

Introduction



The Purposes of This Book

The main purpose of this book is to present a systematic revision and to facilitate identification of the extant species of *Conus* in the Southeastern United States and Caribbean region. To accomplish this goal, each species is discussed and described objectively and consistently, including estimating within-species variation, and as clearly as possible differentiating each from its most similar congeners. In biology a picture is worth far more than the proverbial thousand words, and more than 2100 color photographs of shells, on 109 plates, an average of two per species, seek to illustrate the extent of within-species variation and between-species differences. Both the images and the species accounts emphasize the characteristics of the shells of *Conus*, because most users of the book will probably seek to identify these most durable parts of the animals. In some cases, less commonly used characters, such as shell and radular tooth morphometry, are also described quantitatively. More than 100 text-figures illustrate these and other aspects of *Conus* biology, which are generally not remarked on. They include photographs of living animals of about 40% of the species covered and radular teeth of about one-third, as well as predation by and on *Conus*, egg capsules and larval shells, and other organisms associated with their shells.

Similarities and differences in sequences of key genes are analyzed both as taxonomic characters and to evaluate evolutionary or phylogenetic relatedness among species. The rapid advance of molecular genetics during the late 20th and early 21st centuries belies the author's statement just 17 years ago that "the application of additional character sets, e.g. from molecular biological study, awaits the next generation of researchers" (Röckel, Korn, and Kohn 1995, 13). Although other attributes of Western Atlantic *Conus*—for example, specific habitats, feeding biology, reproduction, and geographic distribution—are far less known than for their Indo-West Pacific rela-

tives, available information on these biological features is included.

Fossil shells of *Conus* in the Western Atlantic region extend back at least to the Late Eocene, about 37 million years ago (Hendricks and Portell 2008), but the geologic record of the genus still remains too poorly known to provide useful insights into the evolution of the region's modern *Conus* fauna. For this reason, known fossils of extant species are mentioned, but other aspects of the geologic history of the genus are largely left to future researchers.

Surveying and evaluating the validity of all available described or nominal species proposed for the focal geographic region is a necessary but secondary purpose of the book. Valid nominal species can only be justified by documenting those that are invalid. To accomplish this, separate accounts in Chapter 5 detail each species concluded to be valid, and list and discuss its synonyms and homonyms. The chapter ends with a table summarizing the concluded dispositions of all nominal species known to occur in the region covered by the book.

Why Is *Conus* Important?

In addition to the fact that for centuries its shells have caught and held the attention of diverse enthusiasts—collectors, naturalists, and artists as well as biologists—*Conus* is important for several reasons, as discussed below.

Biodiversity. *Conus* is the largest genus of marine animals, with probably more than 600 species worldwide in tropical and subtropical seas. It is thus a major contributor to biodiversity in the sea. Different marine habitats support different numbers of species, and diversity gradients observed in nature have aided testing hypotheses of the factors that determine why some environments support more co-occurring species than others. Diversity of *Conus* is highest in the tropical Indo-West Pacific region, where more

than 300 species occur. West Africa and its offshore islands constitute the next most diverse region, with 92 species (Monteiro et al. 2004). Remarkable and geologically recent adaptive radiations of *Conus* in the Cape Verde Islands contribute importantly to this diversity (Cunha et al. 2005; Cunha et al. 2008; Duda and Rolán 2005). The Western Atlantic and Caribbean area ranks third in diversity with at least the 53 species treated here. For reasons explained in Chapter 6, additional species are likely to be validated in the future, and others occur beyond the scope of this volume in Brazil. However, if one calculated diversity as the number of species per unit of the region's ocean area, the Western Atlantic and Caribbean *Conus* fauna would probably be more diverse than that of the Indo-West Pacific. The Eastern Pacific tropics are next with 44 species according to a very recent revision (Tenorio et al. 2012), followed by South Africa with about 20 species south of the Indo-West Pacific region (Tenorio and Monteiro 2008). These figures sum to about 525 species worldwide. This is doubtless a conservative estimate, because new species continue to be discovered, including "cryptic species" whose shells are so similar as to be indistinguishable, but their genes show that they do not interbreed. Of all these regions, the Western Atlantic and Caribbean is taxonomically the least known. That fact most strongly dictated the need for this book.

Distribution and abundance. *Conus* is exceedingly widespread, occurring primarily throughout the world's tropical and subtropical oceans. The animals are relatively large (2–10 cm in shell length in the Western Atlantic region, and to 20 cm in the Eastern Atlantic and Indo-West Pacific. In the latter region they are particularly abundant in intertidal and shallow subtidal habitats, and most diverse in depths of one to several meters of water. In the Western Atlantic and Caribbean, however, *Conus* is generally less abundant, less diverse and less conspicuous in intertidal and shallow subtidal environments. The preferred coral reef habitats are usually deeper, and a higher proportion of species is known only from deeper water than in the Indo-West Pacific. In all geographic regions fewer species occur on continental shelves and slopes. None is known from deeper than 1000 m, less than one-third of the world ocean's average depth.

Some species of *Conus* are narrowly restricted geographically, while others are extremely widespread. In the Indo-West Pacific region, some species appear to maintain continuous populations from eastern Polynesia to the Red Sea, across an area comprising one-fourth of the entire world ocean. Many species occupy rather high proportions of this broad expanse,

and a few cross the Eastern Pacific to the Pacific coast of Central America. In the Western Atlantic and Caribbean, a smaller proportion of species occupy the entire region, and many are more narrowly restricted, in some cases to one or a few islands or to narrow stretches of the continental coast.

Ecology. In addition to its importance for general marine biodiversity, *Conus* is notable in that several to many very similar species often co-occur in the same habitat. Up to 36 co-occurring species are known to inhabit single Indo-West Pacific coral reefs. Ecological studies of these assemblages have helped show why tropical reef-associated habitats support such high biodiversity (e.g., Kohn 1959, 2001). The reduced abundance, diversity, and accessibility of *Conus* populations in the Western Atlantic have impeded comparable studies.

Conus snails possess remarkable chemical expertise, and all whose diets are known are predatory carnivores. They inject potent venoms called conotoxins into their prey through a hypodermic needle-like radular tooth in a unique, rapid-strike process. The venom quickly paralyzes the prey—usually a polychaete worm, fish, or another gastropod—that is then swallowed whole. In past studies, primarily in the Indo-West Pacific and to a lesser extent in the Eastern Pacific, this has aided identification of the natural prey, led to the demonstration that different co-occurring species specialize on different food types, and enhanced understanding of coral reef ecology. As yet very few comparable data exist for Western Atlantic species.

Neurobiology and medicine. Practical applications of *Conus* to neurobiology and medicine are increasing rapidly. All *Conus* species that have been examined produce the potent conotoxins mentioned above. Several of these small peptides have been sequenced and synthesized, some are now available commercially, and their genes are also being sequenced. Because most conotoxins block the transmission of nerve impulses, they are now widely used in research on neurobiology. During the 21st century, an average of 180 scientific reports on conotoxins have appeared every year. The use of conotoxin derivatives in medicine is also expanding rapidly. At least three are in current use, and one, a painkiller, has been marketed since its approval by the US Food and Drug Administration in 2004. Several others are in clinical trials, and about 300 patents for medical uses have been awarded.

Evolution. *Conus* is not only the largest marine gastropod genus, but its number of species is increasing

more rapidly than any other whose speciation rates have been studied. Since its origin about 55 million years ago, the fossil record indicates that the number of species has doubled on the average every 6 million years, a diversification rate at least twice that of most tropical marine gastropod genera and families. Although Indo-West Pacific *Conus* are currently better known, new species may well be evolving more rapidly in the Western Atlantic and Caribbean.

Conservation. Science-based knowledge of the most diverse genus of marine animals is essential for the maintenance and sustainable use of biodiversity. The most important practical applications of such information on *Conus* have been in neurobiology and medicine as mentioned above, but its susceptibility to very low concentrations of the endocrine disruptor tributyltin, until recently a common component of anti-fouling paints applied to ships, has been demonstrated in widely separate parts of the world. This indicates its ability to serve as an early warning system for marine pollutants.

Despite this abundant evidence of its importance, knowledge of the *Conus* fauna of the Western Atlantic region remains in a confused state. In fact, Todd et al. (2002, 572) noted when characterizing general molluscan taxonomy and its Neogene geological history in the modern Caribbean area, “taxonomic compendia covering the whole of this time interval or region are lacking” and “the difficulties inherent in accurate taxonomic compilation have, to our knowledge, previously gone unmentioned.” In addition, the first species-level, molecular-based phylogenetic hypotheses proposed for *Conus* (Duda and Palumbi 1999a, 1999b; Monje et al. 1999) appeared little more than a decade ago, and subsequent studies have expanded the coverage to about 40% of the species in the genus (Duda et al. 2001; Espiritu et al. 2001; Duda and Kohn 2005; Kraus et al. 2011; N. Puillandre, P. Bouchet, T. F. Duda, S. Kauferstein, A. J. Kohn, B. M. Olivera, M. Watkins, and C. Meyer, unpublished data¹). The time is thus appropriate for systematic revisions in the light of modern molecular genetic analyses.

Why Is Systematics Important?

Biological systematics is a rather broad term, often defined as the scientific study of diversity or, as Simpson (1961) put it even more broadly: “Systemat-

ics is the scientific study of the kinds and diversity of organisms and any and all relationships among them.” Taxonomy and classification are parts or subdivisions of systematics. Taxonomy is the naming, describing, and distinguishing of species, genera, and higher taxa of organisms. Classification is the hierarchical ordering of biological diversity in those categories. Taxonomy and classification are essential to enable us to understand and communicate about organisms and biodiversity. They also provide the basic data for interpreting the ecological interactions of species (e.g., Kohn 2001) and the hypotheses of phylogenetic, other evolutionary and biogeographic patterns (e.g., Duda and Kohn 2005). The species-level taxonomy of *Conus* is also increasingly important to human health (e.g., Olivera and Teichert 2007). *Conus* venoms are being modified as painkillers and other medicines. Because every species has up to 100 or more active venom components, and those of every species differ, accurate documenting of source species is required. Thus taxonomy is important because it has a “multitude of end users” (Godfray and Knapp 2004). For *Conus*, these include amateurs and naturalists as well as professional biologists across the spectrum from basic physiologists, ecologists, biogeographers, and evolutionists, to more applied conservation biologists, resource managers, and natural product chemists. This book is thus directed to all with a desire to learn about the systematics of sea life.

The Geographic Scope of This Book

The region covered by this book extends from the northern limits of *Conus* in the western North Atlantic Ocean, along the coast of the United States from North Carolina southward, including the offshore islands of Bermuda and encompassing the Gulf of Mexico and Caribbean Sea, eastward to French Guiana. It is almost exactly the area defined by the United Nations as the Western Central Atlantic or Major Fishing Area 31: “It includes the tropical and subtropical waters of the western Atlantic and is bordered by 35° north latitude corresponding to Cape Hatteras in North America, 40° west longitude, 5° north latitude corresponding to the coast of French Guiana of South America, and in the west by the corresponding coastline of South, Central, and North America” (Carpenter 2002, iv; www.fao.org/fishery/area/Area31/en).

I define the southeastern United States as the Atlantic coastal region from North Carolina to southern Florida, as well as the Gulf of Mexico coastal region from southern Florida to the Texas-Mexico

¹ At the time of writing, a manuscript on species-level molecular phylogeny of *Conus* by these authors was being prepared for publication. Hereafter it is referred to in the text as “Puillandre, et al. unpublished data.”

boundary. The Gulf of Mexico continues southward to the Yucatan Peninsula. A recent compendium also considers the north coast of western Cuba as part of the Gulf of Mexico (Felder and Camp 2009). The Caribbean region is defined as the “Caribbean Sea and all of its contents, plus the facing continental margins of North, South, and Central America” (Iturralde-Vinent and MacPhee 1999, 6). Although the Bahamas are geographically and geologically separate, I include them in the Caribbean region because their marine biota is closely related. The Caribbean region’s boundaries vary with different authors; Petuch (1987) defines it much more broadly (see Chapter 2 of this book). Subdivisions of the region also vary markedly among authors. I use a rather conservative system based on that of the Atlantic and Gulf Rapid Reef Assessment Program (Kramer 2003). It reflects the region’s tectonic history, so it is presented in Chapter 2 following a brief account of historical geology.

I exclude consideration of the *Conus* fauna of Brazil for two main reasons. First, Brazil’s marine as well as its terrestrial biodiversity is very high, and numerous species that occur there appear morphologically within the range of variation of more northerly species. Some workers have treated these as conspecifics while others have considered them distinct. However, character analyses remain very limited and molecular genetic data in particular are even sparser. A study of Brazilian reef corals that combined morphological and molecular data (Nunes et al. 2008) showed that some species considered congeneric with northern forms on morphological grounds more likely evolved from southern members of a quite different genus in striking cases of convergent evolution. Their results provide a cautionary lesson for revisionary systematics of other Brazilian marine taxa. A second reason for excluding Brazil from this treatment is its “good connections with systematics institutions in richer countries and a strong program of its own” (Hine 2008); better positioned Brazilian biologists are beginning to investigate the challenging problems presented by its complex, distinctive, and understudied *Conus* fauna (e.g., Gomes 2004, 2009, 2011; Gomes et al. 2007).

The Format of This Book

This book’s format generally follows that of an antecedent work on the Indo-West Pacific species of *Conus* (Röckel, Korn, and Kohn 1995).

Chapter 1, “Setting the Stage: Approaches,” outlines the general principles and methods followed to resolve problems of determining both the species to

which a specimen belongs and the classification of species of *Conus*. It introduces the newer methodology that has become available since the 1995 book was published and that has been incorporated in this one. Chapter 1 also explains and defends retaining all Western Atlantic species in *Conus* in this book, although some authors have subdivided the original genus into various numbers of other genera.

Chapter 2, “Setting the Stage: The Geological Theater and the Evolutionary Play,” briefly describes the complex geologic history of the focal geographic area and the evolutionary and biogeographic history of *Conus* worldwide and particularly in the Southeastern United States and Caribbean region. It ends with a brief history of the study of *Conus* in the Western Atlantic.

Chapter 3, “How to Use This Book,” discusses how *Conus* species are identified and classified, the salient features that each species account addresses, how each account is organized, and the rationale for the order of accounts that comprise Chapter 5.

Chapter 4, “Behind the Scenes: Technical Aids to the Species Accounts,” gives more details of the topics presented in Chapter 3. It includes glossaries of specialized terms used in shell and radular tooth descriptions and statistical analyses, and brief primers to aid in understanding the statistical methods and molecular genetic analyses.

Chapter 5, “Systematic Section: Species Accounts,” is the heart and most of the bulk of the book. It follows the principles discussed in the earlier chapters to present the results of the study that assesses the validity of the described extant species of *Conus* in the focal geographic region.

Chapter 6, “Synthesis and Conclusions,” summarizes and synthesizes information primarily on taxonomy, natural history, biogeography, and phylogeny, and to a lesser extent on ecology and fossil history; this is based mainly on the species accounts in Chapter 5.

A general glossary, bibliography of literature cited, and index follow.

Access to Additional Information

The *Conus* Biodiversity Website (<http://biology.burke.washington.edu/Conus/>) provides considerable important supplementary information, including PDF’s of original descriptions. It also includes videos of behavior in living animals, a format impossible to convey in a printed book. The website also periodically updates Röckel, Korn, and Kohn (1995), and updates to this book will be posted in the future as well.

A companion web site containing the data files and statistical analyses used in the research for this book has been developed and is available from the publisher's web page (<http://press.princeton.edu/titles/10229.html>). The data files include collection and repository records and shell and radular tooth morphometric data for the specimens studied, and images of some that could not be included in the book. The statistical analyses summarize how the data were used to test whether characters differ between groups hypothesized as indicating different species. As Chapter 4 describes in more detail, tests of statistical significance yield values of P . The

P value is the probability that if the null hypothesis (i.e., that the populations being sampled do not really differ from each other) is correct, the value of the test statistic would be as extreme or more so than the observed value. Thus, the smaller the value of P , the more strongly the test rejects the null hypothesis, and the more likely that the difference between populations is real. The supplementary material therefore presents the analyses resulting in the P values that appear in the text. It enables readers who so wish to replicate, extend, and improve the analyses of data, and it avoids cluttering the species accounts in Chapter 5 with details that not all readers will require.