0.63 - 0.78
PMD	0.78 - 0.89
RSH	0.06 - 0.18

Ground colour white; in form *nanus* (Pl. 8, Figs. 7, 8) usually with a distinct blue shade. Usual pattern of last whorl consists of reddish brown axial flames arranged in 2 spiral rows. Flames often reduced in size or fusing into bands. Base and basal part of columella purplish blue. Teleoconch sutural ramps with reddish to blackish brown blotches between tubercles. Aperture dark bluish violet deep within.

Periostracum yellow to brown, thin, translucent, smooth; sometimes thicker and opaque at the growing edge or in large specimens (Kohn, 1959a).

In form *nanus*, pattern of last whorl either reduced to a few flecks and a small number of dotted and/or dashed spiral lines or completely absent; spire pattern either reduced to spots or dots between tubercles or completely absent; aperture with a light violet tone but with more pronounced brown and blue tones.

Foot narrow; dorsum pale pink or white, maculated with elongate bright white markings; anterior part often with dense red streaks, or solid pink distally with 2 red lateral spots, occasionally with a dark grey central blotch; posterior part occasionally red. Sole of foot red, longitudinally

streaked or variably mottled with white, usually uniformly shaded with pink, ends red; some specimens with a rather uniformly pink sole. Rostrum and tentacles variably red and white. Siphon white to red with axially white markings; tip darker pink to red; entire siphon occasionally solid pink (Kohn, 1959a & unpubl. observ.; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.) (Pl. 74, Fig. 12; Pl. 78, First row, right).

Radular teeth small, with an adapical barb opposite a blade; serration extending from base of barb along the blade; shaft with 2 constrictions, just posterior to the blade and at base; basal knob with a spur (Peile, 1939; Kohn, 1963b; James, 1980).

Habitat and Habits: Abundant on intertidal benches, less common on subtidal coral reefs; some specimens dredged in 100 m (Kay, 1979). Mostly an epifaunal species, in protected and exposed sites. Intertidally on beachrock and limestone benches, usually inhabiting algal turf binding sand, small sand-filled depressions, coral rubble and crevices of rocks; less frequently on larger patches of sand or bare reef limestone. Subtidally, on reef flats, lagoon pinnacles and deeper reef habitats to ca. 18 m, inhabiting sand or reef limestone with algal turf, coral rubble and crevices of dead coral. Typical form and form nanus co-occurring in some mixed populations; however, populations often consisting predominantly or completely of one form (Kohn, 1959a, b, 1966b, 1968b; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Cernohorsky, 1964, 1978; Kay, 1979; Kilburn & Rippey, 1982; Grosch, pers. com., 1989).

*C. sponsalis* feeds exclusively on errant polychaetes (Kohn, 1959 b; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985; Kohn & Almasi, 1993).

In form *nanus*, observed egg diameter of 135 μm predicts a minimum pelagic period of about 29 days (Perron, 1981b; Perron & Kohn, 1985).

Map 12

**Discussion:** C. sponsalis is closely related to C. musicus and C. parvatus. For comparison, see the Discussions of those species.

Some authors (e.g. Richard, 1990) consider *C. nanus* a distinct species. Populations occurring in southeast Polynesia and Hawaii are consistently of the *nanus* form. However, we are unable to separate these forms morphometrically, and both shell colour patterns occur, with intergrades, in some geographic regions, e.g. Marshall Islands.

### 26

### Conus musicus HWASS in BRUGUIÈRE, 1792

(Plate 8, Figures 9-21; Plate 74, Figure 13; Plate 78, First row, left and middle; Map 12)

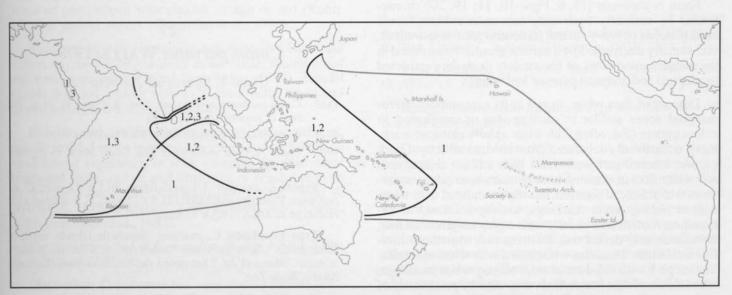
- 1792 Conus musicus Hwass in Bruguière, Encycl. Méth., 1: 629, no. 25
- 1792 Conus ceylanensis Hwass in Bruguière, Encycl. Méth., 1: 636
- 1845 Conus mighelsi Kiener, Coq. Vivant., 2: Pl. 103 fig. 1; 1849: 352-353
- 1857 Conus acutus Sowerby II, Thes. Conch., 3: 16, sp. 119, pl. 6 fig. 142 (non C. acutus Anton, 1839, non C. acutus Deshayes, 1865)

**Types:** *C. musicus*: Lectotype (Kohn, 1968) figured in Tableau (1798: Pl. 322 fig. 4) (18 x 9 mm); *C. ceylanensis*: Neotype (Coomans et al., 1983) in ZMA (10 x 6 mm); *C. mighelsi*: Original figure 32 x 14 mm; *C. acutus*: Original figure 19.5 x 11.5 mm.

**Type Localities:** *C. musicus*: "Les mers de la Chine"; *C. ceylanensis*: "Les côtes de l'isle de Ceylan"; *C. mighelsi*: "la mer des Indes"; *C. acutus*: "Ceylon."

Range: Central Indian Ocean (Sri Lanka, Maldives) to Marshall Is. and Fiji; Ryukyu Is. to W. and E. Australia.

**Description:** Small, light to moderately light. Last whorl conical or ventricosely conical to broadly and ventri-



1: C. sponsalis 2: C. musicus 3: C. parvatus

cosely conical; outline slightly to distinctly convex at adapical half and usually straight below. Aperture may have a transverse ridge at centre. Shoulder angulate to occasionally rounded, weakly to distinctly tuberculate. Spire of low to moderate height, outline slightly concave to slightly convex. Teleoconch sutural ramps flat, in late whorls with 2 increasing to 3-4 spiral grooves. Last whorl with weak to distinct, granulose spiral ribs at base; sometimes extending to centre or even to shoulder.

C. music	us Shell Morphometry
	14 - 30 mm
RW	0.03 - 0.11 g/mm
RD	
typical form	0.59 - 0.77
form ceylanensis	0.61 - 0.78
PMD	
typical form	0.78 - 0.93
form ceylanensis	0.81 - 0.90
RSH	0.02 - 0.15

Ground colour white to pale grey. Last whorl with a grey, orange or reddish brown spiral band on each side of centre; bands occasionally obsolete or fusing into a single basal colour zone. Spiral rows of brown dots and dashes extend from base to shoulder, varying in number and arrangement. Dark dots may alternate with white dashes or dots. Base and basal part of columella dark bluish violet. Late sutural ramps crossed by brown markings between shoulder tubercles. Aperture pale violet to dark bluish violet, usually with a ground-colour band at centre and below shoulder.

Periostracum light brown, thin, variably translucent, smooth.

Form *mighelsi* (Pl. 8, Figs. 12, 18) characterized by a broad pinkish red to orangish red spiral band above centre.

Form *ceylanensis* (Pl. 8, Figs. 10, 11, 19, 20) characterized by variously coalescing brown to reddish brown axial blotches or wavy flames on central area of last whorl, occasionally interrupted by a narrow ground-colour band in the middle; spiral rows of brown dots or dashes restricted to adaptical and abapical parts of last whorl.

Dorsum of foot white, to red at its extremities; lateromarginal zones similar to median area or contrasting in colour pattern (red, often with white axially elongate markings), occasionally separated from median area by a dark groove; anterior part sometimes with a black central spot and white dots at corners; area beneath operculum sometimes white. Sole of foot red, heavily maculated with white dots or oblong white markings, usually solid red at extremities; median area usually with a grey longitudinal line, sometimes only darker red. Rostrum red, sometimes mottled with white. Tentacles white to red with white eyestalks. Siphon pink with red dots or axial oblong white markings; white dots and thin brown lines may also be present; tip of siphon usually red (Pl. 74, Fig. 13) (Chaberman, pers. comm., 1981; Pearson, unpubl. observ.; Kohn, unpubl. observ.).

Radular teeth with an adapical barb opposite a blade; serration, centred waist and basal spur present (Nybakken, 1990, as *C. ceylanensis*).

Habitat and Habits: In 1-18 m, on rock benches, subtidal reef flats, the reef rim and on lagoon pinnacles; on sand-binding algal mats, limestone pavement, dead coral rocks or heads and in crevices of rocks or coral reefs. Somewhat more common in subtidal habitats (Cernohorsky, 1964; Kohn, 1968b; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985; Tucker, 1973).

C. musicus feeds on polychaetes of the families Nereidae and Eunicidae, primarily the former (Kohn, 1968b; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985).

**Discussion:** C. musicus resembles C. sponsalis in the characters of shell and animal. The latter species has larger size and a broader last whorl and less angulate shoulder. The colour pattern of typical C. sponsalis lacks dotted spiral lines; only form nanus sometimes bears sparse spirally arrayed dots, but not the more pronounced, darker dotting of C. musicus. The markings between the tubercles in C. musicus are blackish brown in most shells; they are lighter, usually reddish brown and less regular in C. sponsalis. The pronounced double row of red-brown axial flames in C. sponsalis is absent in C. musicus, including form ceylanensis, but it is also absent in C. sponsalis form nanus.

The form *mighelsi* occurs predominantly in the Pacific. *C. acutus* represents a variant of typical *C. musicus*. Form *ceylanensis* occurs from Sri Lanka to W.Thailand, sympatric with the typical form and intergrading with it in colour pattern and shape. We cannot separate the two forms by shell morphometry. These data do not support separation of form *ceylanensis* from typical *C. musicus* at the species or subspecies level.

# 27 Conus parvatus WALLS, 1979

(Plate 8, figures 22-26; Map 12)

- 1843 Conus pusillus Reeve, Conch. Icon., 1, Conus: Pl. 27 sp. 154 (non C. pusillus Lamarck, 1810)
- 1979 Conus musicus parvatus Walls, The Pariah, 5: 4
- 1986 Conus parvatus sharmiensis Wils, Gloria Maris, 25 (5): 189-190, figs. 71, 72

**Types:** *C. pusillus*: Original figure 20.5 x 12 mm; *C. m. parvatus*: Holotype in DMNH (21.5 x 13 mm); *C. p. sharmiensis*: Holotype in ZMA (19.5 x 12 mm).

**Type Localities:** *C. pusillus*: "Seychelle Islands, north of Madagascar"; *C. m. parvatus*: "South Africa, Natal"; *C. p. sharmiensis*: "Marsa el'At, 7 km noord van Sharm el Sheik, Golf van Akaba, Rode Zee."

Range: E. Africa and Red Sea to W. Thailand.

Description: Small to moderately small, moderately light to moderately solid. Last whorl conical or ventricosely conical to broadly and ventricosely conical; outline convex at adapical half, usually straight below. Large specimens with a transverse central ridge within aperture. Shoulder rounded to subangulate, infrequently angulate, finely tuber-culate to almost smooth. Spire of low to moderate height, outline straight to convex. Teleoconch sutural ramps flat, with 2-3 spiral grooves in late whorls. Last whorl with obsolete to fine and smooth to finely granulose ribs around basal part.

C. J	parvatus Shell Morphometry
L	14 - 30 mm
RW	0.06 - 0.16 g/mm (L 14-24 mm)
RD	0.61 - 0.81
PMD	0.78 - 0.90
RSH	0.02 - 0.17

Ground colour white to pale grey, often suffused with blue. Last whorl with pronounced spiral rows of alternating reddish brown and white dashes and dots from base to subshoulder area or to shoulder. In Red Sea shells (Pl. 8, Fig. 22), rather red than brown dots and dashes alternate with white dashes within the spiral rows. Reddish brown axial blotches and one or a few narrow, light brown spiral bands may be located above centre. Base of columella purplish blue. Outer edges of late sutural ramps with brown dots, fine lines or, more often, bundles of lines between tubercles. Aperture light to dark purplish blue, occasionally with 2 pale bands, at centre and below shoulder.

Periostracum yellow, thin, translucent, smooth.

Dorsum of foot white, streaked with brown. Sole of foot mottled bright and dull white, with pinkish red or orange extremities. Rostrum orange to red. Tentacles white, distal edge may be orange-red. Siphon bright white mottled with white or grey, tipped with pinkish orange or red (Kohn, 1968b & unpubl. observ.; Fainzilber et al., 1992).

Radular teeth with an adapical barb opposite a blade and a short serration ending anterior to the blade; central waist and basal spur present (Red Sea; Rolán, 1993). Bandel (1984) depicted a tooth without distinct barb, blade and central waist (Red Sea, as *C. pusillus*).

Habitat and Habits: Intertidal and upper subtidal, usually in 0.5-5 m; on beachrock benches and reef flats, on sand among vegetation, in rock crevices, on dead coral heads and rocks, and on reef limestone or beachrock with or without a thin layer of sand (Kohn 1968b; Kohn & Nybakken, 1975; Sharabati, 1984; Grosch, pers. comm., 1989; Fainzilber et al., 1992).

Diet similar to that of *C. musicus* (Kohn, 1968b; Kohn & Nybakken, 1975).

**Discussion:** C. parvatus is a very closely related to C. musicus and to C. sponsalis. C. sponsalis differs in the

colour pattern of its shell: no pronounced spiral rows of alternating brown and white dots and dashes; typical form with a double row of reddish brown axial flames; pronounced blotches between shoulder tubercles. The more intensely patterned shells of *C. parvatus* from Réunion have a more straight-sided last whorl than those of *C. sponsalis*.

Kohn (1968b) referred to this species it as the "Indian Ocean form of *C. musicus*." Walls [1979] described it as a geographic subspecies. The colour pattern of *C. parvatus* lacks the broad spiral bands of typical *C. musicus* and form *mighelsi*, and the brown central area of form *ceylanensis*. *C. parvatus* has a slightly more solid shell with a usually less angulate and less tuberculate shoulder and a smoother last whorl. However, because it occurs sympatrically with typical *C. musicus* in Sri Lanka, Andaman Islands and W. Thailand and intergrades have not been observed (Wils, 1986), we favour the status of a separate valid species.

Reeve's *C. pusillus* refers obviously to this species, but it is a junior homonym and therefore not valid. Wils (1986) described shells from the Red Sea as *C. parvatus sharmiensis*, on the basis of minor shape and colour pattern differences, but examination of larger samples indicates that the geographic differences are not consistent.

# 28 Conus ebraeus Linné, 1758

(Plate 8, Figures 27-30; Plate 74, Figure 10; Map 13)

1758 Conus ebraeus Linné, Syst. Nat., 10 ed., 1: 715, no. 268

1811 Conus quadratus Perry, Conchology: Pl. 24 fig. 5 (non Cucullus quadratus Röding, 1798)

Conus judaeus Bergh, Nova Acta Ksl. Leop.-Carol. Deutschen Ak. Naturforscher, 65 (2): 161-163, pl. 4 fig. 91, pl. 6 figs.

**Types:** *C. ebraeus*: Lectotype (Kohn, 1963) in LSL (28 x 19 mm); *C. quadratus*: Holotype figured in Perry (1811: Pl. 24 fig. 5) (40 x 25 mm); *C. judaeus*: Holotype in ZMUC (32 x 21 mm).

**Type Localities:** C. ebraeus: "India"; C. quadratus: "Coast of Africa"; C. judaeus: "M. philippinense."

Range: Entire Indo-Pacific except Red Sea; also W. coast of Central America.

Description: Moderately small to moderately large, moderately solid to solid. Last whorl broadly to broadly and ventricosely conical, occasionally slightly pyriform; outline variously convex adapically, straight or slightly concave toward base. Shoulder angulate or subangulate, strongly to obsoletely tuberculate. Spire of low to moderate height, outline straight to convex. Larval shell multispiral. Postnuclear spire whorls strongly to weakly tuberculate. Teleoconch sutural ramps flat to concave, with 2 increasing to 4-5 often weak spiral grooves. Last whorl with widely spaced, smooth or granulose ribs on basal half.

# C. ebraeus Shell Morphometry L 25 - 62 mm RW 0.22 - 0.57 g/mm (L 27-46 mm) RD 0.69 - 0.78 PMD 0.78 - 0.95 RSH 0.06 - 0.20

Ground colour white, sometimes suffused with pink mainly in juvenile specimens. Last whorl with 3-4 spiral rows of black blotches between base and subshoulder area; blotches squarish to more or less axially elongate, sometimes branching axially or spirally. Apex often pink. Late sutural ramps with rather regularly set black radial blotches. Aperture white to bluish white, external pattern often visible within.

Periostracum yellowish olive, thin, translucent, smooth.

Dorsum of foot black, with a beige pre-marginal zone along latero-posterior sides and with a red anterior edge. Sole of foot buff, anteriorly edged with pink and bordered with black latero-posteriorly; buff median zone variable in width. Rostrum black, sometimes tipped with a narrow red margin. Tentacles red. Siphon either black with a narrow red tip or rusty red with black dots and lighter on proximal portion (Garrett, 1878; Bergh, 1895; Kohn, 1959a & unpubl. observ.; Chaberman, pers. comm., 1981) (Pl. 74, Fig. 10).

According to SEM studies, radular teeth with a basal spur and a reduced adaptical armature of 2 barbs (James, 1980). Troschel (1868), Bergh (1895) and Peile (1939) indicate neither barb nor serration, Troschel and Bergh but neither Peile nor James state that a blade is present.

Habitat and Habits: On intertidal benches and subtidal coral reef platforms, to about 3 m; abundant in both types of habitat, with peak density of population nearer to the shore or halfway across intertidal habitats. On patches of sand bound by algal turf, in sand-filled depressions and crevices, on limestone benches with algal turf, and among or beneath dead coral (Kohn, 1959b, 1966b, 1968b, 1971; Kohn & Orians, 1962; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985; Tirard, pers. comm., 1989; Grosch, pers. comm., 1989).

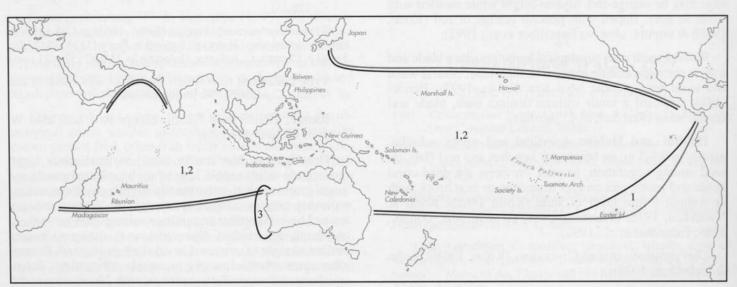
*C. ebraeus* feeds on eunicid and nereid polychaetes; diet composition varies with habitat and locality (Kohn, 1959b; Kohn & Orians, 1962; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985).

Egg capsules measure 7-10 x 6-10 mm. Each capsule contains 1,500-3,000 eggs 170-180 μm in diameter, predicting a minimum pelagic period of about 25-26 days (Risbec, 1932; Ostergaard, 1950; Kohn, 1961b; Perron, 1981b; Perron & Kohn, 1985).

**Discussion:** C. ebraeus and C. chaldaeus are very closely related species; for comparison, see the Discussion of the latter species.

According to Bergh (1895), *C. ebraeus* and *C. judaeus* do not differ in external and internal morphology, except for the armature of the radular teeth (*C. judaeus*: tooth with an adapical barb opposing a sharp blade; serration present). However, Bergh's figures are somewhat contradictory, and as noted above Bergh, Peile and James do not agree with one another. In addition, Bergh's information on *C. judaeus* refers to a single specimen, and the separation of *C. judaeus* from *C. ebraeus* cannot be retained. Walls [1979] assigned *C. judaeus* to *C. chaldaeus*, but this contradicts Bergh's original description.

Map 13



1: C. ebraeus 2: C. chaldaeus 3: C. dorreensis

### 29

## Conus chaldaeus (RÖDING, 1798)

(Plate 8, Figures 31-33; Plate 74, Figure 11; Map 13)

1798 Cucullus chaldaeus Röding, Mus. Bolten., 2: 42, no. 525/47

1810 Conus vermiculatus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 34, no. 17

**Types:** C. chaldaeus: Lectotype (Kohn, 1975) figured in Knorr (1768: Pl. 4 fig. 2) (36 x 22 mm); C. vermiculatus: Type specimen lost.

Type Localities: C. chaldaeus: "Moluccas" (Coomans et al., 1983); C. vermiculatus: "mers chaudes."

Range: Indo-Pacific except for Red Sea and Easter Id.; also W. coast of Central America.

**Description:** Moderately small to medium-sized, moderately solid to solid. Last whorl usually broadly ventricosely conical; outline convex adapically and straight below. Shoulder angulate to subangulate, strongly to weakly tuberculate. Spire of low to moderate height, outline straight to convex. Larval shell multispiral. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat to concave, with 3 increasing to 6-7 spiral grooves. Last whorl with often strong, granulose spiral ribs basally, sometimes to shoulder.

### C. chaldaeus Shell Morphometry

L	25 - 59 mm
RW	0.20 - 0.40 g/mm (L 25-40 mm)
RD	0.71 - 0.87
PMD	0.75 - 0.87
RSH	0.07 - 0.20

Ground colour of last whorl white, suffused with pink mainly in juvenile specimens. Pattern of black axial streaks or flammules usually leaves 2 narrow white bands, at shoulder and near centre. Larval whorls white; apex often suffused with pink. Late sutural ramps white, variously blotched with black. Aperture bluish white behind a brownish black margin.

Periostracum yellow, thin, translucent, smooth.

Dorsum of foot beige, suffused with pink at its extremities; anterior part with solid red frontal zone followed by a large bilobate black blotch; black dots arrayed into a pre-marginal line along lateral and posterior sides. Sole of foot bordered with a discrete black line about 1 mm from the edge. Tentacles white. Rostrum and siphon white dotted with black or brown, with a solid red tip and a few red dots behind (Pl. 74, Fig. 11) (N. Papua New Guinea: Chaberman, pers. comm., 1981). In Hawaii, animal black, with a broad central longitudinal tan stripe on sole of the foot and rostrum and siphon with red tips (Kohn, 1959a). In Maldives, sole reddish yellow, with distinctly red marginal parts; its black

marginal line is not continuous around posterior end (Kohn, unpubl. observ.).

Radular teeth very short, with little or no armature at apex, with a basal spur (James, 1980). Nybakken (1990) stated the presence of an adapical barb opposite a long blade, of a serration terminating in a cusp, and of a central waist.

Habitat and Habits: On intertidal benches, less frequently on slightly subtidal reef platforms; often close to the seaward edge of its habitat. On sand, beachrock, and truncated reef limestone with or without a thin layer of sand or algal turf, in coral rubble with or without sand and on dead coral heads or rocks (Cernohorsky, 1964; Kohn, 1959b, 1966b, 1968b; Kohn & Orians, 1962; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985; Grosch, pers. comm., 1989).

C. chaldaeus is known to feed on errant polychaetes of the families Nereidae and Eunicidae; diet composition varies with habitat. On reef platforms when suitable nereid species become rarer, it may shift to a single eunicid species (Palola siciliensis). In the latter case, it eats worms of the same species as C. ebraeus and C. miles but captures them in a different habitat (Kohn & Orians, 1962; Kohn, 1959b, 1966b, 1968b; Kohn & Nybakken, 1975; Leviten & Kohn, 1980; Reichelt & Kohn, 1985).

**Discussion:** Only *C. ebraeus* closely resembles *C. chaldaeus*. They overlap broadly in shell morphometry, but *C. ebraeus* differs distinctly in colour pattern with usually 3-4 spiral rows of black markings on the last whorl and in fewer and weaker spiral grooves on its late sutural ramps. The granulose spiral ribs of the last whorl are stronger and extend over more of the shell in *C. chaldaeus*. The animals of both species may be very similar (Hawaii) or clearly separable (N. Papua New Guinea). They often occur sympatrically and may share the same habitat, sometimes even the same microhabitat. *C. chaldaeus* typically is less abundant and occurs closer to the seaward margin of its habitat.

### 30

# Conus dorreensis PÉRON, 1807

(Plate 8, Figures 34-36; Map 13)

1807 Conus dorreensis Péron, Voy. Decouv. Terr. Australes, 1: 120

1810 Conus pontificalis Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 38, no. 36

**Types:** *C. dorreensis*: Type (acc. Péron L 40 mm) lost; *C. pontificalis*: Type (acc. Lamarck 45 x 25 mm) lost.

**Type Localities:** *C. dorreensis*: "la Terre d'Endracht"; *C. pontificalis*: "Les parages de Terre de Diemen."

Range: W. Australia from Albany to Monte Bello Is.

**Description:** Moderately small to medium-sized, moderately solid. Last whorl broadly or broadly and ventricosely conical; outline almost straight to slightly convex. Aperture somewhat wider at base than at shoulder.

Shoulder angulate or subangulate, tuberculate to strongly tuberculate. Spire usually high, stepped, with straight to convex outline. Larval shell of about 2.5 whorls, maximum diameter 0.7 - 0.8 mm. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps flat to slightly concave; middle and late ramps with regularly spaced radial threads and 5 increasing to 7 spiral grooves. Last whorl with fine axial and spiral ribbons producing a cancellate surface.

C. d	orreensis Shell Morphometry
Laboration	30 - 48 mm
RW	0.14 - 0.31 g/mm (L 29-42 mm)
RD	0.72 - 0.85
PMD	0.82 - 0.93
RSH	0.21 - 0.35

Ground colour white. Last whorl with 2 often broad zones of pale rose below subshoulder area and at base, occasionally with interrupted spiral bands of irregular light brown markings. Larval shell white. Aperture white or with external rose zones visible.

Periostracum olive, thin, almost opaque and smooth, often absent from spiral zones below shoulder and at base; edges of periostracal bands usually black.

Foot white, with narrow, transverse, rose anterior edges above and below pedal gland. Rostrum white mottled with tan, may be tipped with green. Siphon white tipped with pink, with dark brown transverse markings, fewer and smaller ventro-laterally and sometimes arranged in 2 groups (Kohn, pers. comm., 1993).

Radular teeth with an adapical barb; serration, central waist and basal spur present (Nybakken, 1990; Kohn, pers. comm., 1993).

Map 14

Habitat and Habits: Intertidal and subtidal; on limestone benches in protected pockets of bare limestone, in sand pockets and in algal turf of flats and pockets; on reefs, in pockets of clean sand and sand around rocks, and avoiding mud and muddy sand (Turnbull, pers. comm., 1987; Kohn, 1993).

C. dorreensis feeds mainly on polychaetes (Turnbull, pers. comm., 1987; Kohn & Almasi, 1993).

Oviposition occurs on the outer or inner portion of intertidal flats and under overhanging portions of the platforms. Egg capsules affixed to the underside of red algae plants or to the underside of limestone rocks; spawn arranged in rows of 2-12 capsules. Capsule size from 6-7 x 5-6 mm to 10.5 x 10.5 mm, number of eggs per capsule from ca. 950 to ca. 2,500, and number of eggs per capsule mass from about 10,000 to about 71,000. Egg diameter of 150-160 µm suggests a minimum pelagic period of 28-27 days (Kohn, 1993).

**Discussion:** C. dorreensis does not appear to be closely related to other species of Conus; it cannot be confused with any of its congeners.

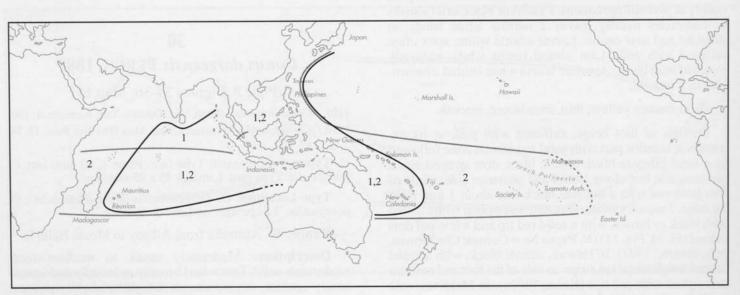
# Conus floridulus A. ADAMS & REEVE, 1848

(Plate 9, Figures 1-5; Plate 74, Figure 14; Map 14))

1848 Conus floridulus A. Adams & Reeve, Zool. Voy. Samarang, Moll., 1: 18, pl. 5 figs. 9a, b

1857 Conus tenuis Sowerby II, Thes. Conch., 3: 3, no. 14, pl. 14 fig. 314 (non C. tenuis Sowerby I, 1833)

**Types:** *C. floridulus*: Holotype in BMNH (37 x 20 mm); *C. tenuis*: Holotype in BMNH (32 x 12 mm).



1: C. floridulus 2: C. muriculatus

Type Localities: Not stated.

Range: Réunion and Maldives to New Caledonia and to Japan.

Description: Moderately small to medium-sized, moderately solid. Last whorl conical to slightly pyriform; outline variably convex adapically and straight to slightly concave below. Shoulder angulate, undulate to tuberculate. Spire of moderate height, outline concave to slightly sigmoid. Larval shell of 3.25 whorls, maximum diameter about 0.8 mm. Early postnuclear spire whorls smoothly edged; late whorls undulate to tuberculate. Teleoconch sutural ramps flat, with arcuate radial threads and 1 increasing to 3-4 spiral grooves. Last whorl with widely spaced, granulose spiral ribs, restricted to basal area or extending to shoulder.

C. T	loridulus Shell Morphometry
L	30 - 59 mm
RW	0.12 - 0.20 g/mm (L 30-44 mm)
RD	0.59 - 0.70
PMD	0.84 - 0.94
RSH	0.15 - 0.22

Ground colour white. Last whorl encircled with 2 variably wide, tan to orangish brown bands, on each side of centre. Populations may include intensely banded and largely white shells. Adapical band often overlaid with or divided by spirally or axially aligned dots. Base, siphonal fasciole and basal part of columella light violet. Larval whorls orange. Teleoconch sutural ramps with tan radial markings matching pattern of last whorl in colour. Aperture light violet at base, translucent white above.

Periostracum greyish olive, thin, and translucent to almost opaque, with finely tufted spiral lines and distinct radial folds on sutural ramps.

Dorsum of foot pale pink, grading to red anteriorly and to brownish red posteriorly; black and white dots centrally and posteriorly; anterior part with a single black spot. Sole of foot beige dotted with white. Rostrum and tentacles red. Siphon red, dotted with black and white, paler proximally (Pl. 74, Fig. 14) (Chaberman, pers. comm. 1981).

Radular teeth slender, with an adapical barb opposite a blade; serration absent but basal spur present (Rolán, pers. comm., 1992).

Habitat and Habits: In 9-80 m; reported to be dredged to 240 m in the Philippines. In Papua New Guinea, in muddy sand or on living coral in 9-80 m; in New Caledonia, on coarse sand or coral rubble and algae in 25-80 m (Estival, 1981; Tirard, pers. comm., 1989; Richards, pers. comm., 1989; Chaberman, pers. comm., 1981).

**Discussion:** C. floridulus resembles the typical form of C. muriculatus in shell and animal. For comparison, see the Discussion of the latter species.

### 32

## Conus muriculatus SOWERBY I, 1833

(Plate 9, Figures 6-11; Plate 74, Figures 15, 16; Map 14)

- 1833 Conus muriculatus Sowerby I, Conch. Ill.: Pt. 24, fig. 1\*
- 1833 Conus muriculatus var. laevigata Sowerby I, Conch. Ill.: Pt. 24, fig. 1 (non C. laevigatus Link, 1807, non C. laevigatus Defrance, 1818).
- 1843 Conus sugillatus Reeve, Proc. Zool. Soc. London, 11: 177-178; 1844: Conch. Icon., 1, Conus: Pl. 45 sp. 247

**Types:** *C. muriculatus*: Lectotype (Kohn, 1992) in BMNH (27 x 15 mm); *C. m.* var. *laevigata*: Original figure 20 x 10 mm; *C. sugillatus*: Original figure 36 x 19 mm.

**Type Localities:** C. muriculatus, C. m. var. laevigata: "Masbate, Philippines."

Range: Indian Ocean: Madagascar and Réunion to W. Australia; Pacific: Japan to New Caledonia, Fiji, and French Polynesia.

**Description:** Small to moderately large, moderately solid to solid; shells of form *sugillatus* larger than those of typical form. Last whorl conical; outline variably convex above centre, straight below. Shoulder angulate, smooth to strongly tuberculate. Spire of low to moderate height, outline slightly concave to slightly convex. Larval shell of about 3 whorls, maximum diameter 0.7-0.8 mm. Early postnuclear spire whorls smooth, late whorls smooth, undulate or tuberculate; tuberculation weaker in form *sugillatus*. Teleoconch sutural ramps flat to weakly concave, with 1 increasing to 3-4 spiral grooves. Sculpture of last whorl varies from smooth spiral ribs at base to strongly granulose spiral ribs on entire whorl; in form *sugillatus* sculpture weaker and restricted to base.

C	c. muriculatus Shell	Morphometry
	typical form	f. sugillatus
L	23 - 31 mm	32 - 62 mm
RW	0.10 - 0.20 g/mm	0.12 - 0.37 g/mm (L 32-46 mm)
RD	0.59 - 0.65	0.54 - 0.64
PMD	0.86 - 0.95	0.84 - 0.90
RSH	0.10 - 0.20	0.05 - 0.15

Ground colour white to greyish white, often suffused with blue shades.

In typical form (Pl. 9, Figs. 8-10), last whorl with a variably broad, yellowish brown spiral band on each side of centre; bands sometimes additionally tinged with olive. Distinctly and obsolety banded shells intergrade. Dashed and dotted or solid brown spiral lines extend from base to subshoulder area, varying in number and arrangement. Base, siphonal fasciole and basal part of columella dark bluish to brownish violet. Larval whorls orange. Teleoconch sutural ramps with sparse to numerous brown radial

markings, sometimes immaculate. Aperture violet at base; remaining area immaculate or external pattern visible within.

Periostracum yellowish brown, thin, and slightly translucent, with widely spaced spiral rows of tufts on last whorl.

In form *sugillatus* (Pl. 9, Figs. 6, 7, 11), colour bands of last whorl usually darker, often tinged with dark bluish green or greenish brown. Central and subshoulder band may be overlaid with yellowish brown. Brown spiral lines usually solid. Teleoconch sutural ramps often greenish brown toward apex. Aperture dark violet, with a pale band at centre and subshoulder area.

Periostracum usually less translucent than in typical form.

In typical form (Pl. 74, Fig. 15), dorsum of foot pink and dotted with white and black, red at its extremities; marginal zone with radiating dotted black lines. Sole of foot, rostrum, tentacles and siphon red, dotted with white and black; an additional pale grey band near centre of siphon (Chaberman, pers. comm., 1981).

In form *sugillatus* (Pl. 74, Fig. 16), entire animal brick to greyish red, heavily dotted with white and black; dorsum of foot darker red at anterior end, with red spot beneath operculum and occasionally lacking white dots; sole of foot less densely dotted, occasionally without dots (Chaberman, pers. comm.; 1981; Estival, 1981).

**Habitat and Habits:** Intertidal to about 70 m; on coarse sand with algae, and on diverse reef substrates. In some areas, found only subtidally (New Caledonia: in 12-40 m; Marshall Is.: slightly subtidal zone to 70 m).

C. muriculatus feeds on eunicid and nereid polychaetes (Marshall Is.; Kohn, 1980a, as C. sugillatus).

On Broadhurst Reef (off Townsville, Queensland), form sugillatus has been observed spawning under coral rubble in 10 m (Loch, pers. comm., 1987). In an aquarium, typical form has deposited egg capsules in groups of 4 (Chaberman, pers. comm., 1981).

**Discussion:** The typical form of *C. muriculatus* closely resembles *C. floridulus* in shell characters and colour pattern of the animal. The latter can be distinguished by its larger size, lighter spiral colour bands, and light violet base, in contrast to the dark bluish or brownish violet base of *C. muriculatus*. Additional differences are seen in the colouration of the animals.

## 33

## Conus sazanka SHIKAMA, 1970

(Plate 9, Figures 12-18; Map 15)

- 1970 Conus (Rhizoconus) sazanka Shikama, Sci. Rep. Yokohama Natl. Univ., 2 (16): 25, pl. 1 figs. 24, 25
- 1973 Rhizoconus yoshioi Azuma, Venus, 32 (1): 10, 14, 15-16, pl. 1 fig. 2; text figs. 9, 9A
- 1974 Conus kurzi Petuch, Veliger, 17 (1): 41-42, figs.1, 2

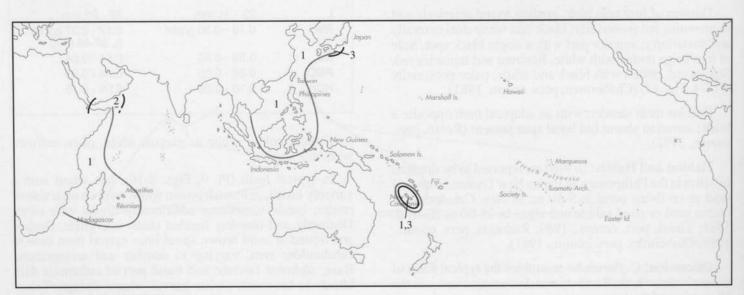
**Types:** *C. sazanka*: Holotype in KPM (38.5 x 21.5 mm); *R. yoshioi*: Holotype in Azuma coll. (42.5 x 22.5 mm); *C. kurzi*: Holotype in CAS (30 x 17 mm).

**Type Localities:** *C. sazanka*: "SW Kochi Prefecture"; *R. yoshioi*: "Off Kirime-zaki, Kii Peninsula"; *C. kurzi*: "approximately 32 km SE of Tosa Shimizu, Shikiku Island, Japan (32° 40' N; 133° 12' E)."

Range: Pacific: Japan, Philippines, E. Indonesia, New Caledonia, Vanuatu, Hawaii; Indian Ocean: Natal, Réunion, Madagascar, Somalia.

**Description:** Moderately small to medium-sized, moderately light to moderately solid. Last whorl conical; outline almost straight to moderately convex with a con-

Map 15



1: C. sazanka 2: C. danilai 3: C. hamamotoi

striction above base. Shoulder subangulate to angulate, undulate to weakly tuberculate. Spire of low to moderate height, outline concave. Larval shell of about 4 whorls, maximum diameter about 1 mm. Postnuclear spire whorls undulate. Teleoconch sutural ramps flat, with 2 increasing to 4-5 spiral grooves. Last whorl with a few weak spiral ribs at base.

C.	sazanka Shell Morphometry
L	25 - 42 mm
RW	0.06 - 0.18 g/mm (L 25-38 mm)
RD	0.56 - 0.64
PMD	0.86 - 0.93
RSH	0.04 - 0.18

Colour reddish to brownish orange, occasionally yellow or violet. Last whorl usually with a lighter spiral band at centre, frequently interspersed with white flecks and adapically edged with brownish spots. In Philippine shells, uniform colouration often replaced by dark and light clouds above centre; white axial streaks below shoulder and across central band. Larval whorls pink to pale yellow. Teleoconch sutural ramps variably maculated with yellow, pink or orange radial blotches. Aperture with external pattern visible.

Periostracum yellowish brown to brown, thin, translucent to opaque, and velvety smooth or with tufted spiral lines on last whorl (Kohn & Weaver, 1962; as "C. sp. cf. C. cumingii Reeve").

In Hawaii, foot buff, mottled with light brown, tinged with vermilion at its extremities. Rostrum and tentacles pale buff. Siphon vermilion, mottled with small darker blotches (Kohn & Weaver, 1962).

Radular teeth with an adapical barb opposite a long blade; serration with coarse denticles from the end of the barb to the center of the shaft; base with a spur (Rolán, pers. comm., 1992).

Habitat and Habits: In 50-200 m; in Hawaii, mainly on coral rubble.

**Discussion:** *C. sazanka* is quite distinct from its Indo-Pacific congeners; for comparison with *C. lischkeanus* and *C. cumingii*, see the Discussions of those species.

Shells of *C. sazanka* from Japan and South Africa are very similar to each other and are strikingly uniform in colour pattern. Philippine specimens are more variable in colouration and pattern, even at the same locality; differences in shape or sculpture cannot be observed. Hawaiian shells vary both in colour (yellow to deep orange) and in sculpture of the last whorl ("partly or entirely encircled by granular spiral lirae", Kohn & Weaver, 1962; as "*C. sp.* cf. *C. cumingii* Reeve"). However, colour and sculptural variants appear to co-occur. The colour pattern variability observed in Hawaii closely matches that known from Philippines.

#### 34

## Conus danilai RÖCKEL & KORN, 1990

(Plate 9, Figures 19-22; Map 15)

1990 Conus danilai Röckel & Korn, Acta Conchyl., 2: 46-49, pl. 10, row 2 figs. 1-5, row 3 fig. 1

Type: Holotype in SNMS (30.5 x 17 mm).

Type Locality: "Ras Fartak, Gulf of Aden, N. W. Indian Ocean."

Range: Gulf of Aden.

**Description:** Moderately small to medium-sized, moderately solid. Last whorl conical to ventricosely conical or slightly pyriform; outline slightly to moderately convex, occasionally concave above base. Base of columella with a weak or distinct posterior plication. Shoulder angulate and tuberculate. Spire of moderate height, stepped; outline concave to straight. Larval shell of about 2 whorls, maximum diameter about 1.4 mm. Postnuclear spire whorls tuberculate. Teleconch sutural ramps flat, with 1-2 subsutural spiral grooves; spiral grooves weak on last 2-3 ramps. Last whorl with weak spiral ribs at base.

#### C. danilai Shell Morphometry

25 - 40 mm
0.17 - 0.24 g/mm
0.67 - 0.72
0.81 - 0.87
0.15 - 0.21

Ground colour white. Last whorl either covered with a coarse network of light brown to orange-brown lines edging small to medium-sized tents, or banded with orange red to orangish brown reticulate lines and triangular spots forming 3 spiral zones below shoulder and on both sides of centre. Larval whorls white. Teleoconch sutural ramps with occasionally sparse orange-red spots or radial lines. Aperture white or pale pinkish violet deep within.

Habitat and Habits: In about 60 m.

**Discussion:** *C. danilai* resembles *C. hamamotoi*. For comparison, see the Discussion of that species.

#### 35

# Conus hamamotoi Yoshiba & Koyama, 1984

(Plate 9, Figures 23-27; Map 15)

1984 Conus hamamotoi Yoshiba & Koyama, Venus, 43 (2): 115-123, pl. 1 figs. 1-5

Type: Holotype in WPMN (23 x 13.5 mm)

**Type Locality:** "at so-called Teradashi to Hattanshö (33°25.8'-33°26.3'N, 135°44.5'-135°44.9'E) 1.0-1.5 km west of Ogokuda Beach, Kushimoto-machi, Nishimuro-gun, Wakayama Pref., Japan, (southern end of Kii Peninsula, Honshu)."

Range: Japan New Caledonia and Coral Sea.

Description: Small and moderately light. Last whorl broadly conical to slightly pyriform; outline convex adapically, straight to concave toward base. Shoulder tuberculate. Spire of moderate height, outline straight. Larval shell of about 3 whorls, maximum diameter 0.9 mm. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps with radial threads; 1-2 weak spiral grooves on early ramps. Last whorl with pronounced spiral grooves basally, separating ribs and ribbons; ribs may be granulose and may extend to shoulder.

C. hamamotoi Shell Morphometry		
L	18 - 24 mm	
RW	0.06 - 0.13 g/mm	
RD	0.70 - 0.79	
PMD	0.85 - 0.93	
RSH	0.15 - 0.22	

Ground colour white. Last whorl overlaid with rose pink, leaving a band of white blotches and a few spiral rows of reddish brown dots at centre; adjacent to central band, rose pink suffused with brown. Base and siphonal fasciole white. Larval whorls pale orange. Teleoconch sutural ramps brownish red, tuberculate marginal areas paler.

Animal "persimmon in colour" (Yoshiba and Koyama, 1984).

**Habitat and Habits:** In 60-70 m, in Coral Sea, 62-120 m (Richard, pers. comm., 1991).

Map 16

**Discussion:** *C. hamamotoi* resembles *C. sazanka*, *C. articulatus* and *C. danilai*. *C. sazanka* is larger (25-42 mm), has a narrower last whorl (RD 0.56-0.64), lower spire (RSH 0.07-0.18), weak tuberculation of the teleoconch spire whorls, and distinct spiral grooves on its sutural ramps; its last whorl pattern lacks both a continuous white band and spiral rows of reddish brown dots centrally. *C. danilai* is also larger (25-40 mm), heavier (RW 0.17 g/mm in similarly sized shells), has a narrower last whorl (RD 0.67-0.72) with less pronounced sculpture, the colour pattern of its last whorl includes white tents, and its larval shell is broader (1.4 mm) comprising only 2 whorls. For comparison with *C. articulatus*, see the Discussion of that species.

# 36 Conus axelrodi WALLS, 1978

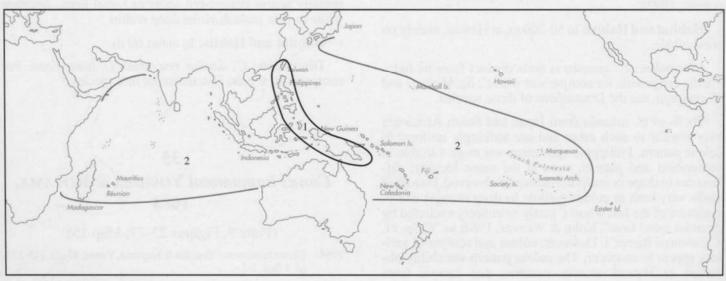
(Plate 9, Figures 28-31; Map 16)

1978 Conus axelrodi Walls, The Pariah, 2: 1, 5 (figs.)

**Type:** Holotype in DMNH (16 x 9 mm). **Type Locality:** "Philippines, Palawan."

Range: Taiwan, Philippines, Papua New Guinea.

Description: Small, light. Last whorl broadly conical, broadly and ventricosely conical or slightly pyriform; outline variably convex adapically and straight to concave below. Shoulder angulate, distinctly tuberculate to undulate. Spire of moderate height, occasionally high; outline straight to slightly concave. Larval shell of about 1.75 whorls, maximum diameter about 1 mm. Postnuclear spire whorls tuberculate to undulate. Teleoconch sutural ramps flat, with 3 increasing to 4-5 spiral grooves; ribs between often crossed by arcuate threads producing a cancellate appearance. Entire last whorl with distinct, widely spaced,



1: C. axelrodi 2: C. litteratus

granulose spiral ribs; interspaces occasionally with a single fine, punctate spiral groove.

C. a	axelrodi Shell Morphometry
L	15 - 20 mm
RW	0.05 - 0.06 g/mm
RD	0.69 - 0.79
PMD	0.77 - 0.90
RSH	0.16 - 0.30

Ground colour white, usually variously suffused with yellowish brown, pink, or rose. Last whorl with a varying number of variably spaced brown dots arrayed on the spiral ribs; in some populations, dots completely absent. Larval whorls white to red. Teleoconch sutural ramps with scattered brown markings or immaculate. Aperture white, pale yellow or pale pink.

Periostracum yellowish brown to olive, thin, translucent, smooth.

#### Habitat and Habits: Shallow water.

**Discussion:** C. axelrodi is similar to the Caribbean C. puncticulatus. C. puncticulatus and its close relatives C. jaspideus (Caribbean) and C. perplexus (E. Pacific) are all clearly distinguished by their non-tuberculate postnuclear whorls, smooth sutural ramps, and spiral ribbons rather than ribs on the last whorl. C. axelrodi has often been identified as C. papillosus Kiener (e.g. Richard, 1990). It conforms generally to the description of that species; however, the original figure of C. papillosus, is 25 mm long, and it is more likely a specimen of C. puncticulatus Hwass (Vink, 1990).

# 37 Conus litteratus LINNÉ, 1758

(Plate 10, Figures 1-4; Pl. 74, figure 18; Plate 78, Second row, left; Map 16)

- 1758 Conus litteratus Linné, Syst. Nat., 10 ed., 1: 712, no. 252
- 1798 Cucullus pardus Röding, Mus. Bolten., 2: 41, no. 519/41
- 1810 Conus arabicus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 40, no. 46
- 1843 Conus grueneri Reeve, Proc. Zool. Soc. London, 11: 175; 1844: Conch. Icon., 1, Conus: Pl. 43 sp. 231

Types: C. litteratus: Lectotype (Kohn, 1963) in LSL (91 x 52 mm); C. pardus: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 60 fig. 667) (88 x 52 mm); C. arabicus: Lectotype (Kohn, 1981) figured in Tableau (1798: Pl. 323 fig. 1) (80 x 43 mm); C. grueneri: Original figure 24 x 12 mm.

**Type Localities:** *C. litteratus* "O. Asiatico"; *C. arabicus*: "l'Océan asiatique"; *C. grueneri*: "Island of Java."

Range: Indo-Pacific, except for Red Sea and Hawaii.

**Description:** Moderately large to large, solid to heavy. Last whorl conical; outline almost straight, sometimes convex below shoulder. Base moderately pointed. Shoulder sharply angulate. Spire low, outline usually sigmoid. Middle and late teleoconch sutural ramps concave, with 3 increasing to 4-6 spiral grooves; grooves often weak to obsolete. Last whorl almost smooth.

C. 1	itteratus Shell Morphometry
L	60 - 170 mm
RW	0.67 - 2.42 g/mm (L 60-115 mm)
RD	0.54 - 0.65
PMD	0.85 - 0.94
RSH	0.00 - 0.08

Ground colour white. Last whorl usually encircled with 3 yellowish orange bands, at centre and within adapical and abapical thirds. Spiral rows of blackish brown, medium-sized, round to squarish spots, sometimes axially elongate or arrow-shaped, extend from base to shoulder. Base and siphonal fasciole bluish brown. Teleoconch sutural ramps with blackish brown oblique radial streaks. Aperture white, usually with a bluish brown basal edge.

Periostracum brown to blackish brown, variably thick, translucent to opaque, and velvety to rough.

Dorsum of foot pink to reddish brown anteriorly, laterally and behind operculum, grey to beige with white radial lines on remaining portion; anterior edge with closely spaced black axial streaks; a dotted black pre-marginal line around entire median zone. Sole of foot solid reddish brown or grey mottled with pinkish cream to brown. Rostrum pink. Tentacles pink, tipped with white and dotted with grey. Siphon brownish red grading to rose distally or pink to violet, dotted with white, black and dark red (Pl. 74, Fig. 18; Pl. 78, Second row, left) (Bergh, 1895; Kohn, unpubl. observ.; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.).

Radular teeth with an adaptical barb opposite a blade/second barb(?); serration ending anterior to the central waist; base with a prominent spur (Nybakken, 1990).

Habitat and Habits: Slightly subtidal to 50 m, juveniles sometimes dredged in 60 m. In channels to large patches of fine or more often coarse sand, rubble and sand, silty rubble, sand with vegetation and even dense beds of sea-weed (Cernohorsky 1964, 1978; Kohn & Nybakken, 1975; Kohn, 1980a; Tirard, pers. comm., 1989; Grosch, pers. comm., 1989).

C. litteratus feeds exclusively on polychaetes, mainly Capitellidae, and serves as prey for C. marmoreus (Endean & Rudkin, 1965; Kohn & Nybakken, 1975; Kohn, 1980a; Reichelt & Kohn, 1985).

Egg capsules with a heavily corrugated surface and crenulated edges, affixed to the substratum by confluent basal plates. Egg diameter of 201-222 µm predicts a minimum pelagic period of 23-21 days (Perron & Kohn, 1985).

**Discussion:** *C. litteratus* appears to be closely related to *C. leopardus*, which often occurs sympatrically, sometimes in the same habitat. It may also resemble *C. eburneus*. For comparison, see the Discussions of those species.

# 38 Conus leopardus (RÖDING, 1798)

(Plate 10, Figures 5-7; Plate 74, Figure 17; Plate 78, Second row, right; Map 17)

- 1798 Cucullus leopardus Röding, Mus. Bolten., 2: 41, no. 520/42
- 1822 Conus millepunctatus Lamarck, Hist. Nat. Anim. s. Vert., 7: 461-462, no. 45 (non C. millepunctatus Röding, 1798)
- 1937 Conus millepunctatus var. aldrovandi Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 171-172 (non C. aldrovandi Risso, 1826, a fossil)

**Types:** *C. leopardus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 60 fig. 666) (78 x 43 mm); *C. millepunctatus*: Lectotype (Walls, [1979]) figured in Tableau (1798: Pl. 323 fig. 5) (137 x 75 mm); *C. m.* var. *aldrovandi*: Lectotype (Coomans et al., 1980) figured in Tableau (1798: Pl. 324 fig. 4) (119 x 66 mm).

Type Localities: C. millepunctatus: "l'Océan asiatique."

Range: Entire Indo-Pacific except for Red Sea.

Description: Large and heavy. Last whorl usually conical; outline almost straight, sometimes convex at adapical fourth. Base truncate. Shoulder angulate, occasionally subangulate. Spire of low to sometimes moderate height, outline slightly concave to slightly convex. Middle and late teleoconch sutural ramps concave, with 3 increasing to 4-6 spiral grooves; grooves usually weak on last ramps of large specimens. Last whorl with weak spiral ribs above base, obsolete in large specimens.

# C. leopardus Shell Morphometry L 80 - 222 mm RW 1.40 - 5.00 g/mm (L 80-170 mm) RD 0.58 - 0.71 PMD 0.81 - 0.93 RSH 0.00 - 0.15

Ground colour white. Last whorl with spiral rows of dark bluish brown spots or short axial streaks. Teleoconch sutural ramps variably maculated with dark bluish brown oblique radial blotches. Aperture white.

In subadults, periostracum yellowish olive, thin, translucent, largely smooth, with short fringes at shoulder edge. In adults, periostracum reddish brown to dark greyish brown, thick, progressively opaque, and velvety or rough.

Foot thick; dorsum tan or mottled brown and white; anterior part with a diffuse dark brown to black pattern centrally, corners sparsely maculated or white; lateral and posterior marginal zone with diffuse black streaks radiating from a dotted black pre-marginal line. Sole of foot white mottled with brown, with darker brown interlaced longitudinal veins and sometimes with purplish brown to black blotches. Rostrum white to tan or orange. Tentacles white to beige. Siphon white, grading to yellow or buff anteriorly, with a black half-ring near centre; often with sparse additional light brown markings, occasionally with an additional latero-ventral black blotch somewhat posterior to the black half-ring. Interior of siphon edged with light brown (Pl. 74, Fig. 17; Pl. 78, Second row, right) (Garrett, 1878; Kohn 1959a & unpubl. observ.; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.).

Radula and venom apparatus poorly developed. Radular teeth small, with an adapical barb opposite a second weak but large barb; long serration terminates in a cusp; base with a spur (Bergh, 1895; Peile, 1939; Kohn, 1959b & 1980a).

Habitat and Habits: Slightly subtidal to about 45 m, usually below 2 m. Mainly in shallow bays with vast subtidal stretches of sand or sand with vegetation; also occupying large areas of sand or sand and rubble on subtidal reef flats; less common where subtidal reef flats pass into smooth intertidal limestone benches (Kohn, 1959a, b, 1968b, 1980a; Kohn & Nybakken, 1975; Cernohorsky, 1964, 1978; Tirard, pers. comm., 1989).

*C. leopardus* feeds exclusively on enteropneusts (*Pty-chodera flava*) by engulfing its prey without stinging it first (Kohn, 1959b, 1980a; Endean & Rudkin, 1965).

Observed to oviposit in 0.2-1.5 m of water on sand and rubble. Egg capsules deposited in irregular rows, affixed to the underside of granite rocks, coral rocks and coral heads by confluent basal plates. Observed to spawn together with *C. textile* and *C. virgo* at the same place without interspecific competition. Capsules measure 26-58 x 19-37 mm and contain 2,900-12,800 eggs; observed number of eggs per capsule mass is more than 744,000. Egg diameter varies between 204-240 µm depending on locality, predicting a minimum pelagic period between 23 and 21 days (Kohn, 1961a, b; Perron, 1981b, c; Perron & Kohn, 1985; Cernohorsky, 1964).

**Discussion:** *C. leopardus* may be mistaken for *C. litteratus*. The latter species can be distinguished by its smaller size, moderately pointed and dark bluish brown rather than truncate, white base, and the less pronounced spiral grooves on its sutural ramps. *C. litteratus* often has yellowish orange bands on the last whorl, absent in *C. leopardus*, and the last whorl of the former is usually narrower (RD 0.54-0.65). These species also differ in the colouration of the animal, the diet, and to some extent the microhabitat.

#### 39

## Conus eburneus HWASS in BRUGUIÈRE, 1792

(Plate 10 Figures 8-19; Plate 74, Figure 19; Map 17)

1792	Conus eburneus Hwass in Bruguière, Encycl. Méth., 1: 640-641,
	no. 89

- 1798 Cucullus quadratulus Röding, Mus. Bolten., 2: 41, no. 512/36
- 1807 Conus alternatus Link, Beschr. Nat. Samml. Univ. Rostock, 3: 101-102
- 1858 Conus crassus Sowerby II, Thes. Conch., 3: 25, no. 203, pl. 12 figs. 254, 255
- 1874 Conus eburneus var. polyglotta Weinkauff, Jahrb. deutsche malak. Ges., 1: 244

**Types:** *C. eburneus*: Lectotype (Kohn, 1968) figured in Tableau (1798: Pl. 324 fig. 1) (46 x 30 mm); *C. quadratulus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 61 fig. 670) (45 x 24 mm); *C. alternatus*: Lectotype (Kohn, 1981) same as lectotype of *C. quadratulus*; *C. crassus*: Lectotype (Walls, [1979]) in BMNH (44 x 29 mm); *C. e.* var. *polyglotta*: Refers to Sowerby II (1858: Pl. 12 fig. 248) (30 x 18 mm).

**Type Localities:** C. eburneus: "aux mers des Indes orientales"; C. crassus: "Feejee Islands"; C. e. var. polyglotta: "Pelew Ins., Gesellsch.-Ins.."

Range: E. Africa, except for Red Sea, to Ryukyu Is., Polynesia, and to Australia; absent from Hawaii.

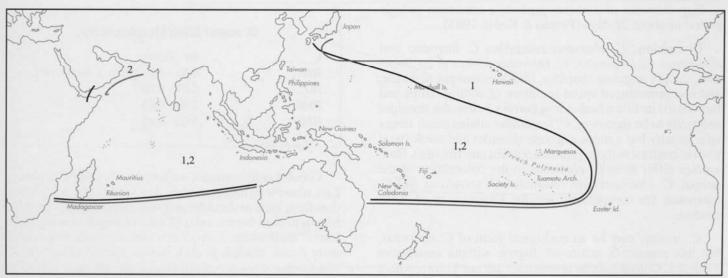
**Description:** Medium-sized to moderately large, moderately solid to heavy. Last whorl conical to broadly and/or ventricosely conical, occasionally conoid-cylindrical; outline convex to bulbous at subshoulder area and straight below; base truncate. Shoulder angulate to rounded. Spire low, outline concave to straight or sigmoid. Larval shell multispiral, maximum diameter about 0.7 mm. Teleoconch sutural ramps almost flat, with 2 narrow but deeply

incised spiral grooves in early whorls and 2-5 grooves in later whorls; intervening ribs and subsutural ridge often pronounced, occasionally weak on last ramps. Last whorl with distinct to weak spiral ribs and ribbons on basal fourth to half.

C. ebur	neus Shell Morphometry
L	35 - 79 mm
- form crassus	35 - 63 mm
RW	0.23 - 1.20 g/mm
- from crassus	0.23 - 0.73 g/mm
RD	0.59 - 0.73
- form crassus	0.63 - 0.72
PMD	0.74 - 0.92
- form crassus	0.81 - 0.89
RSH	0.02 - 0.12
- form crassus	0.02 - 0.10

Ground colour white. Last whorl with spiral rows of variably spaced, reddish brown to black squarish spots, rectangular bars or comma-shaped streaks; 3 yellow, orange or tan bands may underly spiral rows, below shoulder and on both sides of centre. Typical form (Pl. 10, Figs. 8-13) often with less densely spaced markings; occasionally, colour bands obsolete or covering large parts of last whorl. In form *polyglotta* (Pl. 10, Figs. 16-19), black bars or commalike markings tend to fuse into solid narrow spiral bands and wavy axial streaks. Form *crassus* (Pl. 10, Figs. 14-15) has red-brown markings and usually lacks spiral colour bands. Larval whorls white. Teleoconch sutural ramps with reddish brown or blackish brown spots, radial streaks or blotches; intensity of spire pattern matching that of last whorl pattern. Aperture white.

Map 17



1: C. leopardus 2: C. eburneus

Periostracum yellowish orange, thin, translucent, and smooth in subadult specimens, becoming olive-brown and less translucent in adults.

Dorsum of foot ivory, occasionally with beige lateral and posterior sides; marginal zone of central and posterior part with radial markings of grey, black and various shades of brown; anterior part often with 2-3 triangular grainy black blotches radiating from centre, and with 2 grey to black markings near anterior corners. Sole of foot uniformly ivory to pinkish beige, mottled white and tan, or buff with a darker yellow anterior edge. Rostrum pale pink or buff. Tentacles white, sometimes tan distally and dorsally. Distal part of siphon white, edged with pink, yellow or tan; central part tan or white, with 1 or 2 irregular black rings grading to grey latero-ventrally; proximal part light brown, mottled with darker brown and black dorsally (Pl. 74, Fig. 19) (Chaberman, pers. comm., 1981; Estival, 1981; Kohn, unpubl. observ.; Pearson, unpubl. observ.). Typical form and form crassus have identical body colouration (Richards, pers. comm., 1989).

Radular teeth with an adapical barb opposite a large blade; short serration from the end of the barb to the end of the blade; base with a spur (Rolán, pers. observ., 1991).

Habitat and Habits: Intertidal to about 65 m, mostly in 1-25 m; primarly in and on sand bottoms of subtidal reef flats, in sand-filled channels, large patches of sand and among weed on sandy or muddy substrate (Cernohorsky, 1964, 1978; Kohn & Nybakken, 1975; Kohn, 1980a; Reichelt & Kohn, 1985; Tirard, pers. comm., 1989). In E. New Britain, typical *C. eburneus* often in dense colonies in 1-20 m, while form *crassus* is solitary, usually half buried in volcanic sand close to gravel bottoms below 12 m (Richards, pers. comm., 1989).

C. eburneus preys mainly on polychaetes belonging to several families and is also known to feed on fishes. Its venom is toxic to worms, mollusks and small fishes, less dangerous to small mammals (Endean & Rudkin, 1965; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985; Thorsson, 1989).

Egg diameter of 150 µm predicts a minimum pelagic period of about 28 days (Perron & Kohn, 1985).

**Discussion:** *C. eburneus* resembles *C. litteratus* and sometimes *C. leopardus*. *C. litteratus* differs in its larger size, sharply angulate shoulder, bluish brown pointed base, and less pronounced spiral sculpture of sutural ramps and last whorl; its last whorl is less convex below the shoulder and tends to be narrower. *C. leopardus* attains much larger size, usually has a more angulate shoulder and weak basal ribs (in contrast to more pronounced ribs and ribbons). Both species differ from *C. eburneus* in the colouration of the animal. *C. eburneus* also resembles *C. tessulatus* and *C. suturatus*; for comparison, see the Discussions of these species.

C. crassus may be an ecological form of C. eburneus, but this remains a matter of dispute without conclusive evidence. Colour pattern intergrades are not known where both co-exist in the same locality with overlapping depth

ranges; the slight differences in shell morphometry do not separate them. We consider *C. eburneus* var. *polyglotta* a colour form, as described by Weinkauff (1874).

#### 40

# Conus augur [LIGHTFOOT], 1786

(Plate 10, Figures 20-22; Map 18)

- 1786 Conus augur [Lightfoot], Cat. Portland Mus.: 44, no. 1046
- 1791 Conus punctatus Gmelin, Syst. Nat., 13 ed., 1: 3389, no. 40
- 1792 Conus augur Hwass in Bruguière, Encycl. Méth., 1: 685-686, no. 74
- 1798 Cucullus magus Röding, Mus. Bolten., 2: 49, no. 624/115 (non C. magus Linné, 1758)
- 1798 Cucullus pulverulentus Röding, Mus. Bolten., 2: 44, no. 556/66

**Types:** *C. augur* [Lightfoot]: Lectotype (Kohn, 1964) figured in Knorr (1772: Pl. 13 fig. 6) (65.5 x 35 mm); *C. punctatus*: Holotype same as lectotype of *C. augur*; *C. augur* Hwass: No type; *C. magus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 58 fig. 641) (43 x 31 mm); *C. pulverulentus*: Lectotype (Kohn, 1975) same as lectotype of *C. magus*.

**Type Localities:** C. augur [Lightfoot]: "Ceylon" (Coomans et al., 1981); C. augur Hwass: "l'Isle de Ceylan."

Range: E. Africa to W. Thailand; probably Moluccas.

**Description:** Medium-sized to moderately large, solid to heavy. Last whorl conical; outline convex at adapical third, slightly concave at central third and almost straight below. Shoulder subangulate to sharply angulate. Spire usually low; outline concave to convex. Larval shell of about 2 whorls, maximum diameter 0.7 - 0.8 mm. Early postnuclear whorls tuberculate. Teleoconch sutural ramps concave, with densely set, fine to pronounced threads crossing 3-4 major spiral grooves in late whorls; additional spiral threads on last ramps. Last whorl with closely spaced spiral threads from base to shoulder.

### C. augur Shell Morphometry

L	50 - 76 mm
RW	0.53 - 1.27 g/mm (L 50-68 mm)
RD	0.57 - 0.69
PMD	0.85 - 0.93
RSH	0.05 - 0.13

Ground colour cream, suffused with yellow or orange. Last whorl with numerous spiral rows of fine reddish brown dots from base to shoulder and with a spiral band of reddish brown to dark brown axial blotches on each side of centre. Larval shell white. Teleoconch sutural ramps with moderately dense, reddish to dark brown, curved radial streaks, often reduced to a pre-sutural and a sub-sutural row of spots. Aperture white, often variously tinged with orange.

Periostracum greyish to blackish brown, thick, opaque, axially ridged.

**Habitats and Habits:** In 3-25 m; in muddy sand, on coral rubble and beneath rocks.

**Discussion:** *C. augur* is a very distinctive species characterized by a striking conchological uniformity within and between populations.

#### 41

## Conus arenatus HWASS in BRUGUIÈRE, 1792

(Plate 11, Figures 1-7; Plate 74, Figure 23; Plate 78, Third row; Map 18)

- 1792 Conus arenatus Hwass in Bruguière, Encycl. Méth., 1: 621-622, no. 16
- 1798 Cucullus arenosus Röding, Mus. Bolten., 2: 40, no. 494/20
- 1798 Cucullus stercusmuscarum Röding, Mus. Bolten., 2: 40, no. 495/21 (non C. stercusmuscarum Linné, 1758)
- 1883 Conus arenatus var. mesokatharos Melvill in Tryon, Man. Conch., 6 (1): 18, pl. 27 fig. 2
- 1891 Conus armatus "Hwass" E. A. Smith, Proc. Zool. Soc. London, 1891: 402, no. 18 (error for C. arenatus Hwass)
- 1937 Conus arenatus var. aequipunctata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 31, pl. 1 fig. 2
- 1937 Conus arenatus var. undata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 31-32, pl. 1 fig. 3 (non C. undatus Kiener, 1845)
- 1937 Conus arenatus var. granulosa Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 32, pl. 1 fig. 4 (non C. granulosus Röding, 1798, C. granulosus Sowerby I, 1834, and C. granulosus Barros e Cunha, 1933)
- 1981 Conus arenatus bizona Coomans, Moolenbeek & Wils, Basteria, 45 (1-3): 16-18, figs. 98, 131

Map 18

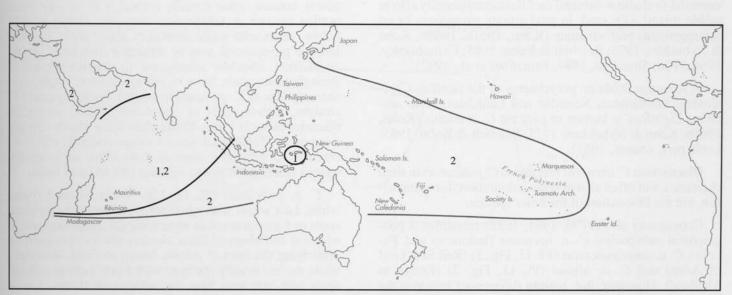
**Types:** *C. arenatus*: Lectotype (Kohn, 1968) in MHNG (35.5 x 19.5 mm); *C. arenosus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 63 fig. 696) (48 x 33 mm); *C. stercusmuscarum*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 63 fig. 697) (25 x 13 mm); *C. a.* var. *mesokatharos*: Holotype in NMWC (28 x 15 mm); *C. a.* var. *aequipunctata*: Holotype in IRSN (55 x 32 mm); *C. a.* var. *granulosa*: Original figure 42 x 22 mm; *C. a. bizona*: Holotype in ZMA (35 x 20 mm).

**Type Localities:** *C. arenatus*: "des Isles Philippines"; *C. a.* var. *aequipunctata*: "the Red Sea coast at Jiddah (Saudi Arabia)" (Coomans et al., 1979b); *C. a.* var. *granulosa*: "Amboine"; *C. a.* var. *undata*: "Amboine"; *C. a. bizona*: "Malindi, Kenya" (Coomans et al., 1981).

Range: E. Africa to Marshall Is. and Tuamotu Archipelago.

Description: Medium-sized to large, moderately solid to moderately heavy; maximum size smaller in eastern populations. Last whorl usually ventricosely conical in eastern populations, conical to sometimes broadly conical in the W. Indian Ocean; outline convex, sometimes straight centrally. Siphonal fasciole distinct, occasionally separated from basal zone by an incision. Shoulder subangulate to rounded, weakly to strongly tuberculate. Spire of low to moderate height, outline straight to moderately convex. Larval shell of 3 or more whorls, maximum diameter about 0.7 mm. Postnuclear spire whorls tuberculate. Teleoconch sutural ramps concave, with 1 increasing to 4-6 spiral grooves. Last whorl with weak spiral ribs at base; in subadults and small adults, ribs may be granulose and extend to shoulder.

Ground colour white. Last whorl with spiral rows of brown or black dots, clustered in 2-3 interrupted spiral bands or in axial zigzag flames; dotted areas often with underlying grey shadows, most conspicuous within spiral bands. White dashes often irregularly alternating with dark dots. Larval whorls white. Teleoconch sutural ramps variably maculated with radial clusters of brown and black dots. Aperture white, brown or pinkish orange deeper within.



1: C. augur 2: C. arenatus

Periostracum thin, velvety smooth and either translucent olive or reddish brown and nearly opaque; large and some subadult shells with a thicker, opaque periostracum.

	C. arenatus	Shell Morphometry
L	35 - 67 mm	(eastern populations)
	35 - 90 mm	(W. Indian Ocean populations)
RW	0.20 - 1.10 g/m	nm (L 35-75 mm)
RD	0.60 - 0.72	
PMD	0.75 - 0.85	(eastern populations)
	0.84 - 0.89	(W. Indian Ocean populations)
RSH	0.08 - 0.19	

Dorsum of foot cream, mottled with yellowish brown, with a dark brown to black central spot at anterior end occasionally followed by a few grey to black dots; sometimes a dotted black pre-marginal line latero-posteriorly. Anterior edge of foot may be orangish brown. Sole of foot white to brown, sometimes darker anteriorly, mottled with tan and sometimes longitudinally streaked with brown; mottling often more pronounced laterally. Rostrum white to yellow. Tentacles white to pale yellow, mottled with black at base. Siphon white or pinkish white, tip orange or mottled with red; central part with a single black dorsal blotch or a narrow black to grey ring; proximal part often mottled with tan (Pl. 74, Fig. 23; Pl. 78, Third row) (Chaberman, pers. comm., 1981; Kohn, unpubl. observ.; Pearson, unpubl. observ.; Fainzilber et al., 1992).

Radular teeth with an adapical barb opposite a large second barb; serration as long as second barb and ending in a cusp; central waist and basal spur present (Peile, 1939; Bandel, 1984: Seychelles). For Red Sea specimens, Bandel (1984), depicted a narrower tooth, with a blade instead of a second barb and a shorter serration.

Habitat and Habits: Intertidal to about 30 m, almost exclusively in sand. Mainly on wide stretches of sand on intertidal to shallow-subtidal reef flats; occasionally also in rubble mixed with sand, in mud among mangroves or on heterogeneous reef substrate (Kohn, 1961b, 1968b; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985; Cernohorsky, 1964, 1978; Sharabati, 1984; Fainzilber et al., 1992).

C. arenatus feeds on polychaetes of the families Capitellidae, Maldanidae, Nereidae and Eunicidae. Melo amphora Lightfoot is known to prey on C. arenatus (Kohn, 1968b; Kohn & Nybakken, 1975; Reichelt & Kohn, 1985; Loch, pers. comm., 1987).

**Discussion:** *C. arenatus* resembles *C. pulicarius* in shell characters and often also in body colouration; for comparison, see the Discussion of the latter species.

Coomans et al. (1979b, 1981, 1982) recognize 3 geographical subspecies: *C. a. arenatus* (Indonesia and Pacific); *C. a. aequipunctatus* (Pl. 11, Fig. 3) (Red Sea; Gulf of Aden) and *C. a. bizona* (Pl. 11, Fig. 2) (Kenya to Thailand). However, the pattern differences between the two western subspecies are not constant. Although *C. a.* 

bizona was described as having two bands and C. a. aequipunctatus as having three, the third band is incomplete or lacking in some specimens from the Red Sea and Gulf of Aden, and it is present in some specimens from Sri Lanka. As noted above, W. Indian Ocean shells differ in size and shape from those farther east. In form mesokatharos the central part of the last whorl is unspotted, form granulosa bears granules on the entire last whorl, and form undata shows dots arranged in flame-like axial clusters.

#### 42

## Conus pulicarius HWASS in BRUGUIÈRE, 1792

(Plate 11, Figures 8-14; Plate 74, Figures 21, 22; Plate 78, Fourth row, left; Map 19)

1792 Conus pulicarius Hwass in Bruguière, Encycl. Méth.,1: 622-623, no. 17

1792 Conus fustigatus Hwass in Bruguière, Encycl. Méth., 1: 623, no. 18

1798 Cucullus punctulatus Röding, Mus. Bolten., 2: 40, no. 497/23

1845 Conus vautieri Kiener, Coq. Vivant., 2: Pl. 100 fig. 3; 1849-1850: 350

**Types:** *C. pulicarius*: Lectotype (Kohn, 1968, as "holotype", Walls, [1979]) in MHNG (45 x 29 mm); *C. fustigatus*: Lectotype (Kohn, 1968) in MHNG (41 x 27 mm); *C. punctulatus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 63 fig. 698) (46 x 26 mm); *C. vautieri*: Original figure 32 x 19 mm.

**Type Localities:** *C. pulicarius*: "les isles de l'Océan Pacifique"; *C. fustigatus*: "l'Océan Asiatique."

**Range:** *C.p. pulicarius*: Central and W. Pacific, Polynesia except Marquesas; Indian O., Cocos (Keeling) Island, and northern Western Australia; *C. p. vautieri*: Marquesas.

**Description:** Medium-sized to moderately large, solid to heavy. Last whorl conical, conoid-cylindrical, or ventricosely conical, often broadly conical in *C. p. pulicarius*; outline convex at subshoulder area and almost straight below, often with slight convexity above base. Siphonal fasciole pronounced, may be separated from basal part by an incision. Shoulder subangulate to rounded, weakly to strongly tuberculate. Spire of low to moderate height, consistently low in *C. p. vautieri*; outline slightly concave to straight. Larval shell of about 3.5 whorls, maximum diameter about 0.7 mm. Postnuclear spire whorls strongly tuberculate. Teleoconch sutural ramps concave, with 1 increasing to 4-5 spiral grooves. Last whorl with variably spaced spiral grooves and adjacent ribs on basal fourth.

C. p. pulicarius (Pl. 11, Figs. 8-12): Ground colour white. Last whorl with spiral rows of irregularly set black spots or bars clustered in an interrupted spiral band within adapical and abapical third; clusters often emphasized by underlying shadows of yellow, brown or violet. Near base, white dashes usually alternate with black markings. Black spots and bars may fuse into solid axial flames. Larval whorls white to grey. Teleoconch sutural ramps with vari-

ously solid black markings, varying in number and arrangement. Aperture white to bluish white, often suffused with yellow or orange.

	C. pulicarius Shell Mo	rphometry
	C. p. pulicarius	C. p. vautieri
L	35 - 75 mm	35 - 74 mm
RW	0.29 - 1.10 g/mm (L 35 - 64 mm)	0.35 - 1.23 g/mm
RD	0.63 - 0.80	0.62 - 0.67
PMD	0.78 - 0.88	0.80 - 0.91
RSH	0.04 - 0.22	0.06 - 0.10

Periostracum of subadults yellow, thin and translucent in Hawaii, fawn-coloured in Fiji; adult periostracum reddish brown, thicker and almost opaque in Hawaii, Fiji and Cook Islands; adults from Guam and northern Queensland with a yellowish olive, translucent, velvety periostracum bearing interlaced axial threads.

C. p. vautieri (Pl. 11, Figs. 13, 14) with brownish grey ground colour and reddish brown pattern; bands around last whorl underlaid with reddish brown; intermittent white dashes often pronounced also adapically; aperture white.

At Hansa Bay (N. New Guinea), dorsum of foot ivory, suffused with cream and grey or sometimes with pink and green; median zone edged with pale tan dots on posterior half or completely dotted; anterior part bears a black central blotch with 2 backward- pointing lines of black dots, and its distal edge is occasionally white. Sole of foot ivory, washed with tan. Rostrum olive-grey or pale tan. Tentacles pale yellow. Siphon may be white, tipped with orange and washed with brown proximally on dorsal side, with a black half-ring anterior to centre, or siphon may match foot in

colouration, with white dots distally and tan dots proximally (Pl. 74, Figs. 21, 22; Pl. 78, Fourth row, left) (Chaberman, pers. comm., 1981). In Hawaii, foot and rostrum pale tan, mottled with yellowish to reddish brown; tip of siphon reddish orange, followed by pale buff and black bands (Kohn, 1959a).

Radular teeth stout, with an adaptical barb opposite a large second barb or a blade; serration short, terminating in a cusp; base with a spur (Troschel, 1868; James, 1980).

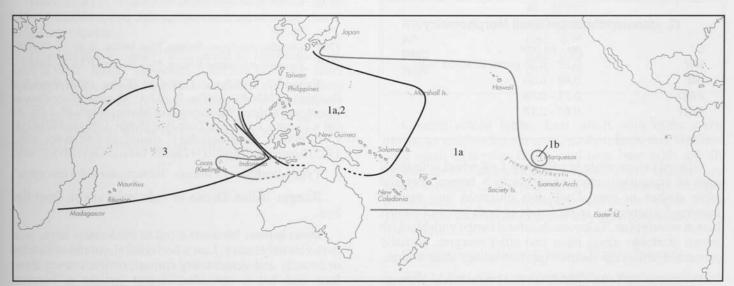
Habitat and Habits: Intertidal to more than 75 m; in deep sand away from limestone outcrops and growing coral; mostly in sand-filled channels and large patches of sand on reef flats and in bays. Reported to be both active only at night and active during the whole day (Cernohorsky, 1964, 1978; Kohn 1959a,b; 1980a; Thorsson, 1989; Tirard, pers. comm., 1989).

*C. pulicarius* feeds on polychaetes (mainly Capitellidae, occasionally also on Nereidae and Eunicidae); in Hawaii, echiurans ("spoonworms") are known to be a part of the diet. Venom toxic to worms but neither to molluscs nor to fishes (Kohn 1959b, 1980a; Endean & Rudkin, 1965).

Egg capsules with crenulate margins; capsules measure 18-19 x 14-15 mm in Hawaii, 13-14 x 15.8-17.5 at Lizard Id. (Australia) and 8-9 x 10-11 mm at Enewetok, Marshall Is. Egg diameter of 150-175 μm predicts a minimum pelagic period of about 27-26 days (Huish, 1978; Perron, 1981b; Perron & Kohn, 1985; Kohn & Perron, 1994).

**Discussion:** *C. pulicarius* resembles *C. arenatus* in shell characters and body colouration. The pattern of the latter species consists of more and smaller spots that form flamelike clusters but do not fuse into solid axial flames; its last whorl has a more convex outline as well as weaker spiral sculpture, and tends to be ventricosely conical but not conoid-cylindrical.

Map 19



la: C. pulicarius pulicarius 1b: C. pulicarius vautieri 2: C. stercusmuscarum 3: C. zeylanicus

C. fustigatus and C. punctulatus refer to C. p. pulicarius. The local race from the Marquesas Is. was described as C. vautieri, but the conchological similarities support its status as a geographic subspecies of C. pulicarius.

#### 43

### Conus stercusmuscarum LINNÉ, 1758

(Plate 11, Figures 15-18; Plate 74, Figure 24; Plate 78, Fourth row, right; Map 19)

- 1758 Conus stercusmuscarum Linné, Syst. Nat., 10 ed., 1: 715, no. 269
- 1798 Cucullus arenatus Röding, Mus. Bolten., 2: 49, no. 627/116 (non C. arenatus Hwass, 1792)
- 1798 Cucullus sabella Röding, Mus. Bolten., 2: 49, no. 628/116\*

**Types:** *C. stercusmuscarum*: Lectotype (Kohn, 1963) in LSL (37 x 20 mm); *C. arenatus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 64 fig. 712) (50 x 27 mm); *C. sabella*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 64 fig. 713) (46 x 22 mm).

Type Localities: C. stercusmuscarum: "Asia."

Range: Japan to Marshall Is. and to Indonesia, Papua New Guinea and Solomon Is.; probably also Fiji.

**Description:** Medium-sized to moderately large, moderately solid to solid. Last whorl usually conoid-cylindrical to nearly cylindrical or slightly ovate, outline slightly convex. Siphonal fasciole prominent. Shoulder sharply angulate. Spire of low to moderate height, outline straight to slightly convex. Larval shell multispiral, maximum diameter about 0.6 mm. First 3 postnuclear whorls weakly tuberculate. Teleoconch sutural ramps flat in early whorls, concave in late whorls, with 2 increasing to 3-4 spiral grooves. Last whorl with regularly spaced, broad spiral ribs, distinct basally but obsolete adapically.

# C. stercusmuscarum Shell Morphometry

L	40 - 64 mm
RW	0.21 - 0.35 g/mm (L 40-56 mm)
RD	0.48 - 0.63
PMD	0.71 - 0.78
RSH	0.07 - 0.18

Ground colour white to pale grey. Last whorl with spiral rows of irregularly alternating blackish brown dots and white dashes or bars. Dark dots clustered into patches forming 2 interrupted spiral bands of both sides of centre. Larval whorls pink. Teleoconch sutural ramps with blackish brown markings along inner and outer margins, partially connected across the ramps. Aperture orange deep within.

Periostracum yellowish olive, thin, translucent, velvety smooth.

Dorsum of foot with a large crown-shaped black zone anteriorly, separated from light brown anterior edge by 2 lateral white blotches; marginal zone cream with radiating black markings, densely clustered at posterior end; median zone white, mottled with black and brown and edged with a black line. Sole of foot white, mottled or transversely streaked with brown. Rostrum cream at tip, streaked with dark brown proximally. Tentacles white with black tips. Siphon white, mottled with light brown dorsally posterior to the tip and with darker brown proximally (Pl. 74, Fig. 24; Pl. 78, Fourth row, right) (Chaberman, pers. comm., 1981; de Couet, pers. comm., 1992).

Radular teeth with a large pointed adaptical barb, a large second barb, and a long backward-pointing third barb terminating in a recurved tip; neither serration nor basal spur present (Endean & Rudkin, 1965).

**Habitats and Habits:** Intertidal and uppermost subtidal; in sand and beneath corals.

C. stercusmuscarum probably preys on fishes (Endean & Rudkin, 1965).

Egg diameter of 235-240 μm predicts a minimum pelagic period of about 20 days (Perron & Kohn, 1985).

**Discussion:** C. stercusmuscarum is very similar to C. arenatus in colour pattern but differs markedly in its conoid-cylindrical to ovate and generally narrower last whorl, non-tuberculate late teleoconch whorls, and pink larval shell. The differences in feeding habits, radular tooth structure, and body colouration also distinguish these species.

#### 44

# Conus zeylanicus GMELIN, 1791

(Plate 11, Figures 19-23; Map 19)

- 1786 Conus undulatus [Lightfoot], Cat. Portland Mus.: 180, no. 3866
- 1791 Conus zeylanicus Gmelin, Syst. Nat., 13 ed., 1: 3389, no. 41
- 1792 Conus obesus Hwass in Bruguière, Encycl. Méth., 1: 623-624, no. 19
- 1798 Cucullus theobroma Röding, Mus. Bolten., 2: 43, no. 549/60
- 1798 Cucullus meningeus Röding, Mus. Bolten., 2: 39, no. 491/17

**Types:** *C. undulatus*: Lectotype (Kohn, 1964) figured in Gualtieri (1742: Pl. 25 fig. I) (67 x 35 mm); *C. zeylanicus*: Lectotype (Kohn, 1966) figured in Martini (1766: Pl. 2 fig. 20) (44 x 23 mm); *C. obesus*: Lectotype (Kohn, 1968) in MHNG (65 x 45.5 mm); *C. theobroma* and *C. meningeus*: Lectotypes (Kohn, 1975) figured in Chemnitz (1788: Pl. 142 fig. 1318) (63 x 35 mm).

Type Localities: C. obesus: "les mers des Indes orientales."

Range: Indian Ocean to Indonesia; absent from Red Sea.

**Description:** Medium-sized to moderately large, solid to moderately heavy. Last whorl conical, conoid-cylindrical or broadly and ventricosely conical; outline convex above base and below shoulder, almost straight in between. Shoulder rounded, irregularly undulate. Spire of low to

moderate height, outline straight to deeply concave. Larval shell of about 2.75 whorls, maximum diameter 0.8-1 mm. Postnuclear spire whorls tuberculate, less so toward shoulder. Teleoconch sutural ramps flat, concave in late whorls, with 1 increasing to 3-4 spiral grooves. Last whorl with variably broad spiral ribs at base.

#### 

Ground colour white, suffused with cream, pink or violet. Last whorl with grey to violet clouds, underlaying numerous short, fine, brown axial dashes, variously shaped and arranged black markings, and spiral rows of small alternating dark and light brown bars. Dark brown elements usually aligned in 2 incomplete spiral bands, on both sides of centre, often forming a weak additional band below shoulder. Larval whorls white. Teleoconch sutural ramps crossed by fine brown curved lines and sparse black blotches. Aperture light to pinkish violet deep within.

Periostracum yellowish brown, thin, slightly translucent, smooth.

Sole and sides of foot brown. Rostrum light brown. Siphon with a dark pink tip, shading lighter proximally, followed by white, brown and white bands (Kohn, 1978a).

Radular teeth stout, with an adapical barb opposite a second barb; serration not longer than second barb; shaft with a cusp and a waist just anterior to the centre; base with a distinct spur (Peile, 1939).

Habitat and Habits: Subtidal, to about 35 m; on mud, sand and rubble.

**Discussion:** C. zeylanicus resembles C. caracteristicus in its shell characters. For comparison, see the Discussion of the latter species.

C. undulatus is usually considered to represent a synonym of C. textile. However, it differs from the latter species in shape and pattern but is similar in colour pattern to certain variants of C. zeylanicus; therefore it is tentatively placed in the synonymy of this species. If this is substantiated, C. undulatus will be an unused senior synonym, and the name C. zeylanicus must be retained.

#### 45

# Conus caracteristicus FISCHER VON WALDHEIM, 1807

(Plate 11, Figures 24-26; Map 20)

- 1807 Conus caracteristicus Fischer von Waldheim, Mus. Démidoff, 3: 139, no. 113-116
- 1810 Conus muscosus Lamarck, Ann. Mus. Hist. Nat. Paris, 15: 281, no. 105
- 1817 Conus characteristicus Dillwyn, Descr. Catal. Rec. Shells, 1: 367, no. 26
- 1874 Conus masoni Nevill & Nevill, J. Asiatic Soc. Bengal, 43 (2): 22, pl. 1
- 1877 Conus brevis E.A. Smith, Ann. Mag. Nat. Hist., 19: 222-223 (non C. brevis J. de C. Sowerby, 1840, a fossil)

**Types:** *C. caracteristicus*: Lectotype (Kohn, 1981) figured in Chemnitz (1795: Pl. 182 fig. 1761) (40 x 27 mm); *C. muscosus*: Holotype in MNHN (44 x 27mm); *C. characteristicus*: Holotype same as lectotype of *C. caracteristicus*; *C. masoni*: Holotype in ZSI (25 x 14.5 mm); *C. brevis*: Holotype in BMNH (18.5 x 11 mm):

**Type Localities:** *C. caracteristicus* "Java Sea" (Coomans et al., 1983); *C. characteristicus*: "the coast of the Island of St. Bartholomew" (Chemnitz, 1795); *C. masoni*: "Andaman Islands."

Range: Bay of Bengal to Philippines and Japan.

Description: Medium-sized to large, solid to heavy. Last whorl conical to broadly conical; outline convex below shoulder, straight toward base. Shoulder angulate to rounded. Spire of low to moderate height; early whorls projecting from an otherwise flat spire. Larval shell multispiral, maximum diameter about 0.7 mm. First 5-6 postnuclear whorls tuberculate. Teleoconch sutural ramps flat, with 2 deep spiral grooves increasing to 3-4 major grooves and several spiral striae. Last whorl with weak or strong, alternating fine and coarse spiral ribs near base.

#### C. caracteristicus Shell Morphometry

L	40 - 88 mm	
RW	0.40 - 1.30 g/mm	
RD	0.65 - 0.76	
PMD	0.85 - 0.92	
RSH	0.04 - 0.18	

Ground colour white. Last whorl with often wavy, brown to reddish brown axial dashes, lines and blotches, with small triangular flecks, and near base with spirally aligned spots. Pattern elements clustered in 3 spiral zones, below shoulder and on both sides of centre; adapical zones accentuated by an underlaying salmon or brown band. Teleoconch sutural ramps crossed by brown blotches. Aperture yellow.

Periostracum yellowish brown, thin, translucent.

Sole of foot white mottled with tan. Rostrum yellowish buff. Siphon with a central black ring separating a white

anterior part from a mottled brown and buff posterior part (Kohn, unpubl. observ.).

Habitat and Habits: Subtidal, to 30 m; on sand.

**Discussion:** *C. caracteristicus* resembles *C. zeylanicus*, which co-occurs in the E. Indian Ocean. However, it differs from the latter in its coarser colour pattern without pink or violet tones, strictly conical last whorl, and more pronounced spiral sculpture of the sutural ramps. The colour patterns of the animals are also different.

# 46 Conus suturatus REEVE, 1844

(Plate 12, Figures 1-8; Map 20)

- 1843 Conus suturatus Reeve, Proc. Zool. Soc. London, 11:178; 1844: Conch. Icon., 1, Conus: Pl. 45 sp. 250
- 1858 Conus turbinatus Sowerby II, Thes. Conch., 3: 25, no. 207, pl. 10 (196) fig. 227
- 1978 Conus suturatus sandwichensis Walls, The Pariah, 2: 3-4, 7, text figs.

**Types:** *C. suturatus*: Original figure 26 x 15 mm; *C. turbinatus*: Holotype in BMNH (42 x 28 mm); *C. s. sandwichensis*: Holotype in DMNH (14.5 x 7 mm, granulose juvenile).

**Type Localities:** C. suturatus: "Port Essington, Australia" (Kohn, 1959 a); C. s. sandwichensis: "Hawaii, Oahu, Pokai Bay."

Range: C. s. suturatus: Papua New Guinea to N. W. Australia and Queensland; C. s. sandwichensis: Hawaii.

**Description:** *C. s. suturatus* (Pl. 12, Figs. 1-6): Moderately small to medium-sized, moderately solid to solid. Last whorl conical, ventricosely conical or broadly conical; outline straight or variably convex adapically. Shoulder subangulate to angulate. Spire low, outline concave to straight.

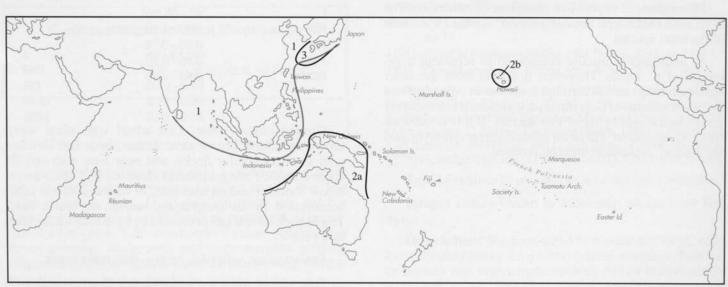
Map 20

Larval shell multispiral, maximum diameter about 0.7 mm. First 5-8 postnuclear whorls tuberculate. Teleoconch sutural ramps with a pronounced subsutural ridge and a distinct ribbon between 2 spiral grooves; in large specimens, last ramp sometimes with 3-4 spiral grooves. Last whorl with variably spaced deep spiral grooves at basal fourth to third; ribs between grading to ribbons adaptically.

C. s. sandwichensis (Pl. 12, Figs. 7, 8) differs in its less solid shell with a strictly conical, narrower and more straight-sided last whorl and a moderately high, stepped spire. Subadults from Hawaii have more pronounced sculpture on the last whorl, with spiral grooves extending to shoulder; intervening ribs usually with minute granules.

	C. suturatus Shell Mo	rpnometry
	C. s. suturatus	C. s. sandwichensis
L	30 - 43 mm	35 - 47 mm
RW	0.20 - 0.44 g/mm	0.17 - 0.34 g/mm
RD	0.62 - 0.73	0.55 - 0.66
PMD	0.80 - 0.90	0.89 - 0.92
RSH	0.03 - 0.12	0.12 - 0.21

C. s. suturatus: Ground colour white, sometimes suffused with pink or violet. Last whorl usually with 3 orange or pink spiral bands, below shoulder and on both sides of centre; adapical band usually pale. Sometimes, additional spiral rows of variously sized, squarish, yellowish brown spots form clusters overlying colour bands; rows vary in number and arrangement and sometimes contain white spots. Base and siphonal fasciole light violet. Larval whorls white. Teleoconch sutural ramps immaculate or with orangish brown radial markings producing separated spots or bars along shoulder edge. Aperture white to violet.



1: C. caracteristicus 2a: C. suturatus suturatus 2b: C. suturatus sandwichensis 3: C. kiicumulus

C. s. sandwichensis matches C. s. suturatus in pattern, except for mostly darker spiral bands on last whorl, a pale orange-brown base, and a usually maculated spire.

Periostracum dark brown, opaque, smooth (Kohn, 1959a; Kohn & Weaver, 1962; Walls, 1978, [1979]).

In *C. s. sandwichensis*, dorsum of foot white mottled with brown, with a narrow darker band close to the posterior end. Rostrum and tentacles buff. Siphon with 3 broad bands of white, black and tan from the tip proximally (Kohn & Weaver, 1962).

**Habitat and Habits:** Rare on exposed intertidal parts of coral reef, more frequent in subtidal habitats in 7-150 m; often on muddy bottoms.

**Discussion:** C. suturatus resembles C. tessulatus, C. eburneus and C. kiicumulus. C. eburneus can be distinguished by its more equally arranged spiral rows of well separated markings, its white base, and its smooth postnuclear whorls. For comparison with C. kiicumulus and C. tessulatus, see the Discussions of those species.

# 47 Conus kiicumulus (AZUMA, 1982)

(Plate 12, Figures 9-12; Map 20)

- 1973 Rhizoconus nebulosus Azuma, Venus, **32** (2): 34, 36, 37, fig. 1 (non *C. nebulosus* Gmelin, 1791, non *C. nebulosus* Hwass, 1792)
- 1982 Rhizoconus kiicumulus Azuma, Venus, 40 (4): 231 (nom. nov. for R. nebulosus Azuma)

Type: Holotype in Azuma coll. (40.5 x 21.5 mm).

Type Locality: "off Nada, Kii."

Range: S. Japan and Ryukyu Is.

Description: Moderately small to medium-sized, moderately solid. Last whorl conical to ventricosely conical; outline slightly to moderately convex below shoulder, straight toward base; left side slightly concave above base. Shoulder subangulate to angulate, smooth to weakly tuberculate. Spire low, outline variably concave. Larval shell of about 2 whorls, maximum diameter 0.8-0.9 mm. First 3-8.5 postnuclear whorls tuberculate, often somewhat stepped. Teleoconch sutural ramps flat, with 0-1 increasing to 4-5 spiral grooves. Last whorl with variably to regularly spaced, punctate or axially striate spiral grooves, weaker on adapical half and separated by ribbons and ribs.

#### C. kiicumulus Shell Morphometry

L	30 - 41 mm
RW	0.10 - 0.19 g/mm (L 23-38 mm)
RD	0.55 - 0.61
PMD	0.80 - 0.92
RSH	0.06 - 0.12

Ground colour white, sometimes tinged with violet. Last whorl with a variably wide, yellowish brown to orange spiral band on each side of centre; adaptical band consistently wider; both bands blend with adjacent ground colour zones. Most shells with axial, partially coalescing, violet or reddish brown clouds on last whorl. In subadults, spiral rows of alternating brown and white dots and bars on surface elevations. Larval shell white. Teleoconch spire immaculate or with brown markings. Aperture white.

Radular teeth relatively narrow, with an adapical barb opposite a blade; serration of 16-18 denticles extends from the posterior tip of the barb nearly to the centre of the shaft; base pronounced, with a distinct spur (Rolán, pers. comm., 1991).

#### Habitat and Habits: In 40-100 m.

**Discussion:** Röckel (1991) noted a striking similarity between specimens of *C. kiicumulus* that lack the axial violet or reddish brown clouds on the last whorl and *C. kashiwajimensis*, as described by Shikama and illustrated by Walls [1979]. However, that species is known only from the holotype, whose whereabouts are unknown. *C. kiicumulus* also resembles *C. suturatus*. Both subspecies of *C. suturatus* can be distinguished by the third spiral colour band below the shoulder, the spiral rows of squarish spots (instead of axial clouds) on the last whorl, and by the more pronounced spiral sculpture on the sutural ramps.

# 48 Conus tessulatus BORN, 1778

(Plate 12, Figures 13-21; Plate 74, Figure 20; Map 21)

- 1778 Conus tessulatus Born, Index Mus. Vindob., 1: 131; 1780: Test. Mus. Vindob.: 151
- 798 Cucullus pavimentum Röding, Mus. Bolten., 2: 41, no. 509/33
- 1910 Conus edaphus Dall, Proc. U.S. Natl. Mus., 38 (1741): 223-224

**Types:** *C. tessulatus*: Lectotype (Kohn, 1964) figured in Martini (1773: Pl. 59 fig. 653) (46 x 29 mm); *C. pavimentum*: Lectotype (Kohn, 1975) same as lectotype of *C. tessulatus*; *C. edaphus*: Holotype in USNM (24.5 x 14 mm).

**Type Localities:** C. tessulatus: "Africa" (Martini, 1773); C. edaphus: "Off Clarion Island."

Range: Entire Indo-Pacific; also in E. Pacific Region.

**Description:** Medium-sized to moderately large, moderately solid to moderately heavy. Last whorl conical to broadly conical, sometimes ventricosely or broadly and ventricosely conical; outline convex at subshoulder area, straight below. Shoulder subangulate to angulate. Spire of low to moderate height, outline concave. Larval shell multispiral, maximum diameter 0.7 mm. Teleoconch sutural ramps with 1 increasing to 2-4 spiral grooves, often 2 major grooves and additional spiral striae. Last whorl with variously spaced, weak or incised, often punctate spiral grooves on abapical third.

# C. tessulatus Shell Morphometry L 30 - 82 mm RW 0.13 - 0.83 g/mm (L 30-67 mm) RD 0.58 - 0.75 PMD 0.78 - 0.92 RSH 0.03 - 0.17

Ground colour white. Last whorl with spiral rows of orange to reddish brown rectangular spots or bars, often alternating with white markings. Dark markings usually cluster or fuse into spiral bands on each side of centre. Base light violet. Larval whorls grey to light orange. Teleoconch sutural ramps with radial markings matching bars on last whorl in size and colour. Aperture white, often suffused with violet or pink.

Periostracum orange or olive brown, thin, variably translucent, and velvety with very fine interlaced axial ridges; in subadults, periostracum very thin and almost colourless but moderately thick and fibrous in large adults.

Foot white to brown; dorsum variably mottled with light brown, with black or brown dots and spots on anterior part forming a triangular pattern, sometimes with a brown premarginal line and a yellow anterior edge; sole often streaked or reticulated with brown. Rostrum uniformly cream or orange ventrally and tan dorsally, with a cream to orange anterior edge. Tentacles white, with scattered black spots, tips sometimes yellow. Siphon white, grading to cream posteriorly, sometimes also mottled with brown, with a broad, sometimes interrupted black ring on anterior part;

distal edge white or yellow (Garrett, 1878; Chaberman, pers. comm., 1981; Pearson, unpubl. observ.; Kohn, unpubl. observ.; Fainzilber et al., 1992).

Radular teeth stout, with an adaptical barb opposite a blade; serration and basal spur present (Peile, 1939).

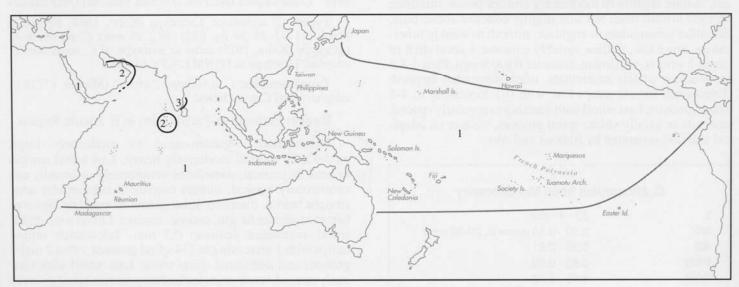
Habitat and Habits: Intertidal and subtidal, usually to 40 m; in Philippines, dredged to 240 m; in W. Mexico reported from 15-72 m. On coral reefs and in bays in fine to coarse sand substrate with or without vegetation, muddy sand, and gravel on sheltered flats (Thorson, 1940; Kohn, 1959a, 1960; Hanna, 1963; Cernohorsky, 1964; Keen, 1968; Estival, 1981; Kilburn & Rippey, 1982; Sharabati, 1984; Tirard, pers. comm., 1989; Grosch, pers. comm., 1989; Fainzilber et al., 1992).

*C. tessulatus* feeds on polychaetes. Its venom hardly affects molluscs and small fishes (Endean & Rudkin, 1965; Reichelt & Kohn, 1985).

In the Persian Gulf, spawn found attached to rocks, empty bivalve shells and polychaete tubes; capsules of 25-26 x 18-21 mm, arranged in parallel rows, each containing 200-300 eggs. Egg diameter of 250 µm predicts a minimum pelagic period of about 19 days (Thorson, 1940; Perron & Kohn, 1985).

**Discussion:** *C. tessulatus* resembles *C. suturatus* and *C. eburneus*. *C. suturatus* differs in having the first 5-8 postnuclear whorls tuberculate, and in its hardly tessellated colour pattern with 3 background bands. *C. eburneus* differs in its smaller, dark brown spots and yellowish orange to tan background bands on the last whorl, and its white base. The colour patterns of the animals are also different.





1: C. tessulatus 2: C. melvilli 3: C. tuticorinensis

#### 49

#### Conus melvilli SOWERBY III, 1879

(Plate 12, Figures 22-26; Map 21)

- 1834 Conus pusio Sowerby I, Conch. Ill.: Pt. 55, fig. 69 (non C. pusio Hwass, 1792)
- 1879 Conus melvilli Sowerby III, Proc. Zool. Soc. London, 1878: 795-796, pl. 48, fig. 1
- 1972 Conus (Chelyconus) boschi Clover, Venus, 31: 117-118, text figs. 1-5.

**Types:** *C. pusio*: Holotype in NMWC (18.5 x 12 mm); *C. melvilli*: Holotype same as holotype of *C. pusio*; *C. boschi*: Holotype in NSMT (28 x 15.5 mm).

Type Localities: C. melvilli: "Key West"; C. boschi: "Museera Is. to Muscat Oman in South East Arabia."

Range: Oman to Persian Gulf; probably also in Maldives.

Description: Small to moderately small, moderately light to moderately solid. Last whorl conical to broadly or ventricosely conical, outline convex. Shoulder angulate to rounded. Spire of low to moderate height, outline straight to slightly convex or sigmoid. Larval shell of 2-2.25 whorls, maximum diameter 1.3-1.7 mm (shells from Oman) to 2.1 mm (a shell from Persian Gulf). Teleoconch sutural ramps nearly flat, with closely spaced radial threads and obsolete spiral striae only on latest ramps; sutures usually depressed and moderately wide. Last whorl sculpture grades from a few spiral ribbons at base to variably spaced spiral ribs on basal half.

### C. melvilli Shell Morphometry

20 - 32 mm
0.09 - 0.17 g/mm (L 20-30 mm)
0.66 - 0.75
0.75 - 0.88
0.10 - 0.19

Ground colour white to bluish grey. Last whorl with a red-brown "brick wall" pattern of about 16-26 fine spiral lines and irregular, numerous to very sparse axial dashes. Shells with a spiral row of variously sized dark greyish blue or brown flecks just above centre and often within basal third (described as *C. boschi*) intergrade with shells with large axial blotches across entire last whorl except for subshoulder area (represented by the holotype of *C. melvilli*) (Pl. 12, Fig. 22). Larval whorls white. Teleoconch sutural ramps with dark brown radial streaks or lines; lines often overlying broad reddish brown spots. Aperture dark violet.

Periostracum brownish grey, thin, translucent, smooth.

Radular teeth with a small adaptical barb and distinct basal spur; serration absent (Clover, 1972, as C. boschi).

Habitat and Habits: Shallow water; on sand at protected sites (Bosch & Bosch, 1982).

**Discussion:** C. melvilli is very similar and closely related to C. tuticorinensis; for comparison, see the Discussion of the latter species.

In Oman, shells similar in shape to the holotype of *C. melvilli* and intergrading in colour pattern with specimens described as *C. boschi* strongly suggest the two to be conspecific (Moolenbeek, pers. comm., 1992). A shell from the Persian Gulf corresponding with the specimens from Oman in all conchological characters except for a wider larval shell (ca. 2.1 vs. 1.3-1.7 mm) is provisionally assigned to *C. melvilli*.

#### 50

# Conus tuticorinensis RÖCKEL & KORN, 1990

(Plate 12, Figures 27-29; Map 21)

1990 Conus tuticorinensis Röckel & Korn, Arch. Moll., 119 (4/6): 277-291, pl. 1 fig. 1, pl. 2 fig. 2

Type: Holotype in SMF (26 x 16.5 mm).

Type Locality: "bei Tuticorin, S. E. Indien."

Range: S. E. India.

**Description:** Small to moderately small, moderately solid. Last whorl broadly or broadly and ventricosely conical; outline convex adapically, less so toward base. Shoulder angulate. Spire low, outline straight to slightly concave. Larval shell of 1.5-1.75 whorls, maximum diameter 1.3-1.7 mm. Teleoconch sutural ramps flat, with 1 increasing to 3 distinct major spiral grooves and additional minor grooves; sutures narrow and deep. Last whorl with flat spiral ribbons from base to shoulder.

#### C. tuticorinensis Shell Morphometry

L	23 - 30 mm
RW	0.12 - 0.18 g/mm
RD	0.73 - 0.76
PMD	0.82 - 0.92
RSH	0.09 - 0.12

Ground colour white, suffused with pale violet on last whorl. Last whorl with an orange-brown "brick-wall" pattern of about 12 spiral lines and irregular axial lines; similarly coloured irregular flecks spirally aligned below shoulder and on each side of centre. Larval whorls white. Teleoconch sutural ramps with orange-brown radial markings. Aperture reddish violet.

Habitat and Habits: Reported from about 50 m.

**Discussion:** C. tuticorinensis is closely related to C. melvilli. The latter species differs in its wider sutures and the absence of spiral grooves from its sutural ramps. In

addition, *C. melvilli* has a dark violet aperture, a less angulate shoulder, and tends to have a narrower last whorl.

# 51 Conus suratensis HWASS in BRUGUIÈRE, 1792

(Plate 13, Figures 1-3; Map 22)

1792 Conus suratensis Hwass in Bruguière, Encycl. Méth., 1: 669-670, no. 63

**Type:** Lectotype (Mermod, 1947, as "holotype") in MHNG (51.5 x 31.5 mm).

Type Locality: "mers des grandes Indes."

Range: India and Sri Lanka to Philippines, Papua New Guinea, Solomon Is., and Queensland; probably Madagascar.

**Description:** Large and heavy. Last whorl usually ventricosely conical, outline convex at adapical third, straight below. Shoulder subangulate to rounded. Spire low, outline variably concave. Larval shell multispiral, maximum diameter 0.8-0.9 mm. Teleoconch sutural ramps flat to slightly concave, with a few spiral grooves grading to spiral striae in late whorls. Last whorl with distinct or weak spiral grooves on basal third, separating ribbons of varying width.

# C. suratensis Shell Morphometry L 80 - 161 mm RW 1.00 - 3.00 g/mm (L 80-128 mm) RD 0.59 - 0.69 PMD 0.78 - 0.86 RSH 0.02 - 0.06

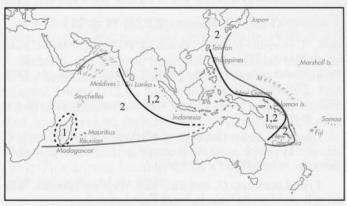
Ground colour cream to tan, variably suffused with orange-brown. Last whorl with spiral rows of brown dots, spots, dashes or narrow bars mostly also aligned in axial rows. Dark markings sometimes alternate with white dashes. Occasionally, narrow orange-brown bands encircle last whorl at various sites. Base, siphonal fasciole and basal part of columella pale orange, often immaculate. Late sutural ramps radially or irregularly maculated with dark brown streaks and a few blotches. Aperture orange or pale brown in subadults, white in adults.

Habitat and Habits: Usually shallow subtidal.

In Philippines, egg diameter of about 207  $\mu$ m predicts a minimum pelagic period of about 23 days (Perron & Kohn, 1985).

**Discussion:** *C. suratensis* may only be confused with *C. betulinus*; for comparison, see the Discussion of the latter species.

Map 22



1: C. suratensis 2: C. betulinus

# 52 Conus betulinus LINNÉ, 1758

(Plate 13, Figures 4-11; Map 22)

- 1758 Conus betulinus Linné, Syst. Nat., 10 ed., 1: 715, no. 266
- 1798 Cucullus medusae Röding, Mus. Bolten., 2: 43, no. 546/48
- 1906 Conus betulinus var. immaculata Dautzenberg, J. Conchyl. (Paris), 54: 27
- 1937 Conus betulinus var. alternans Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 48
- 1937 Conus betulinus var. tabulata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 48-49
- 1937 Conus betulinus var. plurizonata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 49
- 1937 Conus betulinus var. scripta Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 49 (non C. scriptus Sowerby II, 1858)
- 1937 Conus betulinus var. paucimaculata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 50
- 1979 Conus zulu Petuch, Nemouria, 23: 19-20, figs. 28-31

**Types:** *C. betulinus*: Lectotype (Kohn, 1963) in LSL (101 x 67 mm); *C. medusae*: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 142 fig. 1321) (73 x 43 mm); *C. b.* var. *alternans*: Lectotype (Coomans et al., 1980) figured in Tableau (1798: Pl. 334 fig. 8) (126 x 75 mm); *C. zulu*: Holotype in DMNH (62 x 35 mm).

**Type Localities:** *C. betulinus*: "island of Java, Indonesia" (Coomans et al., 1982); *C. b.* var. *immaculata*: "Ambodifoutra (Côte est de Sainte Marie de Madagascar)"; *C. zulu*: "off the mouth of the Umfolozi River, Zululand Coast, Natal, South Africa."

Range: Indian Ocean to Ryukyu Is., New Caledonia, Solomon Is., and Queensland; absent from Red Sea.

**Description:** Moderately large to large, solid to heavy. Last whorl ventricosely conical to broadly and ventricosely conical, less frequently conical, broadly conical or approaching pyriform; outline usually straight at abapical two-thirds and convex to strongly convex above, sometimes slightly concave near base. Shoulder subangulate to rounded. Spire of low to moderate height, outline variably concave. Maximum diameter of larval shell 0.8-0.9 mm. Teleoconch sutural ramps flat to slightly convex, with

numerous spiral striae. Basal third of last whorl with variably broad spiral ribs.

C. L	petulinus Shell Morphometry
L	55 - 177 mm
RW	0.50 - 4.60 g/mm (L 55-165 mm)
RD	0.63 - 0.81
PMD	0.77 - 0.87
RSH	0.03 - 0.14

Ground colour yellowish tan to orangish brown, less often cream white mottled with yellow or orange; occasionally, ground overlaid with grey. Last whorl generally with spiral rows of brown markings, varying from a great number of closely set rows to absence of rows. Markings vary from narrow spiral dashes to bars and from dots to round or squarish spots and axial flecks. Dark markings alternate regularly with white markings that are often absent from adapical two-thirds. Basal part of last whorl may be of darker colour. Larval whorls white. Early teleoconch sutural ramps immaculate; late ramps variously maculated with dark brown spots or radial streaks and blotches. Aperture white, sometimes pale yellow or violet; smaller shells often suffused with violet-brown deep within.

Periostracum brown, thin to thick, translucent to almost opaque, with fine to strong and interlaced axial ridges.

Foot yellowish tan, axially streaked with violet. Rostrum violet. Siphon pale yellow at base, blackish brown distally (Quoy & Gaimard, 1835).

Radular teeth with an adapical barb opposite a large weakly pointed second barb; serration consists of a double row of strong denticles, extends as far as the second barb or halfway down the shaft and ends in a cusp; shaft with a slight constriction at centre, base with a pronounced spur (Bergh, 1895; Peile, 1939; Kohn, unpubl. observ.).

Habitat and Habits: Intertidal to about 50 m; in sheltered bays and on reefs, in sand pockets, sand flats and muddy sand. Typical form mostly above 20 m; form *zulu* reported from 30-50 m (Petuch, 1979).

C. betulinus probably feeds on worms (Kohn, 1978a).

**Discussion:** C. betulinus is similar to C. suratensis, C. figulinus, C. loroisii, and C. glaucus. C. suratensis is often difficult to distinguish from C. betulinus. It does not attain as large size as the latter species, generally has a narrower last whorl (RD 0.59-0.69) as well as a lower spire (RSH 0.02-0.06); the spiral sculpture of its last whorl consists of ribbons, and its pattern has more but smaller brown markings that are also axially aligned. For comparison with C. figulinus, C. loroisii, and C. glaucus, see the Discussions of those species.

We assign specimens from the E. African coast between Natal and Mozambique described as *C. zulu* (Pl. 13, Figs. 9-11) to *C. betulinus*, although they may represent hybrids between *C. betulinus* and *C. figulinus*. At these localities

and Madagascar and India, C. figulinus (L 45-90 mm), typical C. betulinus (L 75-175 mm) and moderately large adults (L 55-80 mm) appearing intermediate in shape and colour pattern co-occur in the same habitat. Should the latter shells be assigned to C. betulinus or be regarded as hybrids? Their last whorl, which may be slightly pyriform, often has a mixed grey, greenish and brownish ground colour with a contrasting shoulder band and variably fine dashed and dotted spiral lines; their spire may be relatively higher (0.05-0.14 vs. 0.03-0.10 in more typical C. betulinus). The morphometry of their last whorl (RD 0.66-0.78; PMD 0.82-0.86), the pronounced intermittent white dashes of their abapical spiral rows and the axial blotches of their sutural ramps suggest that they are assignable to C. betulinus rather than representing true intermediates with C. figulinus (RD 0.52-0.74; PMD 0.74-0.84). The shells from Natal and Mozambique described as C. zulu differ from the shells from Madagascar in a less conical last whorl, a mostly steeper shoulder ramp and a consistently fine pattern. Although these characters make C. zulu slightly more similar to C. figulinus, we provisionally regard all the questionable Indian Ocean shells as forms of C. betulinus. However, the possibility of hybridization between C. betulinus and C. figulinus cannot be excluded.

The variants described by Dautzenberg all refer to colour pattern forms:

- 1. form *alternans* has alternating rows of large and small markings, a fairly common pattern;
- form tabulata has spiral rows of regularly alternating dark and light markings;
- 3. form *plurizonata* has spiral rows with large spiral bars;
- 4. form *scripta* has spiral rows of axial blotches on a white ground;
- 5. form *paucimaculata* has sparse dark blotches on a white ground;
- form immaculata lacks dark markings on the last whorl.

# 53 Conus figulinus LINNÉ, 1758

(Plate 13, Figures 12-16; Map 23)

- 1758 Conus figulinus Linné, Syst. Nat., 10 ed., 1: 715, no. 267
- 1798 Cucullus buxeus Röding, Mus. Bolten., 2: 42, no. 530/49
- 1933 *Conus figulinus violascens* Barros e Cunha, Mem. Estud. Mus. Zool. Univ. Coimbra, (1) **71**: 37-38

**Types:** *C. figulinus*: Lectotype (Kohn, 1963) in LSL (65 x 42 mm); *C. buxeus*: Lectotype (Kohn, 1975) figured in Martini (1773: Pl. 59 fig. 656) (57 x 37 mm); *C. f. violascens*: 2 syntypes in MZUC (L 48 and 42 mm).

Type Localities: C. buxeus: "Amboina" (Martini, 1773).

Range: Indian Ocean: Natal to India and Indonesia, absent from Red Sea; Pacific: Japan to Philippines and Queensland to Fiji.

Description: Medium-sized to large, solid to heavy. Last whorl ventricosely conical to broadly and ventricosely conical or slightly pyriform; outline convex adapically, straight or slightly concave toward base; left side consistently sigmoid. Shoulder rounded. Spire usually low, outline variably sigmoid or concave. Maximum diameter of larval shell about 0.8 mm. Teleoconch sutural ramps flat to slightly convex, with many spiral striae. Last whorl with variably pronounced and spaced spiral grooves on basal third, separating ribs and ribbons.

C. 1	figulinus Shell Morphometry
L	45 - 135 mm
RW	0.30 - 1.50 g/mm
RD	0.52 - 0.74
PMD	0.74 - 0.84
RSH	0.05 - 0.13

Ground colour varies from yellowish or orangish cream through reddish to greyish or blackish brown. Last whorl with variably spaced, solid or occasionally dashed or dotted spiral lines of brown or black; lines usually absent from a narrow band below shoulder edge; subshoulder band may contrast in colour from adjacent area of last whorl, ranging from yellow to dark reddish brown. Larval whorls white. Teleoconch sutural ramps orange-brown to blackish brown, darker than last whorl; occasionally with variably broad, irregularly set radial streaks. Aperture white or bluish white.

Periostracum brown, of varying thickness, translucent to opaque, either uniformly rough or with raised spiral ridges.

Operculum ovate. Radular teeth with an adapical barb opposite a blade; serration longer than blade (Peile, 1939).

Habitat and Habits: Intertidal and uppermost subtidal; in semi-sheltered or protected sites, on fine to very fine sand of flats, often among vegetation (Kohn, 1960; Cernohorsky, 1964; Kilburn & Rippey, 1982; Grosch, pers. comm., 1989).

*C.figulinus* probably feeds on polychaetes (Kohn, 1960; Endean & Rudkin, 1965).

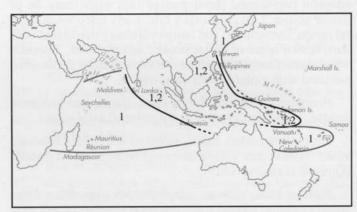
C. figulinus lives on soft substratum without suitable solid objects to affix its egg capsules, and it exhibits a special form of capsule clusters: About the first five capsules are empty and lack an exit window. They are buried in the substrate and serve as an anchor for the later capsules containing eggs. The capsules are attached to each other forming an irregularly branching cluster, becoming more randomly attached during oviposition. The surface of the capsules has a rather regular network of corrugations. Anchoring capsules measure 16-19 x 7-12 mm and vary in shape (19x7 to 17x12 mm). Definitive capsules measure 18-19 x 11-13 mm, each containing 5,700-8,600 eggs (Sri

Lanka); from N. Queensland, larger capsules (25.5-29 x 10-17 mm) have been collected (AMS), with neighbouring capsules exhibiting confluent basal plates. In Sri Lanka, egg diameter is 190-210 µm, predicting a minimum pelagic period of about 23 days (Kohn, 1961b; Perron & Kohn, 1985).

**Discussion:** *C. figulinus* is most closely related to *C. betulinus* and *C. loroisii. C. betulinus* attains larger size and has a broader last whorl; the spiral rows on its last whorl contain intermittent white markings and its sutural ramps bear dark radial blotches. Some specimens of *C. figulinus* from Natal, Mozambique and Madagascar have dashed or dotted lines without the intermittent white markings and with irregular dark streaks on the sutural ramps. For specimens agreeing with the description of *C. zulu*, see the Discussion of *C. betulinus*.

For differences between *C. figulinus* and *C. loroisii*, see the Discussions of the latter species.

Map 23



1: C. figulinus 2: C. loroisii

# 54 Conus loroisii Kiener, 1845

(Plate 13, Figures 17-25; Plate 75, Figure 26; Plate 79, Second row, left; Map 23)

- 1845 Conus loroisii Kiener, Coq. Vivant., 2: Pl. 65 fig. 1; 1847: 91-92
- 1850 Conus (Dendroconus) agrestis "Spgl. mus." Mörch, Cat. Conch. Kierulf: 16, 31, no. 405
- 1937 Conus figulinus var. insignis Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 108, pl. 1 fig. 6 (non C. insignis Sowerby I, 1833)
- 1989 Conus huberorum da Motta, La Conchiglia, 21 (242-245): 9-11, 2 text figs.

**Types:** *C. loroisii*: Original figure 73 x 48 mm; *C. agrestis*: Paratype in ZMUC (Coomans et al., 1979b) (76 x 49.5 mm); *C. f.* var. *insignis*: Figured type in IRSN (75 x 48 mm); *C. huberorum*: Holotype in MHNG (48 x 24.5 mm).

Type Localities: C. loroisii: "la mer de l'Inde"; C. agrestis: "Insulas Nicobaricas"; C. f. var. insignis: "Amboine"; C. hubero-

rum: "off the Coromandel Coast, Bay of Bangal, northward from Madras, India."

Range: India and Sri Lanka to Philippines, Papua New Guinea, and Solomon Is.

Description: Medium-sized to large, solid to heavy. Last whorl usually ventricosely conical to broadly and ventricosely conical; outline convex adapically, straight toward base. Shoulder subangulate to rounded. Spire usually low, sometimes of moderate height; outline variably concave. Maximum diameter of larval shell about 0.7 mm. Teleoconch sutural ramps flat to slightly concave or slightly convex, with closely spaced spiral striae. Basal third of last whorl with variably spaced spiral grooves separating ribs and ribbons.

Form *insignis* (Pl. 13, Figs. 19-22) with a less rounded shoulder and sometimes pyriform subadults.

Form huberorum (Pl. 13, Figs. 23-25) generally smaller and lighter in weight. Last whorl ventricosely conical to distorted conoid-cylindrical with straighter outline. In distorted specimens, aperture wider at base than near shoulder. Spire of low to moderate height, outline slightly sigmoid to concave; in distorted specimens, early postnuclear whorls stepped.

	sii Shell Morphometry
L	50 - 120 mm
- form huberorum	45 - 73 mm
RW	0.40 - 2.10 g/mm (L 50-100 mm)
- form huberorum	0.30 - 0.70 g/mm
RD	
- typical form	0.66 - 0.76
- form insignis	0.62 - 0.76
- form huberorum	0.55 - 0.68
PMD	
- typical form	0.77 - 0.86
- form insignis	0.76 - 0.83
- form huberorum	0.75 - 0.83
RSH	
- typical form	0.03 - 0.09
- form insignis	0.01 - 0.09
- form huberorum	0.07 - 0.19
A STATE OF THE PARTY OF THE PAR	

Ground colour grey mixed with pale blue, brown and sometimes violet. Colours arranged in blending spiral and axial zones. Last whorl with contrasting light narrow spiral bands at shoulder and below centre; shoulder band always present but often very narrow and inconspicuous; subcentral band may be absent. Solid or interrupted reddish to blackish brown lines occur infrequently on last whorl. Base of columella and siphonal fasciole partially or completely brown to violet-brown. Larval whorls white. Early teleoconch sutural ramps brown; late ramps match last whorl in colouration, with obsolete to distinct brown radial streaks. Aperture usually white to bluish white, sometimes orange.

Periostracum brown, fairly thick, opaque, with raised spiral ridges (Kohn, 1978a) or tufted spiral lines (India).

In form *huberorum*, ground colour grades to darker olive-grey with a greater number of more pronounced violet or brownish violet axial zones on last whorl and radial streaks on late sutural ramps. Shoulder band often darker than in typical form, shading from cream to violet grey; subcentral band often weak or absent. Dashed or dotted spiral lines on last whorl as rare as in typical form. Colouration of aperture usually darker than in typical form.

In form *insignis*, last whorl tinged with grey or various shades of brown; colours arranged in blending spiral zones. Shoulder band usually pronounced, shading from white to brown or grey; subcentral band usually present, often somewhat wider than in other forms and similar to shoulder band in colour. Closely spaced and variably fine, blackish brown lines extend from base to shoulder band, usually weak or absent on basal fourth. Reddish brown and blackish brown lines often alternate; occasionally, lines are dashed or dotted. Staining of columella and siphonal fasciole more pronounced than in other forms. Teleoconch sutural ramps brown to blackish brown, either solidly coloured or irregularly streaked with shades of brown.

Periostracum brown, thin, translucent, with widely set spiral rows of tufts (Philippines; Papua New Guinea).

Typical form from India with an ovately triangular operculum. Foot brown, darker on sole. Siphon buff, mottled with grey on proximal part and with broad longitudinal dorsal and lateral bands of black and dark grey on distal part (Kohn, 1978a).

In N. Papua New Guinea (Pl. 75, Fig. 26; Pl. 79, Second row, left), dorsum of foot dark violet, edged with grey and with black dots clustering at posterior end, and along sides of grey area anterior to rostrum; anterior edge with an orange spot at centre. Sole of foot beige, edged with violet. Rostrum grey, progressively darker proximally; tip cream. Tentacles purplish grey. Siphon violet, shaded with grey, darker dorsally and distally; tip mostly black, sometimes white (animals probably representing *C. l.* form *insignis*; Chaberman, pers. comm., 1981).

Radular teeth with an adaptical barb opposite a blade; serration ending anterior to the central waist; base with a spur (Nybakken, 1990).

**Habitat and Habits:** In 5-70 m; reported from sandy bottoms. Typical form in 9-18 m; form *huberorum* in 35-70 m

Specimens from India are known to feed on polychaetes (Kohn, 1978a).

**Discussion:** C. loroisii and C. figulinus are very similar. C. figulinus often has a narrower last whorl (RD 0.52-0.74) and a more rounded shoulder than typical C. loroisii and form insignis. Similarly sized specimens of C. loroisii are relatively heavier than C. figulinus. In addition, typical C. loroisii from India has an ovately triangular operculum, and form insignis has more closely spaced lines around the last whorl. C. loroisii often has a thinner and spirally tufted

periostracum and contrastingly light-coloured bands at the shoulder and below the centre of the last whorl, while *C. figulinus* lacks a subcentral band and its subshoulder band may be either contrastingly lighter or darker than the rest of the last whorl. Typical *C. loroisii* and *C. loroisii* form *huberorum* are separated from *C. figulinus* by their greyish ground colour. Its tendency toward a conoid-cylindrical distortion of the last whorl additionally distinguishes form *huberorum* from *C. figulinus*.

We consider C. huberorum to represent an ecological form of C. loroisii, because they intergrade in shape and colour pattern. Form huberorum is sympatric with the typical form along the Coromandel coast but has a different bathymetric range. Distortion during growth causes the differences in relative diameter and spire height. Dautzenberg's var. insignis and typical C. loroisii are almost identical in shell morphometry and differ only in colour pattern. Specimens with and without closely spaced spiral lines occur sympatrically both in the Bay of Bengal and in Philippines. Specimens with spiral lines on the last whorl intergrade with typical non-lineate C. loroisii in the former region; in the Philippines, the lineate pattern of C. insignis may be reduced. These data strongly suggest that C. insignis is a variant of C. loroisii. Tucker (1984) separates C. loroisii and var. insignis on the subspecies level but intergradation in Philippines and the absence of geographic variation does not support this. For different taxonomic views, see Walls ([1979]: var. insignis and C. loroisii assigned to C. figulinus); Coomans et al. (1979b: C. loroisii assigned to C. figulinus); Tucker (1984: C. figulinus separated from C. buxeus; the latter species with 2 subspecies: C. b. loroisii and C.b. buxeus [=var. insignis]); Richard (1990: C. loroisii as a valid species; var. insignis assigned to C. figulinus; C. huberorum as a valid species).

# 55 Conus glaucus LINNÉ, 1758

(Plate 14, Figures 1-3; Plate 75, Figure 25; Map 24)

1758 Conus glaucus Linné, Syst. Nat., 10 ed., 1: 714, no. 261
 1798 Cucullus fraxineus Röding, Mus. Bolten., 2: 40, no. 506/31

**Types:** *C. glaucus*: Lectotype (Kohn, 1963) figured in Rumphius (1705: Pl. 33 fig. GG) (43 x 29 mm); *C. fraxineus*: Lectotype (Kohn, 1975) figured in Chemnitz (1788: Pl. 138 figs. 1277,1278) (45 x 29 mm).

Type Localities: C. glaucus: "Asia."

Range: Indonesia to Philippines, Papua New Guinea, Solomon Is., and Vanuatu.

**Description:** Medium-sized to moderately large, moderately solid to moderately heavy. Last whorl ventricosely conical to broadly and ventricosely conical, occasionally slightly pyriform; outline convex adapically, less so toward base; left side may be concave near base. Shoulder subangulate to rounded. Spire low, outline almost

straight to concave. Teleoconch sutural ramps slightly convex to slightly concave, with spiral striae. Last whorl with pronounced spiral ribs of varying width at base.

U.	glaucus Shell Morphometry
L	35 - 65 mm
RW	0.25 - 1.10 g/mm (L 35-63 mm)
RD	0.67 - 0.76
PMD	0.72 - 0.84
RSH	0.04 - 0.09

Ground colour bluish grey. Last whorl with spiral rows of fine brown dots and dashes and intermittent, often obsolete white dashes. Base, siphonal fasciole and basal part of columella immaculate, sometimes brown. Early teleoconch sutural ramps brown; late ramps with blackish brown to black radial streaks or blotches, sometimes extending on last whorl, where they are lighter and form axial streaks. Aperture pale brown in subadults, bluish white in adults.

Dorsum of foot grey, anteriorly edged with orange, suffused with brown on its posterior half, and with a white spot beneath the tiny operculum. Sole of foot beige, with dark spots. Rostrum dull orange. Tentacles beige. Siphon brown (Pl. 75, Fig. 25) (Chaberman, pers. comm., 1981).

**Habitat and Habits:** Intertidal and shallow subtidal; mainly on sand.

**Discussion:** *C. glaucus* differs from *C. betulinus* and *C. suratensis* in its smaller size and its distinctive grey rather than yellow or white ground colour. *C. suratensis* can also be separated by its generally narrower last whorl with spiral ribbons instead of ribs at base. Where both species co-occur, *C. betulinus* has a coarser pattern. *C. glaucus* closely resembles some *C. loroisii* from the Indian Ocean in colour pattern. The latter species is larger (L 50-120 mm), its ground colour is brownish grey rather than bluish grey, the radial blotches on its sutural ramps are lighter and confluent rather than separate, and the spiral lines on its last whorl consist of longer, more closely spaced markings.

# 56 Conus quercinus [LIGHTFOOT], 1786

(Plate 14, Figures 4-7; Plate 75, Figure 27; Map 24)

- 1786 Conus quercinus [Lightfoot], Cat. Portland Mus.: 67, no. 1501
- 1791 Conus cingulum Gmelin, Syst. Nat., 13 ed., 1: 3378, no. 72
- 1792 Conus quercinus Hwass in Bruguière, Encycl. Méth., 1: 681-682, no. 71
- 1817 Conus buxeus Link, Beschr. Nat. Samml. Univ. Rostock, 2: 99 (non C. buxeus (Röding, 1798))
- 1858 Conus ponderosus "Beck" Sowerby II, Thes. Conch., **54** (index): Pl. 11 figs. 239, 240 (cited as synonym of *C. quercinus*)

- 1887 Conus akabensis Sowerby III, Thes. Conch., 5: 273 sp. 528; pl. 36 figs. 752, 753
- 1914 Conus egregius Sowerby III, Ann. Mag. Nat. Hist., 14: 475-476, pl. 19 fig. 9
- 1915 Conus quercinus var. albus Shaw, Proc. Malac. Soc. London, 11: 210 (non C. albus Sowerby III, 1887)
- 1942 Conus fulvostriatus Fenaux, Bull. Inst. Océan. (Monaco), 814: 2 fig. 4
- 1966 Cleobula albonerosa Garrard, J. Malac. Soc. Australia, 10: 11-12, pl. 1 fig. 1

Types: *C. quercinus* [Lightfoot]: Lectotype (Kohn, 1964) figured in Martini (1773: Pl. 59 fig. 657) (54 x 38 mm); *C. cingulum*: Holotype figured in Martyn (1784-1792: Pl. 39) (85 x 52 mm); *C. quercinus* Hwass: Lectotype (Kohn, 1968) in MHNG (82.5 x 55 mm); *C. buxeus*: Holotype figured in Martini (1773: Pl. 59 fig. 657) (72 x 50 mm); *C. akabensis*: Holotype in BMNH (44 x 23 mm); *C. egregius*: Holotype in BMNH (3.5 x 2 mm); *C. q.* var. *albus*: Holotype in BMNH (58 x 34 mm); *C. fulvostriatus*: Original figure 71 x 39 mm; *C. albonerosa*: Holotype in AMS (110 x 62 mm).

Type Localities: C. cingulum: "Insulas amicas"; C. quercinus Hwass: "des Indes orientales"; C. akabensis: "Akaba (Red Sea)"; C. egregius: "New Caledonia"; C. q. var. albus: "Aden"; C. fulvostriatus: "I. Bourbon"; C. albonerosa: "off Wide Bay, southern Queensland."

Range: Entire Indo-Pacific.

**Description:** Moderately large to large, moderately heavy to heavy. Last whorl conical to broadly conical, sometimes ventricosely conical to broadly and ventricosely conical; outline convex adapically, straight below. Shoulder angulate to rounded. Spire of low to moderate height, outline concave. Larval shell of about 4.5 whorls, maximum diameter about 0.8 mm. Teleoconch sutural ramps flat, with 2 increasing to 7-12 spiral grooves; spiral sculpture obsolete in some specimens. Last whorl with variably spaced spiral ribs on basal third.

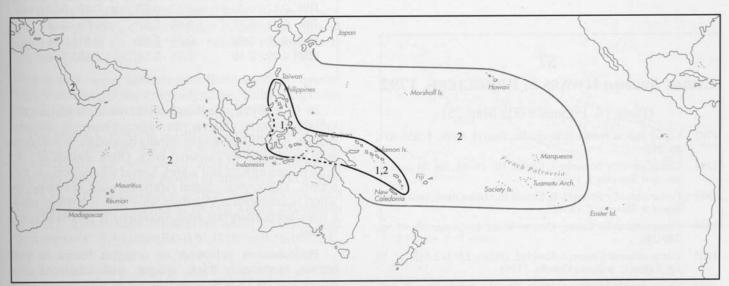
Ground colour varies from white (in forms akabensis and albus) to various shades of yellowish brown in most shells. Last whorl usually with pale to pronounced, fine brown spiral lines, either numerous and closely set or sparse and more widely spaced; lines often obsolete in large specimens, sometimes absent from all post-larval stages. Larval and adjacent postnuclear spire whorls brown. Aperture white.

C. q	uercinus Shell Morphometry
L	60 - 140 mm
RW	0.70 - 2.00 g/mm (L 60-107 mm)
RD	0.62 - 0.76
PMD	0.82 - 0.91
RSH	0.06 - 0.15

Periostracum dark brown or greenish brown, thick, opaque, with interlaced axial ridges; light brown, thin, translucent and smooth in juvenile specimens.

Dorsum of foot almost white anteriorly, grading to yellowish or brownish grey posteriorly, broadly edged with darker grey; median zone bordered by a narrow black band and transversely shaded with dark grey, with transverse rows of black longitudinal dashes on anterior two-thirds and with scattered black dashes, white dots and a light brown pre-opercular spot on posterior third. Sole of foot yellowish grey, mottled with brown. Rostrum and tentacles cream, dotted with black. Siphon white to brownish grey, mottled and ringed with dark grey and black (Pl. 75, Fig. 27); tip dark red in some specimens (Kohn, 1959a; Chaberman, pers. comm., 1981).

Map 24



1: C. glaucus 2: C. quercinus

Habitat and Habits: Subtidal, to more than 70 m, rarely and probably only seasonally entering the lower intertidal zone. A sand-dweller throughout its entire range, in bays on vast flats of sand, often among vegetation but avoiding habitats with rocks and coral or limestone outcrops. A highly gregarious species, active both night and day, tolerates muddy, somewhat brackish waters (Kohn, 1959a, b, 1963b; Cernohorsky, 1964, 1978; Bosch & Bosch, 1982; Grosch, pers. comm., 1989; Tirard, pers. comm., 1989; Fainzilber et al., 1992).

*C. quercinus* preys on enteropneusts and polychaetes in Hawaii (Kohn, 1959b).

In Hawaii, animals migrate to shallower water during the spawning season, ovipositing on sand banks in 0.6-2 m. Egg capsules arranged in rows and affixed to algae and sponges by confluent basal plates. Capsules 17-26 x 17-22 mm contain about 10,000 eggs 185-200  $\mu$ m in diameter in Hawaii and about 180  $\mu$ m in the Philippines, suggesting a minimum pelagic period of 25 (estimated) to 30 (observed in Hawaii) days (Perron, 1981a, b, c; Perron & Kohn, 1985; Kohn, 1959b, 1961a).

**Discussion:** *C. quercinus* resembles *C. fergusoni* from the Panamic Province. *C. fergusoni* has a white shell, with two broad, orange spiral bands in smaller specimens, tuberculate early teleoconch whorls, weaker spiral sculpture on its sutural ramps, and a red animal.

Based on the absence of spiral grooves on its sutural ramps and its golden brown periostracum, Coomans et al. (1979b) regard *C. albonerosa* as a separate species. However, *C. quercinus* shells may have obsolete spiral sculpture on the sutural ramps (India), a golden brown periostracum (Indian Ocean) and an immaculate white colouration (forms *akabensis* and *albus*). These observations suggest the synonymy of *C. albonerosa* and *C. quercinus*.

C. cingulum, C. quercinus Hwass, C. buxeus Link, C. ponderusus, and C. fulvostriatus are synonyms; C. egregius is a juvenile of C. quercinus (Moolenbeek, 1992).

#### 57

# Conus hyaena HWASS in BRUGUIÈRE, 1792

(Plate 14, Figures 8-21; Map 25)

- 1792 Conus hyaena Hwass in Bruguière, Encycl. Méth., 1: 656-657, no. 55
- 1834 Conus unicolor Sowerby I, Conch. Ill.: Pt. 54, fig. 59 (non C. unicolor Sowerby I, 1833)
- 1841 Conus concolor Sowerby II, Conch. Ill.: Index (nom. nov. for C. unicolor Sowerby I, 1834)
- 1844 Conus mutabilis Reeve, Conch. Icon., 1, Conus: Pl. 45 sp. 249-250
- 1865 Conus tribunus Crosse, J. Conchyl. (Paris), 13: 312-313, pl. 10 fig. 2 (non C. tribunus Gmelin, 1791)
- 1882 Conus kobelti Löbbecke, Jahrb. deutsche malak. Ges., 9: 189-190, pl. 4 figs. 4, 5

1983 Conus halli da Motta, Publ. Ocas. Soc. Portuguesa Malac., 2: 3-7, 8 figs.

Types: C. hyaena: Lectotype (Kohn, 1968) in MHNG (61 x 33.5 mm); C. unicolor: Lectotype (Kohn, 1992) in BMNH (46 x 23.5 mm); C. mutabilis: Syntype in BMNH (34 x 20 mm); C. tribunus: Holotype in BMNH (29 x 16.5 mm); C. kobelti: Holotype in LMD (42 x 23 mm); C. halli: Holotype in MHNG (53 x 28 mm).

**Type Localities:** *C. hyaena*: "la côte ouest de l'Afrique"; *C. concolor*: "Solomon Islands" (Röckel & Korn, 1992 as *C. h. concolor*); *C. tribunus*: "California"; *C. halli*: "Pasir Putih, about 180 kilometers east of Surabaya, Java, Indonesia."

**Range:** *C. h. hyaena*: India and Sri Lanka to Indonesia, and South China Sea to Hong Kong; *C. h. concolor*: Solomon Is. and Papua New Guinea; possibly also Lombok, Indonesia.

**Description:** Medium-sized to moderately large, moderately solid to solid. Last whorl conical to ventricosely conical, sometimes approaching pyriform; outline variably convex adapically, less so or straight below; left side concave near base. Shoulder angulate to rounded. Spire of low to moderate height, outline straight to slightly concave or sigmoid. Larval shell multispiral, maximum diameter about 0.8 mm. Early postnuclear whorls weakly tuberculate. Teleoconch sutural ramps flat to convex, with 2 increasing to 6-8 (occasionally to 10-11) spiral grooves, often obsolete on latest ramps. Last whorl with variably distinct wrinkled spiral ribs at base.

C. h. concolor (Pl. 14, Figs. 19-21) differs from C. h. hyaena (Pl. 14, Figs. 8-18) in an usually straighter outline of the last whorl, a consistently angulate shoulder and a consistently low spire.

# C. hyaena Shell Morphometry

	C. h. hya	ena	C. h. concolor
	India	Indonesia	
L	40 - 73 mm	39 - 50 mm	40 - 57 mm
RW	0.17 - 0.53 g/mm	0.15 - 0.26 g/mm	0.15 - 0.35 g/mm
RD	0.61 - 0.71	0.55 - 0.67	0.56 - 0.62
PMD	0.78 - 0.86	0.79 - 0.88	0.81 - 0.89
RSH	0.09 - 0.18	0.11 - 0.14	0.06 - 0.12

In *C. h. hyaena*, ground colour white to bluish grey, variably overlaid with various shades of brown or yellowish orange. Axially streaked or spirally banded shells intergrade with nearly solidly coloured ones. Often, dashed or solid brown lines around last whorl. Larval whorls beige to pale brown. Teleoconch sutural ramps streaked, matching last whorl in colouration. Aperture white to bluish white behind a translucent marginal zone, occasionally pale violet deep within.

Periostracum yellowish or orangish brown to dark brown, moderately thick, opaque, with interlaced axial ridges and 10-18 widely and almost equally spaced, often tufted spiral ridges on last whorl including shoulder. C. h. concolor brown to dark brown. Occasionally last whorl either maculated with lighter axial streaks or encircled with weak rows of darker dots. Larval whorls beige or pale pink; adjacent teleoconch sutural ramps light brown.

Periostracum brownish grey, thin, translucent, with interlaced axial ridges and 6-10 widely spaced tufted spiral ridges on last whorl.

In N.W. India, sole of foot greyish brown, streaked with darker grey; sides of foot brown, anterior edge buff. Rostrum pale reddish brown, grading to buff posteriorly. Tentacles white with a grey dorsal streak. Siphon tipped with black, grading to grey posteriorly (Kohn, 1978a & unpubl. observ.). Operculum elongately paddle-shaped (length ratio operculum/shell 0.19). Da Motta (1983) described the animal of *C. halli* as similar in colour; the operculum is stoutly paddle-shaped (length ratio operculum/shell 0.15). In N.W. Borneo, animal pale pink to orange, with reddish tones usually more distinct on foot; siphon tipped with light to dark red (Lace, pers. comm., 1989). In *C. h. concolor*, operculum small and ovate (length ratio operculum/shell 0.11).

In N.W. India, Java and Solomon Is., radular tooth length 1-1.5 % of the shell length, with an adapical barb opposite a blade; serration of 22-37 denticles extends backwards almost to the middle of the shaft, terminating in a well-separated cusp; shaft waisted just posterior to the cusp, base with a strong prominent spur. Specimens from Java agreeing with the description of *C. halli* have fewer but stronger denticles than specimens in N. W. India (22-26 vs. 32-37); specimens of *C. h. concolor* are intermediate in number of denticles (27-29).

Habitat and Habits: Intertidal and upper subtidal; *C. h. hyaena* common in intertidal and slightly subtidal habitats, with deeper populations (to 50 m) known only from S. India; *C. h. concolor* in 3-30 m. *C. h. hyaena* inhabits fine sand to coarse gravel or rock in intertidal habitats at Bombay (Kohn, 1978a), coral rubble with sparse eel-grass vegetation within a "mangrove and coral shore-line of sandy mud" at Pasir Putih (Java; da Motta, 1983), and rock crevices or silty sand beneath dead coral slabs at N.W. Borneo (Lace, pers. comm., 1989). *C. h. concolor* is found on flats of coarse sand and on mud, often beneath rotting plants (Röckel & Korn, 1992).

In shallow-water habitats near Bombay, *C. h. hyaena* feeds on errant polychaetes mainly of the family Onuphidae but also Eunicidae and Nereidae (Kohn, 1978a).

**Discussion:** C. biliosus, occurring sympatrically with C. h. hyaena in India and Indonesia, differs from the latter in its tuberculate late teleoconch whorls (often including shoulder), different colour pattern of both shell and animal and in its different ecological attributes. C. biliosus from India has a straighter outline in its last whorl; Indonesian shells of C. biliosus have a broader last whorl than sympatric specimens of C. h. hyaena (RD 0.65-0.76 vs. 0.58-0.67). C.

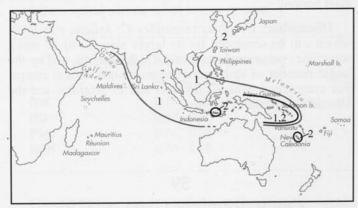
h. concolor resembles the sympatric C. gilvus; for comparison, see the Discussion of the latter species

Indian shells of C. h. hyaena tend to grow larger and have a broader last whorl than those from Indonesia. Some authors (da Motta, 1983; Richard, 1990) separate them as a distinct species (C. mutabilis) from the Indonesian C. hyaena (also described as C. halli). However, neither the type specimens of C. mutabilis, C. hyaena and C. halli nor specimens from the two regions can be clearly distinguished by conchological characters. Shell morphometry and colour pattern overlap considerably between the western and the eastern populations. The animals from Bombay and Java are very similar in colouration and have only minor differences in radular tooth morphology. We therefore consider both populations to represent geographical variants of the same taxon. Shells from Hong Kong cannot be distinguished from the Indian shells (da Motta, 1985 & pers. comm.; Richard, 1990).

The lectotype of C. concolor (RD 0.57; RSH 0.11) agrees closely with shells from Solomon Is. and Papua New Guinea in shape and colouration (Röckel & Korn, 1992). These populations are considered to represent an eastern subspecies of C. hyaena (C. h. concolor). The Indonesian shells of C. h. hyaena overlap in morphometry with C. h. hyaena from India as well as with C. h. concolor. They include specimens with nearly straight last whorl outline and angulate shoulder as well as specimens with convex outline and subangulate shoulder. This gradual change from west to east is evidence against separation of C. h. concolor at the species level. The differences in shape of operculum and radular teeth and the minor differences in shell morphometry favour subspecies status, but more conclusive evaluation of all these populations will require additional analyses of characters and distribution.

Both C. tribunus and C. kobelti are orangish-brown coloured specimens of C. hyaena.

Map 25



1: C. hyaena 2: C. gilvus

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## Conus gilvus REEVE, 1849

(Plate 14, Figures 22-24; Map 25)

1849 Conus gilvus Reeve, Conch Icon., 1, Conus suppl.: Pl. 6 sp. 255

Type: Type in BMNH (25 x 14 mm).

**Type Locality:** "Saldanha Bay, South Africa", corrected in "Solomon Is." (Delsaerdt, 1990).

Range: Papua New Guinea and Solomon Is; probably Indonesia (Flores) and New Caledonia.

**Description:** Moderately small, moderately solid. Last whorl conical, outline nearly straight. Shoulder angulate to subangulate. Spire of low to moderate height, outline straight to slightly convex. Teleoconch sutural ramps flat, with 1-2 increasing to 3-4 spiral grooves; spiral sculpture often weak on last ramps. Last whorl with widely spaced spiral ribs at base.

#### C. gilvus Shell Morphometry

L	24 - 32 mm
RW	0.09 - 0.15 g/mm
RD	0.59 - 0.66
PMD	0.86 - 0.89
RSH	0.10 - 0.14

Last whorl brownish olive or bluish brown, with a bluish grey line at shoulder edge and a bluish grey spiral band at centre; central band usually with spiral rows of brown dots. Dotted brown spiral lines may also be present on basal third. Larval shell brown. Teleoconch sutural ramps irregularly maculated with tannish olive and bluish grey; outer margins bluish grey with irregular brown markings. Aperture bluish white or light violet deeper within; central pale band variably distinct.

**Habitat and Habits:** Intertidal to about 100 m; on dark sand bottom.

**Discussion:** *C. gilvus* resembles *C. hyaena concolor*, which can be separated by its larger size (L 40-57 mm), sometimes narrower last whorl (RD 0.56-0.65), and by the larger number of spiral grooves on its late sutural ramps. For comparison with *C. flavidus* and *C. frigidus*, see the Discussions of those species.

#### 59

# Conus achatinus GMELIN, 1791

(Plate 15, Figures 1-8; Plate 75, Figure 28; Map 26)

1791 Conus achatinus Gmelin, Syst. Nat., 13 ed., 1: 3386, no. 25

- 1792 Conus ranunculus Hwass in Bruguière, Encycl. Méth., 1: 671, no. 65
- 1792 Conus achatinus Hwass in Bruguière, Encycl. Méth., 1: 671-673, no. 66
- 1798 Cucullus ventricosus Röding, Mus. Bolten., 2: 49, no. 623/114 (non C. ventricosus Gmelin, 1791)
- 1937 Conus achatinus var. infumata Dautzenberg, Mém. Mus. Roy. Hist. Nat. Belgique, 2 (18): 12

Types: C. achatinus Gmelin: Lectotype (Kohn, 1966) figured in Chemnitz (1788: Pl. 142 fig. 1317) (74 x 42 mm); C. achatinus Hwass: Lectotype (Kohn, 1968) in MHNG (68.5 x 40.5 mm); C. ranunculus: Holotype (Kohn, 1968) in MHNG (45 x 23 mm); corrected (Kohn, 1992) in: Lectotype (Clench, 1942) figured in Seba (1758: Pl. 43 fig. 36) (49 x 25.5 mm); C. ventricosus: Lectotype (Kohn, 1975) same as lectotype of C. achatinus Gmelin; C. a. var. infumata: Lectotype (Walls, [1979]) figured in Chemnitz (1788: Pl. 142 fig. 1320) (60 x 31 mm).

**Type Localities:** *C. achatinus* Gmelin: "Oceano americano", corrected in "Java" (Coomans et al., 1979a); *C. achatinus* Hwass: "I' Océan asiatique"; *C. ranunculus:* "I' Océan Amériquain"; "Dutch Guiana" (Clench, 1942).

Range: Indian Ocean: Mozambique and Tanzania to W. Australia (absent from Red Sea); W. Pacific: Philippines to Melanesia and N. and N.E. Australia.

**Description:** Medium-sized to moderately large (usually larger in India than in the Pacific), moderately solid to solid (lightest specimens from N. Australia). Last whorl usually ventricosely conical; outline slightly to distinctly convex. Specimens from N. Australia with narrowest last whorls, specimens from Oman broadest. Aperture somewhat wider at base than near shoulder. Shoulder angulate to rounded. Spire of moderate height, outline slightly concave to slightly convex. Larval shell of about 3.5 whorls, maximum diameter 0.7-0.8 mm. About first 5-8 postnuclear whorls tuberculate. Teleoconch sutural ramps flat to slightly concave, with 2 increasing to 4-6 spiral grooves. Last whorl with variably spaced smooth to granulose spiral ribs at base, occasionally to shoulder.

#### C. achatinus Shell Morphometry

L	40 - 82 mm	
RW	0.13 - 0.52 g/mm	
RD		
- N. Australia	0.54 - 0.59	
- Oman	0.62 - 0.69	
- other localities	0.56 - 0.65	
PMD	0.73 - 0.86	
RSH	0.11 - 0.19	

Ground colour white. Last whorl with large axial clouds of olive or orange to blackish brown. Surface pattern emphasized by bordering blue-grey background clouds. In some subadult specimens, ground orange to red; this colouration may persist to the adult stage. Spiral rows of alternating dark and light coloured dots and dashes extend from base to shoulder, on spiral ribs where these occur, producing a pronounced lineate pattern. Some specimens