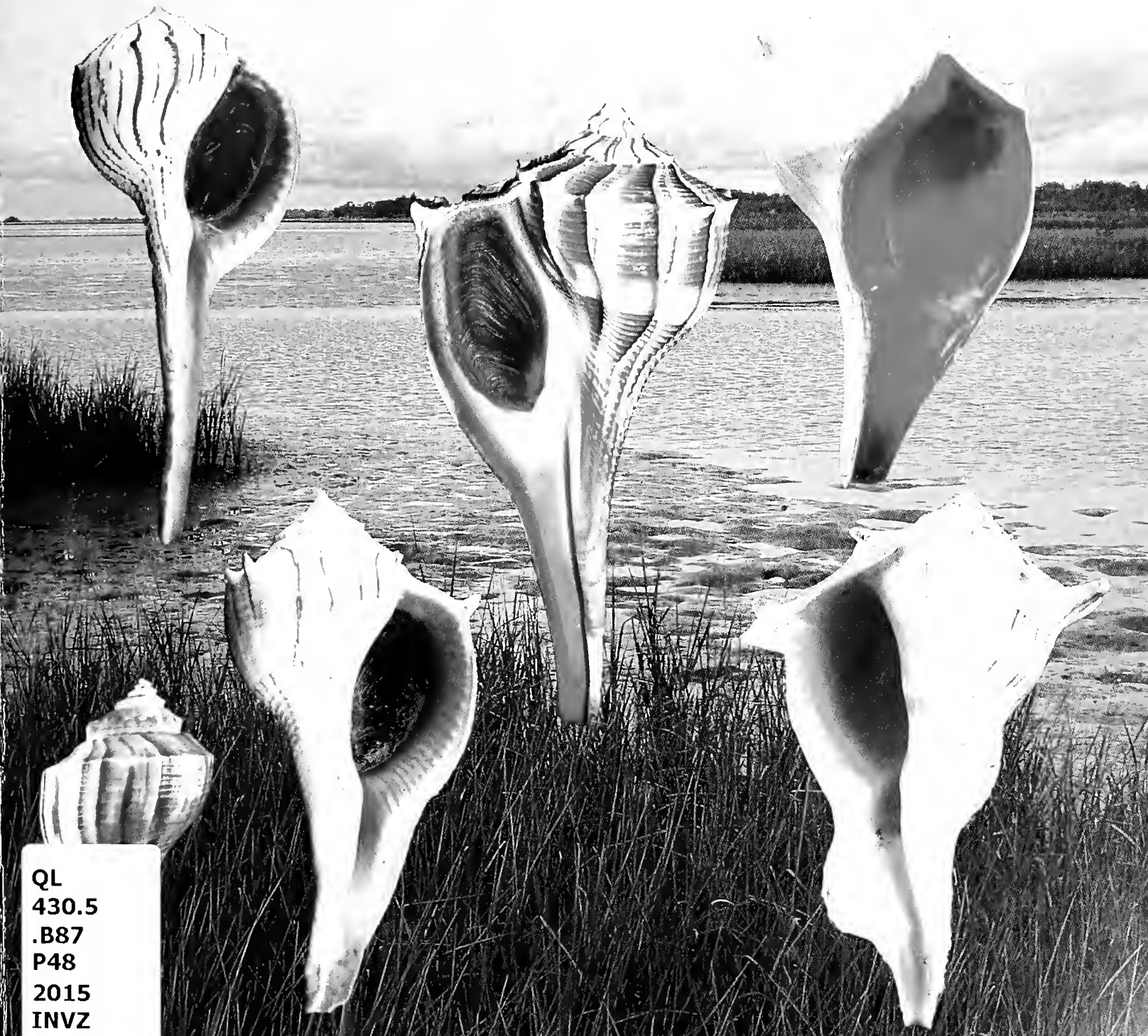
The Living and Fossil Busycon Whelks: Iconic Mollusks of Eastern North America

Edward J. Petuch, Robert F. Myers, and David P. Berschauer



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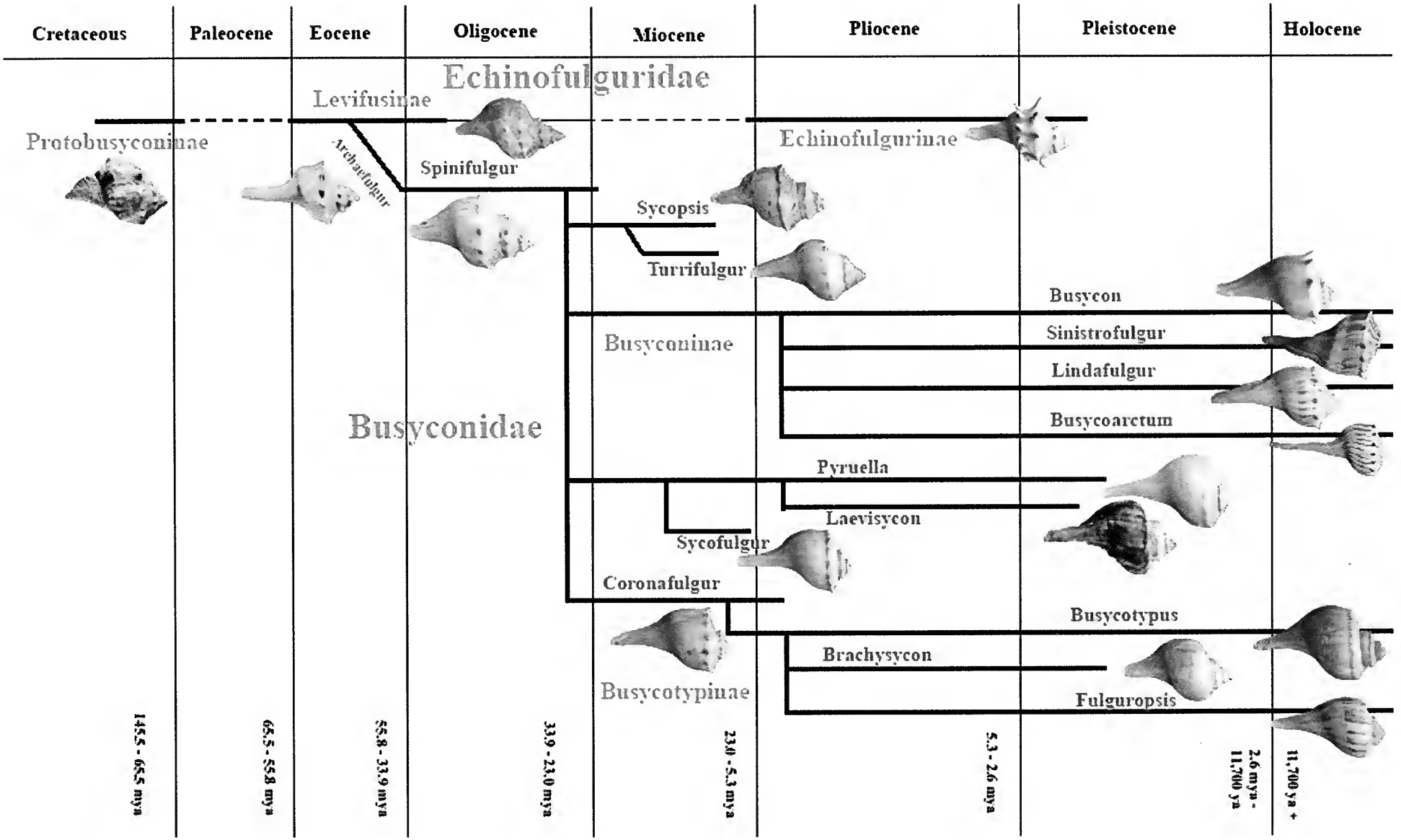
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Pleistocene
Holocene
Echinofulguridae
Levifusinae
Protobusyconinae
Archaeofulgur
Spinifulgur
Echinofulgurinae
Sycopsis
Turrifulgur
Busycon
Busyconinae
Sinistrofulgur
Lindafulgur
Busycoarctum
Busyconidae
Pyruella
Laevisycon
Sycofulgur
Coronafulgur
Busycotypus
Brachysycon
Busycotypinae
Fulguropsis
145.5 - 65.5 mya
65.5 - 55.8 mya
55.8 - 33.9 mya
33.9 - 23.0 mya
23.0 - 5.3 mya
5.3 - 2.6 mya
2.6 mya - 11,700 ya
11,700 ya +

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Dedication

To Linda Petuch, Eric Petuch, Brian Petuch, Jennifer Petuch

and

to Patrice Marker, Laura Myers, and Robbie Myers

and

to Felicia Weisbrot Berschauer, Jonathon Berschauer, Morgan Berschauer

and

to the Memory of James F. Myers

Close-up of a Calusa Indian digging tool made from a large Left-Handed Whelk, *Sinistrofulgur sinistrum*. A stick was inserted through the two large holes as a handle and the smaller holes may have acted as drains for water while digging in wet soil. This artifact, which is at least 500 years old, was excavated on Chokoloskee Island, Collier County, Florida and now resides in the collection of A. Kenneth ("Kenny") Brown, Jr. The Calusa Indians of southern Florida made many types of tools from the shells of Left-Handed Whelks.

FOREWORD

Taxonomic revisions of individual groups of animals remain, to this day, a golden standard for systematic biology and paleontology. Putting these together includes scrupulous collection and verification of information from a wide variety of sources combined with personal knowledge, available study material, and production of state-of-the-art images and illustrations. These basic requirements have remained surprisingly uniform for at least two centuries. This team of authors, including Professor Edward Petuch, whose extensive personal experience include decades of collecting and study of both Recent and fossil whelks from Maryland to South Florida, David Berschauer, a long time marine biology and malacology enthusiast and shell collector, and marine biologist and outstanding photographer Robert Myers, has produced a remarkable and attractive taxonomic and pictorial revision of the busycon whelks of eastern North America. The book, dedicated to the uniquely and unmistakably North American group of large and conspicuous gastropods, commonly known as whelks and collectively known to those in the business as "busycons", follows the best traditions of systematic zoology volumes. The book not only reviews a wealth of information known to date about the group, but adds new and often previously unpublished data on occurrences, habitats, biogeography, and ecology of these taxa. Anyone would be hard pressed to name a more classical eastern North American shell which would be more easily recognizable than the busycons. Living whelks currently serve as a State Shells for three states – the Lightning whelk *Sinistrofulgur pulleyi* for Texas (1987) and Knobbed whelk - *Busycon carica* – for Georgia (1987) and New Jersey (1995). If anyone would ever decide to select a national seashell for the United States of America, busycons, without doubt, should be on the very top of the list of candidates.

The data presented in this book provides a wealth of information on living and fossil whelks, including the patterns of evolution for the entire group throughout the Cenozoic, which has not been outlined anywhere before. The book presents detailed information on 6 living and 8 extinct genera belonging to 4 subfamilies, and on 17 Recent and 112 fossil species of whelks. The book contains the descriptions of a new family, three new subfamilies, and a new genus of ancestral Busyconidae that were not previously recognized. In addition to the purely taxonomic value, the book is written in a vernacular style and is full of fascinating natural history facts. The book is also remarkably well illustrated, with high quality photographs and informative maps. These features will certainly make it a very desirable reading for people with most diverse marine biological and ecological backgrounds. No one would ever look at a whelk, washed up on an eastern North America beach, the same way after reading this book!

Anton E. Oleinik, Ph.D.
Florida Atlantic University

Close-up view of an aggregation of Rucks' Whelk (*Busycon rucksorum* Petuch, 1994), in an exposure of the Fort Drum Member of the Nashua Formation (Gelasian Pleistocene) found within the Dickerson Aggregates Indrio Pit near Fort Pierce, St. Lucie County, Florida.

INTRODUCTION:

The Busycon Whelks of Eastern North America

A trip to an open shoreline anywhere along the eastern United States will quickly introduce a beachcomber to the busycon whelks. These iconic American shells are abundant in shallow water areas from Cape Cod south to Florida and throughout the Gulf of Mexico, and are often the most conspicuous large mollusks to wash up onto beaches after storms. Along coastal New York, New Jersey, Delaware, and Maryland, two large whelks, the Lightning Whelk (*Busycon carica*) and the Channeled Whelk (*Busycotypus canaliculatus*), are frequently encountered on beaches and often accumulate in huge piles after strong winter storms. These two whelks are the largest mollusks found along these coastlines and their beautifully-shaped shells are frequently seen decorating the gardens and porches of seaside homes all the way from Cape Cod to Virginia. Farther south, from Cape Hatteras to Cape Canaveral, the busycon whelk fauna becomes richer, with small Pear Whelks and large Left-Handed Whelks occurring together, in shallow water, with the Channeled and Lightning Whelks. In southern and western Florida and along the coast of Texas, the Channeled and Lightning Whelks are absent, and only Left-Handed and Pear Whelks are found on these beaches. Although three separate types of busycon assemblages occur along eastern North America (one ranging from Cape Cod to Cape Hatteras, one ranging from Cape Hatteras to Cape Canaveral, and one extending around Florida into the entire Gulf of Mexico), these whelks are always among the most prominent and conspicuous types of mollusks found on beaches and in shallow lagoons.

Besides their beautiful and fascinating shell shapes and colors, busycon whelks are also an important food resource and they are harvested in huge quantities in the Northeast. Often incorrectly labeled as "Conchs" in local fish markets (a name reserved for the true conch shells of the family Strombidae), the busycon whelks are harvested by dredging boats off southern New Jersey and they form the basis of a large commercial fishing industry. The meat of the Channeled and Lighning Whelks, together, is referred to as "scungilli" by Italian-Americans and is considered a delicacy. The sliced whelks are served either hot, in a marinara sauce over pasta, or cold, as an "insalata di mare" (sliced cooked whelks served chilled in a salad). Scungilli is a traditional Italian Christmas dish and is also served as the centerpiece for the "Feast of the Seven Fishes." From deeper water off southern New Jersey, a third whelk species occurs along with the Channeled and Lightning Whelks; the large Northern Left-Handed Whelk or the "Snow Whelk", *Sinistrofulgur laeostomum*. The meat from this uncommon offshore species is also sold, together with that of the other two species, as scungilli. As only the foot, head, and main body of these three whelks is used for the Italian seafood dishes, the remainder of the snails, including their livers, digestive glands, and gonads, are discarded as by-products. The commercial fishermen collect and sell these organs to pet supply companies, where they are most often made into cat food. Busycon whelks also appear in other guises, particularly as the "Fried Clam Strips" sold by many restaurants and frozen seafood companies. These are actually slices of busycon whelks and are not made from real clams.

Besides their aesthetic and commercial importance, the busycon whelks also have a special status within the American molluscan fauna, as they are the only group of large gastropods that is essentially confined to the coastal waters of the United States. With the exception of one

species that is endemic to the Yucatan Peninsula of Mexico, the other 16 living species and subspecies recognized in this book are either geographically-restricted to the Eastern Seaboard and the Gulf of Mexico or extend up the Texas coast from farther south on the Campeche Banks. Throughout their entire evolutionary history, spanning over 30 million years, the busycon whelks have always been residents of the southeastern and eastern United States and are the only wholely northeastern American group of gastropods. All the other large mollusks that live along with the busycon whelks can trace their ancestries back to worldwide families that evolved within the Eocene Tethys Sea circumtropical belt ocean. Because they had circumglobal distributions, these groups now have relatives scattered within all of the tropical, subtropical, and temperate seas around the world, including the western Atlantic. Only the busycons are a truly "home grown" family, having evolved directly from specialized groups that appeared within the isolated American inland seas during the Cretaceous and Paleogene Periods (these will be discussed in the following chapters). But while home-grown, all-American families can have a retrobate member; in this case, in the form of an invasive species. By accident in 1938, *Busycotypus canaliculatus* was introduced into San Francisco Bay in a batch of East Coast oysters brought there to start a new fisheries industry. The Channeled Whelks have been thriving there ever since, at the expense of the local clam harvesting industry, which has diminished substantially due to heavy whelk predation. Fortunately, the open Pacific water outside the bay is too cold for the Channeled Whelks and they are perpetually trapped within their isolated West Coast estuarine world.

Over the past 200 years, much has been written about the taxonomy, systematics, ecology, biogeography, fossil record, and biostratigraphy of the busycon whelks, all by specialists in each of these separate disciplines. Although available, this widely scattered data on busyconid biology and paleontology has never been compiled into a single work. The compilation of all this data has led to many interesting and unexpected discoveries. In the course of our preliminary research, we found that the systematics of the Pear Whelks (genus *Fulguropsis*) was much more complicated than we originally thought, involving complex biogeographical patterns and disjuct distributions. This led to the discovery of a previously-unnamed living species, which is described here for the first time. We also discovered that the origins of the family Busyconidae most probably lie within a previously-undescribed family, a previously-undescribed subfamily, and an unnamed genus, all of which are described in this book for the first time. A new genus of Florida fossil whelks is also described here for the first time, giving insight into the busyconid evolutionary explosion that took place in that area during the Pliocene and early Pleistocene. All of these discoveries, and many more, are shown throughout our book. We bring together as many aspects of busyconid biology and paleontology as possible, including an iconography of both the living and fossil species and distribution maps for each living species and subspecies. Hopefully, these data will give a higher-resolution view of the origins and evolutionary patterns of this important and iconic American molluscan family.

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View of an immense accumulation of the Left-Handed Whelk, *Sinistrofulgur sinistrum*, along a beach on the southern coast of Rabbit Key, Ten Thousand Islands, Collier County, Florida.

CHAPTER ONE

Systematics and Evolutionary History of the Family Busyconidae

Although the busycon whelks are recognized as being one of the most conspicuous and common groups of marine mollusks in eastern North America, their systematic classification and taxonomic nomenclature is still in total confusion. Over the past 100 years, these iconic American mollusks have been placed in no fewer than four different families, underscoring the wide range of opinions regarding the systematic placement of this group. These families have included the Melongenidae (Sohl, 1964; Abbott, 1974; Golikov and Starobogatov, 1975; Berlocher, 2000), the subfamily Busyconinae under the family Buccinidae (Poppe and Tagaro, 2006), the family Busyconidae (Wade, 1917; Gardner, 1944; Hollister, 1958; Kantor, 2003; Petuch, 2004, 2013; GBIF Global Biodiversity Information Facility, 2014), the family Fasciolariidae (Dall, 1890; in part, MacNeil and Dockery, 1984), and the family Buccinidae (Dall, 1915; Olsson, 1967; Bouchet *et al.*, 2005). Each of these workers approached aspects of the systematic and nomenclatural problems from different angles, some of which included shell morphology, protoconch structure, fossil record, and stratigraphic placement, and for living species, their biogeography, anatomy, radula, periostracum structure, and biochemical (DNA) differences. The arrival at such disparate systematic placement resulted from the emphasis on only one, or a few, of these systematic characters and not a more holistic approach that combines several of these aspects.

In the current literature, the generic-level taxa of the busyconids are just as confused as are the family-level taxa. There has been a wide range of opinions on the usage of the generic taxa for the living species, with some, such as Abbott (1974: 222-223), using only a single genus (*Busycon*) and four subgenera (*Busycon* s.s., *Sinistrofulgur*, *Busycoarctum*, and *Busycotypus*), with Gill (1867) and Grabau (1903) both using two genera (*Fulgur* and *Sycotypus*). Others, such as Hollister (1958) recognized two genera (*Busycon* and *Busycotypus*) and five subgenera (*Busycon* s.s., *Sinistrofulgur*, *Busycoarctum*, *Busycotypus* s.s., and *Pyrofulgur*), and yet others, such as Petuch (2013: 18-19), recognized six full, distinct genera (*Busycon*, *Sinistrofulgur*, *Lindafulgur*, *Busycoarctum*, *Busycotypus*, and *Fulguropsis*). There is slightly more of a consensus between some recent workers on the number of living species, with Abbott (1974) recognizing 11 species and subspecies, with Hollister recognizing 15 living species and subspecies, and with Petuch (2013) recognizing 17 living species and subspecies. Older workers, such as Gill (1867) recognized only 5 living species and Grabau (1903) only eight. In this book, we utilize several busyconid classification tools, including classic morphological characters such as shell shape, protoconch structure, and periostracal structure, and also the evolutionary history, fossil record, and biogeographical patterns for each genus and species complex. When applicable, references to recent molecular / DNA studies on select groups are also included in our final systematic analysis. These are all combined in different ways to gain insight into a more precise systematic placement of these large and important marine animals.

Systematics of the Busyconidae

In 1958, the single most important work on the systematics of the busycon whelks was published by S.C. Hollister in the *Palaeontographica Americana* series of the Paleontological Research Institution. This large monographic paper was a synthesis of the previous 200 years of research on the group, giving the precise nomenclatural history and synonymies of each whelk species, illustrating the holotypes of many of the more poorly-known taxa, and designating lectotypes and neotypes for species that had no extant holotype. This taxonomic reorganization was essentially undertaken to create a stable nomenclatural scheme for the family, genera, and species. With this work, Hollister set the stage for our present interpretation of busyconid systematics. At the same time, he also described two new genera, *Sinistrofulgur* and *Busycoarctum* (both originally described as subgenera of the genus *Busycon*) and five new species-level taxa; *Sinistrofulgur sinistrum*, *Sinistrofulgur pulleyi*, *Sinistrofulgur aspinosum* (considered to be only a form or variety in this book), and *Fulguropsis plagosus texanus*, and *Fulguropsis plagosus galvestonensis* (with *F. texanus* being considered to be full species in this book).

Since 1958, intensive field research along the eastern coast of the United States and deep water dredging in the Gulf of Mexico have resulted in numerous important discoveries that have built upon, and enhanced, the body of knowledge that was originally compiled by Hollister. Some of the more important of these recent discoveries (described in more detail later in this book) include the discovery, by Bretton Kent in 1982, of a large Left-Handed Whelk from off southern New Jersey, which he named *Sinistrofulgur laeostomum*. At the same time as the description of the new *Sinistrofulgur* species, the senior author described the extinct busyconid genus *Pyruella*, along with eight new species (Petuch, 1982), from fossil beds in southern Florida. Five years later, the senior author named a new deep water living species, *Lindafulgur lyonsi* (Petuch, 1987), from off western Florida, the deepest-dwelling busyconid. The following year, the senior author also described the new genus *Turrifulgur* from the Miocene fossil beds of Maryland (Petuch, 1988).

In the 1990's and 2000's, extensive research on the fossil busycon whelks of the eastern United States, also conducted by the senior author, led to the description of an additional 33 new extinct species from fossiliferous outcrops in Florida and North Carolina. These new species, along with the new genera *Spinifulgur* and *Brachysycon* and the new subfamilies Busyconinae and Busycotypinae, were described and illustrated in the *Atlas of Florida Fossil Shells* (Petuch, 1994). This research into the paleontology of the busyconids culminated in the description of the new genera *Coronafulgur* and *Lindafulgur*, along with new species of *Turrifulgur*, *Spinifulgur*, *Busycon*, and *Pyruella*, and these were described in *Cenozoic Seas: The View from Eastern North America* (Petuch, 2004). A review of the Chesapeake Miocene busyconids, with the description of a new species, was later published in the *Molluscan Paleontology of the Chesapeake Miocene* (Petuch and Drolshagen, 2010). While collecting Pear Whelks of the genus *Fulguropsis* along the coasts of Florida, the senior author also discovered a new living species in the Florida Keys (*Fulguropsis keysensis* Petuch, 2013), along with uncovering the disjunct distribution of the eastern Florida and western Florida *Fulguropsis* species. This led to the discovery of a new East Coast species, which we will be naming later in this book (*Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species).

We here propose a new classification of the Busycon Whelks, based upon their fossil record, shell morphologies, and in the case of the living species, their anatomical and biochemical differences. These data, altogether, support the following scheme for the 17 living taxa:

Class Gastropoda
Subclass Orthogastropoda
Superorder Caenogastropoda
Order Sorbeoconcha
Infraorder Neogastropoda
Superfamily Buccinoidea
Family Busyconidae Wade, 1917
Subfamily Busyconinae Petuch, 1994
Genus *Busycon* Röding, 1798 (Type: *B. carica*)
Busycon carica (Gmelin, 1791)
Busycon carica eliceans (Montfort, 1810)
Genus *Sinistrofulgur* Hollister, 1958 (Type: *S. sinistrum*)
Sinistrofulgur sinistrum (Hollister, 1958)
Sinistrofulgur laeostomum (Kent, 1982)
Sinistrofulgur pulleyi (Hollister, 1958)
Sinistrofulgur perversum (Linnaeus, 1758)
Genus *Lindafulgur* Petuch, 2004 (Type: *L. lindajoyceae*)
Lindafulgur candelabrum (Lamarck, 1816)
Lindafulgur lyonsi (Petuch, 1987)
Genus *Busycoarctum* Hollister, 1958 (Type: *B. coarctatum*)
Busycoarctum coarctatum (Sowerby I, 1825)
Subfamily Busycotypinae Petuch, 1994
Genus *Busycotypus* Wenz, 1943 (Type: *B. canaliculatus*)
Busycotypus canaliculatus (Linnaeus, 1758)
Genus *Fulguropsis* Marks, 1950 (Type: *F. pyrum= spiratum*)
Fulguropsis spiratus (Lamarck, 1816)
Fulguropsis rachelcarsonae, new species
Fulguropsis keysensis Petuch, 2013
Fulguropsis pyruloides (Say, 1822)
Fulguropsis plagosus (Conrad, 1863)
Fulguropsis plagosus galvestonensis (Hollister, 1958)
Fulguropsis texanus (Hollister, 1958)

The 111 described fossil species are listed in a special section at the end of this book. Besides the fossil representatives of the six living genera, the busyconid fossil record also contains eight extinct genera, which include:

Superfamily Buccinoidea
Family Busyconidae Wade, 1917
Subfamily Busyconinae Petuch, 1994
Genus *Spinifulgur* Petuch, 1994 (Type: *S. spiniger*; extinct in the early Miocene)
Genus *Sycopsis* Conrad, 1867 (Type: *S. tuberculatum*; extinct in the late Miocene)

Genus *Turrifulgur* Petuch, 1988 (Type: *T. fusiforme*; extinct in the late Miocene)
Subfamily Busycotypinae Petuch, 1994
Genus *Coronafulgur* Petuch, 2004 (Type: *C. coronatum*; extinct in the late Miocene)
Genus *Brachysycon* Petuch, 1994 (Type: *B. amoenum*; extinct in the early Pleistocene)
Genus *Pyruella* Petuch, 1982 (Type: *P. harasewychi*; extinct in the early Pleistocene)
Genus *Laevisycon*, new genus (Type: *L. laevis*; extinct in the early Pleistocene)
Genus *Sycofulgur* Marks, 1950 (Type: *S. rugosum*: extinct in the late Miocene)

In this book, we recognize the Busyconidae as a separate, full family within the Superfamily Buccinoidea. Based on the presence or absence of a sutural channel and differences in the periostraca, we also recognize two separate subfamilies under the family Busyconidae; the subfamily Busyconinae and the subfamily Busycotypinae. Each of the living genera has a rich and diverse fossil record and we have chosen to illustrate many of the more representative species under each genus in the following chapters. Our overall systematic scheme, based on both the living and fossil taxa, will also be expanded upon under each of the following chapters of this book.

Origin and Evolution of the Busyconidae

The Busyconidae is geologically a very young family, having only first appeared, in any recognizable form, in the early Oligocene Epoch (approximately 32 million years). Throughout its evolutionary history, the family Busyconidae has been completely restricted to Eastern North America, from the Mississippi River Valley (the Paleogene Mississippi Embayment), the entire Gulf of Mexico, and the Eastern United States as far north as Cape Cod. The general consensus among workers such as Dall (1890), Harris and Palmer (1947), and Maury (1909) is that the family arose from the genus *Levifusus* Conrad, 1865 during the latest Eocene. Like the busyconids, this precursor genus (Figure 1.1) has been placed in several different families by previous workers, including the Neptuneidae (Harris and Palmer, 1947), the Fasciolariidae (Dockery, 1980; MacNeil and Dockery, 1984), and the Melongenidae (Petuch, 1994: 306).

The species in the genus *Levifusus*, as typified by the late Eocene *L. branneri* (Figure 1.1A) and the middle Eocene *L. trabeatus* (Figure 1.1B; type species of *Levifusus*), generally have two rows of distinct knobs or short spines, one around the mid-body and one around the shoulder. Some other closely-related Eocene forms have only a single row of large spines around the shoulder and lack the second row of spines around the mid-body. These are now placed within the new genus *Archefulgur*, which is described in the following section. Some specimens of *L. branneri*, such as the one illustrated here, also lack a row of spines around the mid-body and closely approximate the general shell shape of *Archefulgur* and the Busyconidae. The genus *Archefulgur* is the only late Eocene gastropod group that resembles the busycon whelks and there is little doubt that it represents the predecessor lineage of the entire family Busyconidae.

The Paleocene and Eocene complex of *Levifusus* species appears to represent a lineage of Late Cretaceous buccinoideans that survived the terminal Maestrichtian mass extinction. Prior to the asteroid impact and extinction, a small species radiation of the genus *Protobusycon* (Sohl, 1964:194-195, plates 23 and 24), had evolved within the southeastern section of the Western Interior Seaway, along the southern coast of the continent of Appalachia (modern eastern North

America). Members of this Late Cretaceous complex, particularly the type species, *Protobusycon cretaceum* (Wade, 1917), resembled small busyconids, having a protracted siphonal canal, inflated body whorl, and single row of large spines around the shoulder (see Wade, 1917a and 1917b). Other species within the complex, such as *Protobusycon binodosum* Sohl, 1964 (Figure 1.2D), had two rows of spines around their body whorl and resembled stockier, heavier versions of the early Cenozoic genus *Levifusus*. Although placed in the family Melongenidae by Sohl (1964), these Late Cretaceous busyconoids differ from typical members of that family in having a distinct constriction at the body whorl-siphonal canal junction and in having a deep spiral groove along the base of the body whorl. These distinctive shell characters indicate that the three species of *Protobusycon* are not closely related to the Melongenidae.

In the Plio-Pleistocene fossil record of southern Florida and the Everglades Region (the "Okeechobean Sea", Petuch, 2004; Petuch and Roberts, 2007), there exists another group of busyconoid gastropods with two prominent rows of spines and long siphonal canals. Originally placed in the genus *Fulgur* by Dall (1890) and later placed in a new genus named *Echinofulgur* by Olsson and Harbison (1953), this complex of spiny whelks (examples shown here on Figure 1.2) was endemic to the Okeechobean Sea area and has never been found at any other locality. The genus *Echinofulgur*, which comprises seven named species (Petuch, 1994), first appears in southern Florida in the Buckingham Member of the Tamiami Formation (late Zanclean-early Piacenzian Age of the Pliocene) and ranges into the Ayers Landing Member of the Caloosahatchee Formation (late Gelasian Age of the early Pleistocene), a time period of almost 3 million years. The oldest-known species, *Echinofulgur cannoni* Petuch, 1994 (Figure 1.2C) from the Buckingham Member of the Tamiami Formation, closely resembles a large, low-spired *Levifusus* species. Stratigraphically-higher taxa, such as *Echinofulgur dalli* Petuch, 1994 from the Pinecrest Member of the Tamiami Formation (Figure 1.2B) and *Echinofulgur echinatum* (Dall, 1890) from the Fort Denaud Member of the Caloosahatchee Formation (Figure 1.2A; originally "*Fulgur echinatum*"), developed higher spires and longer spines, but retained the general body form of Eocene *Levifusus* species such as *L. trabeatus* and *L. branneri*. Based on these close similarities in shell morphology, the *Echinofulgur* and *Levifusus* species complexes are now seen to belong to the same general group of buccinoidean gastropods. Dockery (1977) also recognized these morphological similarities and placed *L. branneri* in *Echinofulgur*, which he considered to be a subgenus of *Busycon*.

In 1994, the senior author placed the genus *Echinofulgur* in the family Melongenidae and erected a new subfamily to accommodate this group of shells with long siphonal canals and two rows of spines (the Echinofulgurinae; see *Atlas of Florida Fossil Shells*, 1994). Although very similar to *Levifusus*, the genus *Echinofulgur* differs in having larger, heavier shells and in having open sutures along the juncture of the spire whorls and the body whorl. Although superficially similar, both of these groups differ from the Cretaceous genus *Protobusycon* in having longer and better-developed siphonal canals and in lacking the spiral groove along the body whorl-siphonal canal juncture. Enough similarities exist between the Cretaceous, Eocene, and Plio-Pleistocene species complexes to show that all three of these groups belong to the same family and should not be placed within the Melongenidae. Throughout their geologic ranges, the *Protobusycon* and *Levifusus* complexes were restricted to the area of the Mississippi River Valley and eastern coast of the United States, with *Protobusycon* being confined to the southeastern edge of the Western Interior Seaway and with *Levifusus* being found from the

Eocene Mississippi Embayment ("Mississippi Sea") northward as far as Maryland (Martin, 1901). The genus *Echinofulgur* appears to represent a Neogene relictual offshoot of *Levifusus* that managed to survive only within the Okeechobean Sea of southern Florida. Altogether, these three main groups appear to constitute a new family of buccinoidean gastropods that was restricted biogeographically to the Eastern United States and Gulf of Mexico region. This new family, which is described next, was the precursor group of the Busyconidae.

The Ancestral Family Echinofulguridae

Since the taxon Echinofulgurinae was originally proposed as a subfamily (Petuch, 1994: 305), it is available as the oldest family-level name for the entire group of Cretaceous-to-Pleistocene buccinoideans with long siphonal canals and two rows of spines. For this reason, we here propose the new family **Echinofulguridae** to accommodate all the similar taxa discussed in the previous section of this chapter. Three distinct groups are contained within the new family: the *Protobusycon*-type shells of the late Cretaceous Western Interior Seaway, here placed in the new subfamily **Protobusyconinae**; the *Levifusus* complex of the Eocene East Coast and Mississippi Embayment, here placed in the new subfamily **Levifusinae**; and the *Echinofulgur* complex of the Pliocene and early Pleistocene of southern Florida, here retained in the subfamily **Echinofulgurinae Petuch, 1994**. Having been geographically-confined to eastern North America, the family Echinofulguridae may, itself, have had its origins in a relict group of the subulitoidean gastropods from the Jurassic Sundance Sea. Remnants of these Jurassic molluscan faunas may have survived within the Early Cretaceous Western Interior Seaway, eventually evolving into the ancestors of *Protobusycon*. The fact that the entire subfamily Protobusyconinae was restricted to the southern coast of the continent of Appalachia (the proto-Mississippi Embayment area of modern southwestern Tennessee and northern Mississippi) indicates that the subfamily had survived as a localized relict of a once more-widespread group of primitive buccinoideans. Echinofulgurinae, originally described as a subfamily of the Melongenidae, is here transferred to Echinofulguridae. The new family and two new subfamilies are described here.

Class Gastropoda
Subclass Orthogastropoda
Superorder Caenogastropoda
Order Sorbeoconcha
Infraorder Neogastropoda
Superfamily Buccinoidea

Echinofulguridae Petuch, Myers, and Berschauer, new family

Diagnosis: The new family comprises three morphologically-similar groups of extinct, small-to-medium sized gastropods with inflated, pyriform or fusiform shells, most often ornamented with two rows of spines or knobs, one around the mid-body and one around the shoulder; some species have only a single row of spines around the shoulder; shell surface smooth and silky or sculptured with numerous very fine spiral threads; siphonal canals elongated, narrow, separated from the body whorl by a distinct constriction; siphonal canals often ornamented with strong spiral cords or a single large scaly ridge; spire whorls generally elevated, protracted, or

scalariform, most often ornamented with one or two rows of spines; parietal region glazed; apertures wide and flaring; protoconchs rounded, composed of two whorls.

Type Genus: *Echinofulgur* Olsson and Harbison, 1953; Pliocene and early Pleistocene of southern Florida (Type species: *Echinofulgur echinatum* (Dall, 1890), early Pleistocene of southern Florida).

Geochronologic Range: The new family ranges from the Maestrichtian Cretaceous (Ripley Formation of Tennessee), through the Eocene (Wilcox, Claiborne, and Jackson Stages of the Mississippi River Valley; Bashi, Cook Mountain, Kosciusko, White Bluff, Yazoo, Moodys Branch, Danville Landing, and Gosport Formations; Nanjemoy Formation of Maryland)), to the Pliocene and early Pleistocene (of southern Florida only; Tamiami and Caloosahatchee Formations).

Subfamilies in Echinofulguridae: Three subfamilies are presently known to belong in this family, the Protobusyconinae (described next), the Levifusinae (described later), and the Echinofulgurinae Petuch, 1994.

Discussion: Although the new family has a geologic range that extends from the Late Cretaceous to the early Pleistocene, the individual subfamilies are much more chronologically constrained. The subfamily Protobusyconinae is confined to the Late Cretaceous and does not cross the K/T (Cretaceous-Tertiary) boundary. The subfamily Levifusinae appears in the early Eocene (possibly late Paleocene) and persists until the mass extinction at the end of the Lutetian Age of the late Eocene. The family is conspicuously absent from the rich Miocene fossil beds of Maryland, Virginia, the Carolinas, and northern Florida, indicating that the echinofulgurids were almost extinct during that time and probably found a refugium only in the Okeechobean Sea of southern Florida. Unfortunately, the Miocene fossil beds of southern Florida are heavily leached (Petuch and Roberts, 2007) and any traces of the echinofulgurid aragonitic shells were dissolved away. Once the conditions for carbonate preservation returned to the Okeechobean Sea in the Pliocene, the fossil record of the Echinofulguridae resumed, revealing the presence of an entirely new subfamily of echinofulgurids, the Echinofulgurinae. This last vestige of the family proliferated within the Okeechobean Sea and finally went extinct during the extreme climatic degeneration during the early Pleistocene. The fact that the Echinofulguridae has been geographically-confined to only the Mississippi River Valley and Florida throughout its entire geologic history demonstrates that the family is not descended from the Tethyan worldwide families Buccinidae or Melongenidae, but represents a local eastern North American evolutionary radiation.

Protobusyconinae Petuch, Myers, and Berschauer, new subfamily

Diagnosis: The new subfamily comprises only three known species of extinct, small echinofulgurids, all confined to the Late Cretaceous; shells distinctly fusiform, with wide, inflated body whorls that taper gradually into the elongated siphonal canal; shoulders angled; body whorls ornamented with one or two rows of large rounded knobs or short spines, one around shoulder and one around the mid-body (which is absent on the species with only shoulder spines); body whorls sculptured with variable amounts of fine, thin spiral cords and threads;

spires elevated, subpyramidal, slightly scalariform on some species; siphonal canal-body whorl juncture marked by a single deeply-impressed, large spiral groove; the groove corresponds to a small rounded projection on the outer lip; siphonal canals sometimes ornamented with large spiral cords; apertures proportionally large and flaring.

Type Genus: *Protobusycon* Wade, 1917; Maestrichtian Cretaceous of Tennessee and northern Mississippi (Type species: *Protobusycon cretaceum* Wade, 1917, Late Cretaceous of Tennessee and Mississippi).

Geochronologic Range: The new subfamily is known only from the Maestrichtian Cretaceous (Ripley Formation of Tennessee and northern Mississippi).

Genera in the Protobusyconinae: At present, the new subfamily is known to contain only one genus, *Protobusycon* Wade, 1917.

Discussion: This new subfamily, which contains only one known genus and three known species (see Sohl, 1964: 193-195), is the oldest group that is referable to the family Echinofulguridae. The relationship of the Protobusyconinae to the other echinofulgurid subfamilies can readily be seen in *Protobusycon binodosum* Sohl, 1964 (Figure 1.2D), which shares the same type of shell ornamentation composed of two rows of large spines. The large spiral groove around the siphonal canal-body whorl juncture disappears from all echinofulgurid taxa after the Cretaceous and is replaced, in all subsequent groups, by a small blade-like extension of the outer lip. As the Western Interior Seaway filled in and dried up at the end of the Cretaceous, *Protobusycon* managed to survive along the southern coast of Appalachia. When this proto-continental area connected with the western section of North America in the latest Maestrichtian, the newly-formed Mississippi Embayment became a refugium for the subfamily Protobusyconinae. There, the subfamily evolved an offshoot group that gave rise to the subfamily Levifusinae. This subfamily, which is described next, underwent a species radiation within the Mississippi Embayment and later gave rise to the family Busyconidae.

Levifusinae Petuch, Myers, and Berschauer, new subfamily

Diagnosis: The new extinct subfamily comprises small-to-medium sized, distinctly fusiform echinofulgurids with thin, fragile shells; most species within the Levifusinae are ornamented with two rows of short spines, one around the shoulder and one around the mid-body; some species with only a single row of spines along the shoulder and no spines on the mid-body; spires are elevated, protracted, and often scalariform, with distinctly sloping spire whorls; shoulders sharply-angled, often subcarinate; body whorls very inflated; apertures wide and flaring; parietal area glazed, often with a thickened parietal shield; constriction at anterior end of body whorl very pronounced, tapering abruptly into a straight, narrow siphonal canal.

Type Genus: *Levifusus* Conrad, 1865; Eocene of the Mississippi River Valley (Type species: *Levifusus trabeatus* (Conrad, 1833), Eocene (Claiborne Stage) of Alabama and Mississippi); also found in the early Eocene beds of Maryland (Clark and Martin, 1901).

Geochronologic Range: The new subfamily is known only from the formations of the Wilcox, Claiborne, and Jackson Stages, Eocene of the Mississippi River Valley, Alabama, and Maryland.

Genera in the Levifusinae: At present, the new subfamily is known to contain only two genera; *Levifusus* Conrad, 1865 and *Archefulgur* Petuch, Myers & Berschauer, new genus (described next).

Discussion: The name "*Levifusus*" is a "catch-all genus", having been applied to many unrelated Eocene taxa that share the same general pyriform shell shape. Some of these include heavily-corded and costate species such as "*Levifusus*" *mortoniopsis* (Gabb, 1860) and "*Levifusus*" *carexus* (Harris, 1895) and small fusiform species with reduced costae and numerous fine spiral cords, such as "*Levifusus*" *moodianus* Cook, 1926. Further study may show that these taxa actually belong in the family Fasciolariidae, and they would then need new generic-level names. Only the fusiform shells with two rows of small spines are here considered to be true *Levifusus* species. Of these, only a few species are known and include the type species *Levifusus trabeatus* (Conrad, 1833) (Figure 1.1B), the large *Levifusus branneri* Harris, 1894 (Figure 1.1A), and *Levifusus trabeatoides* Harris, 1895. Two other "*Levifusus*" species are differentiated from the typical forms by having only a single row of spines on the shoulder and by completely lacking the row of spines around the mid-body. This group, which is described next as the new genus *Archefulgur*, is represented by only two species; *Archefulgur fulguriparens* (Maury, 1909) (Figure 1.1C, D) from the Jackson Stage of the late Eocene and an undescribed high-spired species from the Cook Mountain Formation of Mississippi (Claiborne Stage of the middle Eocene; illustrated by Dockery, 1980: plate 36, figures 7 and 8). This middle and late Eocene offshoot of *Levifusus* closely resembles the Oligocene and early Miocene busyconid genus *Spinifulgur* and is here considered to be the ancestor of the family Busyconidae.

Archefulgur Petuch, Myers, and Berschauer, new genus

Diagnosis: The new genus encompasses small, pyriform levifusine echinofulgurids that differ from the rest of their subfamily by having only a single row of spines around the shoulder; like typical levifusines, members of the new genus have very long and narrow siphonal canals and a distinct constriction at the body whorl-siphonal canal juncture; the siphonal canals are ornamented with strong spiral threads; in place of a row of spines around the mid-body, *Archefulgur* species have a large, wide, and flattened smooth band just posterior to the constriction; body whorl sculpture varies from smooth and silky (as on the type species) to being covered with small, coarse spiral threads (as on the undescribed species illustrated by Dockery, 1980); protoconch composed of 2 or 3 proportionally-large rounded whorls; apertures wide and flaring, with the interiors being ornamented with strong lirae.

Type Species: *Archefulgur fulguriparens* (Maury, 1909) (originally "*Levifusus*" *fulguriparens*, shown here on Figure 1.1C, D), Moodys Branch Formation of Louisiana, Jackson Stage of the late Eocene.

Other Species in *Archefulgur*: Only one other *Archefulgur* is known, an unnamed species from the Cook Mountain Formation of Mississippi, Claiborne Stage of the middle Eocene (illustrated in Dockery, 1980, plate 36, figures 7 and 8).

Geochronologic Range: The new genus is known only from the middle and late Eocene (Claiborne and Jackson Stages) of Mississippi and Louisiana.

Etymology: The new genus is named as a combination of "archaea", "ancient", and "fulgur", the old name for the busycon whelks.

Discussion: With its distinctive busyconoid shape and single row of large, knob-like shoulder spines, *Archefulgur* is unquestionably the progenitor of the family Busyconidae. The type species, *Archefulgur fulguriparens*, closely resembles some of the low-spired *Spinifulgur* species from the late Chattian Oligocene, such as *Spinifulgur stellatum* (Dall, 1890), and from the Burdigalian Miocene, such as *Spinifulgur armiger* Petuch, 2004 (Figure 1.3 B). The new genus differs in having a proportionally larger and better-developed rounded cord along the anterior end of the body whorl, and in having a protoconch composed of larger and more rounded whorls. Although *Archefulgur* became extinct at the end of the Eocene, its offshoot group, the family Busyconidae, was represented throughout the Oligocene by the primitive busyconid genus *Spinifulgur*.

Echinofulgurinae Petuch, 1994

Diagnosis (taken from the original description): "Shells [originally "Melongenids"] with inflated body whorls, well-developed siphonal canals, high, pyramidal spires, and 2 rows of large spines, one around the shoulder and one around anterior of body whorl near body whorl-siphonal canal junction; sutures often loosely bound, open, with last part of body whorl disconnected from previous whorls, siphonal canals long and slender" (Petuch, 1994: 306).

Type Genus: *Echinofulgur* Olsson and Harbison, 1953 (Type species: *Echinofulgur echinatum* (Dall, 1890), Fort Denaud Member, Caloosahatchee Formation of southern Florida.

Discussion: The senior author originally placed the genera *Tropochasca* Olsson, 1967 (confined to the Tamiami Formation, Piacenzian Pliocene of southern Florida) and *Cornulina* Conrad, 1853 (Eocene of the Mississippi River Valley) in the subfamily Echinofulgurinae. This assignment was based upon the presence, in both genera, of two rows of spines that are arranged in a similar pattern to those seen on members of the genus *Echinofulgur*. Both *Cornulina* and *Tropochasca*, however, have globose, compact shells with low spires and short, stubby siphonal canals and appear much closer, morphologically, to members of the Melongenidae, particularly the extinct northern South American genus *Torquifer* Roth, 1981. *Cornulina* and *Levifusus* occur together in several Eocene formations in Alabama, Mississippi, and Louisiana, demonstrating that *Cornulina* was not an offshoot of *Levifusus*. Based upon their overall compact and massive shell shapes, we here consider the genera *Tropochasca* and *Cornulina* to be members of the family Melongenidae and not to be members of the family Echinofulguridae. The double row of spines seen in both families appears to be an example of convergent evolution and does not reflect a close phylogenetic relationship.

Extinct Genera of the Subfamily Busyconinae

Of the two busyconid subfamilies, the Busyconinae is oldest, first appearing in the early Oligocene as the genus *Spinifulgur* (see Petuch, 1994: 309). Although very similar to the Eocene

Archefulgur in overall shell shape and size, *Spinifulgur* differs in the structure of the protoconch, which is usually composed of two and one-half whorls as opposed to the one and one-half or two whorls seen on *Archefulgur*. The superficial similarity of the multinucleate protoconchs of the oldest *Spinifulgur* species to those of the Eocene genus *Levifusus* led MacNeil and Dockery (1984: 148-150) to place these primitive busyconids in the genus *Levifusus*. The protoconchs of the *Levifusus* (as typified by *L. trabeatus*) and *Archefulgur* species, however, are proportionally smaller and more elongated than those of *Spinifulgur*, which has more bulbous protoconch whorls (illustrated by MacNeil and Dockery, 1984: plate 54, figures 8 and 9). These proportionally-large protoconchs presage the rounded, bulbous protoconchs of modern busyconids and we consider the "*Levifusus*" species discussed by MacNeil and Dockery to belong to the most primitive busyconid group, the genus *Spinifulgur* (examples shown on Figure 1.3).

The Genus *Spinifulgur* Petuch, 1994

Based on shell morphology, at least three species of *Spinifulgur* are known to occur in the Rupelian Age of the Oligocene. All of these, however, were lumped under a single species name, *Spinifulgur spiniger* (Conrad, 1849) (Figure 1.3D), by MacNeil and Dockery (1984). The oldest of the "*spiniger*" morphs is a low-spired form from the early Rupelian Red Bluff Formation of Mississippi (see MacNeil and Dockery, 1984: plate 54, figure 5) and this earliest-known true busyconid closely resembles the late Eocene *Archefulgur fulguriparens* in overall shell shape and size. Specimens of "*spiniger*" from the younger Rupelian Mint Springs Formation of Mississippi (illustrated by MacNeil and Dockery, 1984: plate 54, figure 6) have higher spires and stronger corded sculpture on their body whorls. Although identified as "*spiniger*" by MacNeil and Dockery, both of these important small busyconids need to be named, as they are stratigraphically and morphologically distinct and represent the first major pulse of evolution in the family Busyconidae.

Classic specimens of *Spinifulgur spiniger*, such as the individual illustrated here (Figure 1.3D), are confined to the upper Rupelian beds, particularly the Byram Formation of the Vicksburg Group. These examples of the true *S. spiniger* have high, elevated spires and resemble tiny *Busycon* species. The complex of early *spiniger*-type taxa gave rise, in a relatively short period of time, to a number of closely related species that spread across the area of the southern Mississippi Embayment, northern Florida, and Georgia. Some of these included the ornate *Spinifulgur gemmulatum* Petuch, 1997 from the late Rupelian Suwannee Formation of northern Florida, and the flat-spired *S. proterum* (Gardner, 1944) from the contemporaneous Flint River Formation of southern Georgia. By the Chattian Age of the late Oligocene, the genus *Spinifulgur* had spread as far north as North Carolina, where it is represented in the fossil record by a small, spiny species from the Belgrade Formation ("Silverdale Marls"), *S. onslowensis* (Kellum, 1926) (Figure 1.3A). At the same time, farther south in what is now central western Florida, the genus was undergoing a species radiation within the coral reef systems of the Tampa area. These late Oligocene reef systems, referred to as the "Tampa Reef Tract and Archipelago" (Petuch, 2004: 70-78), provided the habitats for the evolution of three endemic species, including *S. tampaensis* (Dall, 1890), *S. stellatum* (Dall, 1890), and *S. perizonatum* (Dall, 1890) (illustrated in Dall, 1915).

The genus *Spinifulgur* persisted into the early Miocene (Burdigalian Age), but was confined to the Choctaw Sea embayment area of northern Florida and southern Georgia (see Petuch, 2004: 79-87). Here, in the richly-diverse fossil beds of the Chipola Formation, the last species of the genus, *S. epispiniger* (Gardner, 1944) (Figure 1.3C) and *S. armiger* Petuch, 2004 (Figure 1.3B), co-occurred with the first species of the genus *Busycon* (*B. burnsi* and *B. diegelae*; discussed in Chapter 3). By the end of Chipola time, these last relictual taxa disappeared and the genus *Spinifulgur* was extinct. The odd, flat-spired and carinated "*Busycon*" *sicyoides* Gardner, 1944, sometimes placed in *Spinifulgur*, is here transferred to *Pyruella* (subfamily Busycotypinae) and is considered to be the oldest member of its genus and the progenitor of its subfamily (discussed later in this chapter). The genus *Spinifulgur* is represented by 10 described species and these are listed in Appendix 1 at the end of the book.

The Genus *Sycopsis* Conrad, 1867

This small genus, comprising only three described species and one undescribed species, is geographically confined to the fossil beds of Chesapeake Bay, Maryland. During the Burdigalian, Langhian, Serravallian, and Tortonian Ages of the Miocene, this area constituted the "Salisbury Sea" (Petuch, 2004: 7-8) and evolved a highly endemic molluscan fauna, complete with numerous endemic genera (Petuch, 1993: 155-173; 2004: 87-123). The Salisbury Sea also represented the faunal center of the Transmarian Molluscan Province (Petuch, 1988; 1993; 2004: 29-34). One of these Transmarian endemic taxa, the busyconid genus *Sycopsis*, resembles a large, inflated *Spinifulgur* and is obviously the direct descendant of the older Oligocene and early Miocene genus. Indeed, the shell morphology of the two genera is so similar that Martin (1904) even referred to an undescribed species from the Serravallian-aged Choptank Formation as "*Fulgur spiniger* var." (this shell was later named *Sycopsis lindae* by the senior author in 1988). The genus *Sycopsis* differs from *Spinifulgur* in having much larger, more inflated and thinner shells, with more rounded shoulder areas and more sloping spire whorls. *Sycopsis* species also lack the strong rib-like apertural lirae that are typical of *Spinifulgur* species, having, instead, wide and flaring apertures with smooth interiors.

In Maryland, *Sycopsis* is known from only three geological formations of the Chesapeake Group: the Calvert Formation (Langhian Age), with an undescribed species in the Plum Point Member; the Choptank Formation (Serravallian Age), with *Sycopsis lindae* Petuch, 1988 in the Drumcliff Member (Figure 1.4C); and the St. Mary's Formation (Tortonian Age), with *Sycopsis carinatum* (Conrad, 1862) in the Cove Point Member (Figure 1.4B) and *Sycopsis tuberculatum* (Conrad, 1839) in the Windmill Point Member (Figure 1.4A). The genus is absent from the rich fossil beds of the younger Eastover Formation of Virginia (latest Tortonian and Messinian Ages), demonstrating that *Sycopsis* became extinct during the late Tortonian Age. Throughout its short geological range, the genus *Sycopsis* was apparently never very common in any ecological assemblage of the Salisbury Sea, as specimens are only infrequently collected in the stratigraphic units of the lower Chesapeake Group. The only exception is *Sycopsis lindae*, which is relatively common in beds of the Drumcliff Member of the Choptank Formation exposed along the Patuxent River. The known *Sycopsis* species are listed in Appendix 1.

The Genus *Turrifulgur* Petuch, 1988

This genus of small, elongated whelks is known from only nine described species, five of which are endemic to the Maryland Miocene. A tenth, undescribed species is also known from the Chattian Oligocene Belgrade Formation ("Silverdale Marls") of North Carolina, and this represents the oldest-known member of the genus. The Miocene species of *Turrifulgur*, listed here in Appendix 1, fall into two distinct groups: an early and middle Miocene complex from northern Florida, composed of *Turrifulgur atractoides* (Gardner, 1944) and *T. foerstei* (Gardner, 1944) (both from the Langhian Age Oak Grove Formation) and *T. alrichi* (Gardner, 1944) and *T. dasum* (Gardner, 1944) (both from the Serravallian Age Shoal River Formation); and an early and late Miocene complex from Maryland, composed of *T. marylandicum* Petuch, 1993 and *T. prunicola* Petuch, 1993 (both from the Langhian Age Calvert Formation), and *T. covepointensis* Petuch, 2004 (Figure 1.5B), *T. fusiforme* (Conrad, 1839) (Figure 1.5A), and *T. turriculus* Petuch, 1988 (Figure 1.5C) (all three from different members of the Tortonian Age St. Mary's Formation). With the exception of the unnamed late Oligocene species from North Carolina, the entire genus *Turrifulgur* is confined to the Miocene Epoch, occurring primarily in the Langhian, Serravallian, and Tortonian Ages. As in the case of *Sycopsis, Turrifulgur* is absent from the late Tortonian and Messinian Eastover Formation of Virginia, demonstrating that the genus became extinct after the middle of the Tortonian.

Turrifulgur species have a distinct shell morphology that sets them aside from all other small Miocene busyconids. Typically, members of the genus have elongated, fusiform shells with high, protracted spires, and thick, proportionally long siphonal canals that are often equal in length to the entire body whorl and spire combined. The body whorls and spires are relatively smooth and polished, often with a silky surface texture. The siphonal canal, on the other hand, is heavily sculptured with variable amounts of strong spiral cords and threads and this siphonal sculpture extends the entire length of the canal, from the body whorl-siphonal canal juncture to the anterior tip. The shoulders of *Turrifulgur* species are relatively low on the body whorl, are sharply angled, and ornamented with numerous small knobs or low spines. The subsutural area posterior of the shoulder angle is characteristically wide and sharply sloping, producing a protracted, subpyramidal shape to the spire whorls.

Generally, specimens of *Turrifulgur* are quite rare in Miocene fossil shell beds, particularly in northern Florida and in the Calvert Formation of Maryland. On the other hand, *T. covepointensis* from the Cove Point Member of the St. Mary's Formation, is abundant at Little Cove Point, Calvert County, Maryland and is the most frequently collected busyconid at that locality. In the stratigraphically-higher Windmill Point Member of the St. Mary's Formation, along the St. Mary's River, St. Mary's County, Maryland, the descendant species *T. fusiforme* is equally abundant. These are the only two known localities where representative specimens of the genus can be collected in large quantities. The known *Turrifulgur* species are listed in Appendix 1 at the end of this book.

Extinct Genera of the Subfamily Busycotypinae

The subfamily Busycotypinae first appears roughly 10 million years after the evolution of the subfamily Busyconinae. The oldest species that is referable to the subfamily Busycotypinae is

Pyruella sicyoides (Gardner, 1944) (Figure 1.8C), a flat-spired *Spinifulgur*-type shell from the Burdigalian Miocene Chipola Formation of northern Florida. By the Langian Miocene, offshoots of this primitive form had moved northward into the Salisbury Sea of Maryland (see Petuch, 2004; Petuch and Drolshagen, 2010) and underwent the first species radiations of the subfamily Busycotypinae. Altogether, nine different species in the genera *Coronafulgur* Petuch, 2004 and *Sycofulgur* Marks, 1950 evolved during the Langhian, Serravallian, and Tortonian Ages along the Maryland coast and some of these became the stem stock for the younger Plio-Pleistocene *Brachysycon* and *Busycotypus* species radiations. Unlike the ancestral *Pyruella sicyoides* and *P. blountense*, these Maryland Miocene busycotypine species were large animals, often reaching lengths of over 200 mm. Some of these over-sized canaliculate busyconids, among the largest-known Miocene gastropods in North America, include species of the genus *Sycofulgur*, such as *S. choptankensis* (Petuch, 1993), *S. martini* (Petuch and Drolshagen, 2004) (Figure 1.15B), and *S. rugosum* (Conrad, 1843) (Figure 1.15A). The similar but smaller busycotypine genus, *Coronafulgur* (examples shown on Figure 1.6), also evolved in the Salisbury Sea and spread southward into Virginia (*Coronafulgur kendrewi* Petuch, 2004) and to northern Florida (*Coronafulgur propecoronatum* (Mansfield, 1935)) by the late Messinian Age.

At the end of the Miocene, the predecessor genera *Coronafulgur* and *Sycofulgur* had become extinct, but some surviving lineages had given rise to three separate Pliocene and Pleistocene offshoot groups; the canaliculate genera *Busycotypus* Wenz, 1943, *Brachysycon* Petuch, 1994, and *Fulguropsis* Marks, 1950. These were the first busyconid genera to extend along the entire length of the Eastern United States, being found in fossil shell beds from New Jersey south to Florida and along the northern Gulf of Mexico. At the same time that these complexes of large, canaliculate species were evolving along the Eastern Seaboard, the genus *Pyruella* Petuch, 1982 was undergoing a large species explosion in the Okeechobean Sea of southern Florida (see Petuch, 2004), resulting in over 14 species alone during the Pliocene and early Pleistocene (examples shown here on Figures 1.8 to 1.12). This species radiation also resulted in the evolution of an offshoot group, the smooth and unsculptured *Pyruella*-type shells of the genus *Laevisycon* Petuch and Myers, new genus (examples shown here on Figures 1.13 and 1.14). Unlike the closely-related genus *Pyruella*, which is found in early Pleistocene fossil beds as far north as Virginia, the genus *Laevisycon* was confined to the Okeechobean Sea and has never been found outside of southern Florida.

The Genus *Coronafulgur* Petuch, 2004

Members of the channeled whelk genus *Coronafulgur* (examples shown on Figure 1.6) resemble smaller, more slender, and spinier versions of *Sycofulgur* species (discussed later in this section). Although contemporaneous in several Maryland formations, the two genera are consistently different, with *Coronafulgur* having a narrower and less deeply-incised sutural channel and in having more numerous, smaller, and sharper spines along the edge of the shoulder. *Coronafulgur* species also have higher and more protracted spires, which often exhibit scalariformation (such as seen in the high-spired *Coronafulgur kendrewi* Petuch, 2004, Figure 1.6C). Both *Sycofulgur* and *Coronafulgur* occur together in the Calvert, Choptank, and St. Mary's Formations of the Maryland Miocene, but only *Coronafulgur* continues on into the Messinian Miocene Eastover Formation of Virginia, where it is the only genus belonging to the subfamily Busycotypinae. *Coronafulgur* is also a more geographically-expansive group than

Sycofulgur, being found in fossil beds in New Jersey, Maryland, Virginia, and northwestern Florida.

Throughout its geologic time span of around 15 million years, *Coronafulgur* evolved five distinct species. The genus first appears in the Langhian Age of the Miocene (Calvert Formation of Maryland; Kirkwood Formation of Delware and New Jersey) and ranges to the end of the Messinian Age of the Miocene (Eastover Formation of Virginia; Red Bay Formation of northwestern Florida). The oldest species, *Coronafulgur calvertensis* (Petuch, 1988) resembles a small, flat-spired *Sycofulgur scalaspirus* (Conrad, 1863), but differs in having a much smaller and less-developed sutural channel. The genus is absent from the rich fossil beds of the Serravallian Age Choptank Formation of Maryland, and may have moved into deeper water during that time of environmental degradation. Warm marine conditions returned during the Tortonian Age (see Petuch, 2004; Petuch and Drolshagen, 2010) and two species of *Coronafulgur* evolved within the Salisbury Sea at this time; the low-spired *C. chesapeakensis* (Petuch, 1988) from the Cove Point Member of the St. Mary's Formation (Figure 1.6B) and higher-spired *C. coronatum* (Conrad, 1839) from the Windmill Point Member of the St. Mary's Formation (Figure 1.6A). The genus persisted on into the Messinian Age and is represented by the slender, scalariform *C. kendrewi* (Petuch, 2004) from the Cobham Bay Member of the Eastover Formation of Virginia (Figure 1.6C). The last species of the genus appears to be the low-spired *C. propecoronatum* (Mansfield, 1935), which persisited to the very end of the Messinian Age in northwestern Florida and is found in the Red Bay Formation of the Alum Bluff Group. The known *Coronafulgur* species are listed in Appendix 1 at the end of the book.

The Genus *Brachysycon* Petuch, 1994

Members of the channeled whelk genus *Brachysycon* resemble small, truncated, inflated versions of *Busycotypus* species. These distinctive shells, with examples shown here on Figure 1.7, differ from members of the genus *Busycotypus* in having shorter, stubbier siphonal canals, larger and more distinct spines and knobs on the shoulder, and narrower and shallower sutural channels. In some species, such as *B. amoenum* (Conrad, 1875) (Figure 1.7A) and *B. kissimmeensis* Petuch, 1994 (Figure 1.7C), the sutural channel is very shallow and essentially absent. This lack of a deep sutural channel is a good way of distinguishing full grown *Brachysycon* species from juvenile *Busycotypus* species. The genus was one of the most geographically-widespread busyconid groups, being found from Virginia and North Carolina, south across the entire Florida Peninsula, and along the northeastern Gulf of Mexico.

This distinctive group of inflated, pear-shaped channeled whelks was short-lived geologically, having evolved in the early Piacenzian Age of the Pliocene and becoming extinct at the end of the Gelasian Age of the early Pleistocene, a period of only about 2.5 million years. Within this time span, however, *Brachysycon* evolved four distinct species, with the oldest and most primitive being *B. propeincile* (Mansfield, 1930) (Figure 1.7D) from the early Piacenzian Age lower beds of the Jackson Bluff Formation of northern Florida. During the later Pliocene, two other species evolved, the high-spired *B. kissimmeensis* Petuch, 1994 from the mid-Piacenzian Age Pinecrest Member (Kissimmee facies) of the Tamiami Formation of southern Florida (Figure 1.7C) and the beaded-shouldered *B. canaliferum* (Conrad, 1862) from the late Piacenzian Age Chowan River Formation of Virginia and North Carolina and the contemporaneous

Fruitville Member of the Tamiami Formation of southern Florida (Figure 1.7B). By the beginning of the Pleistocene, a descendant species had evolved; the knobbed *B. amoenum* (Conrad, 1862) from the Gelasian Age James City Formation of Virginia and North Carolina and the contemporaneous Nashua Formation of eastern Florida (Figure 1.7A). During the early Pleistocene in Virginia, North Carolina, and eastern Florida, *Brachysycon* species coexisted, often in immense aggregations, with other busyconid genera such as *Busycon*, *Sinistrofulgur*, *Busycotypus*, and *Pyruella*, and these formed the richest busyconid assemblages ever seen at any time in the United States. A list of the described *Brachysycon* species is given in Appendix 1 at the end of this book. Several still-undescribed species are known from the Pliocene and early Pleistocene of Florida.

The Genus *Pyruella* Petuch, 1982

The genus *Pyruella* Petuch, 1982 is the most species-rich group of busyconids known, with 19 described species (examples shown here on Figures 1.8 through 1.12). Of these 19 taxa, only two species, *Pyruella bladenense* (Gardner, 1948) (Figure 1.10C) and *P. willcoxi* (Gardner, 1948), are known to have occurred outside of Florida. All the rest of the known *Pyruella* species are confined to Florida, with two species having lived in the Miocene Choctaw Sea of northern Florida (the Burdigalian Age *P. sicyoides* (Gardner, 1944) from the Chipola Formation and the Messinian Age *P. blountense* (Mansfield, 1935) from the Red Bay Formation) and the other 14 species being confined to the Okeechobean Sea of southern Florida (found in the Tamiami Formation; see Petuch, 2004; Petuch and Roberts, 2007). Of the 19 known species, the Gelasian Age *Pyruella bladenense* is the most widespread taxon, being found in the James City Formation of Virginia and North Carolina, the Waccamaw Formation of North and South Carolina, and the Nashua Formation of eastern Florida. The genus first appears in the Burdigalian Miocene as a single species, *Pyruella sicyoides*, and then underwent a large species radiation in the Piacenzian Pliocene (Tamiami Formation), producing 12 species (see Petuch, 1982; 1994; 2004). The genus persisted into the middle Pleistocene (Calabrian Age) as *Pyruella tomeui* Petuch, 2004 from the Bermont Formation (the last-living species; Figure 1.9B). As a genus, *Pyruella* is geologically the longest-lived group of all the busyconids, ranging from the Burdigalian Miocene to the late Calabrian Pleistocene, a time span of over 19 million years.

Morphologically, *Pyruella* is the most primitive group within the Busycotypinae, with many early Pliocene forms, such as *Pyruella harasewychi* Petuch, 1982 (Figure 1.8B) and *Pyruella miccosukee* Petuch, 1991, diverging very little from the basic shell form of the ancestral *P. sicyoides*. The genus contains two separate and distinct lineages; one that retains a flat spire and has the body whorl sculpture composed of large, heavy spiral cords, and one that has an elevated, stepped spire and has the body sculpture composed of numerous fine spiral threads and fine cords. The first of these contains species such as *Pyruella harasewychi*, *P. blountense*, and *P. miccosukee*, and also *P. rugosicostata* Petuch, 1982 (Figure 1.8A), *P. seminole* Petuch, 1982 (Figure 1.12B), *P. streami* Petuch, 1994 (Figure 1.11A), and *P. waltfrancei* Petuch, 1982 (Figure 1.9C). The second group contains the largest number of species and includes *P. basingerensis* Petuch, 1994 (Figure 1.10B), *P. bladenense*, *P. carraheri* Petuch, 1994 (Figure 1.11B), *P. eismonti* Petuch, 1994 (Figure 1.10A), *P. federicoae* (Figure 1.12C), *P. osceolai* Petuch, 1982, *P. sarasotaensis* Petuch, 1982 (Figure 1.12A), *P. schmidti* Petuch, 1994 (Figure 1.9A), *P. tomeui*, and *P. willcoxi*. These two subgroups may eventually prove to be of subgeneric rank. The genus

Pyruella is the only group within the Busycotypinae that has a variable degree of development of the sutural channel. Some species, like *P. harasewychi* and *P. streami*, completely lack a sutural channel, while others, such as *P. sarasotaensis* and *P. schmidti*, have very narrow, but deep, sutural channels. A list of the described *Pyruella* species is given in Appendix 1 at the end of the book.

The Genus *Laevisycon* Petuch, Myers, and Berschauer, new genus

Diagnosis: Shells small for the subfamily, thin and fragile, distinctly pyriform, with high, stepped spires and long, narrow siphonal canals; shoulders are broadly angled, with rounded, unornamented edges; body whorl and spire whorls completely smooth and shiny, completely without spiral sculpture, or with only a small amount of spiral ornamentation around the anterior end of the body whorl; sutural channel absent on most species, but only poorly-formed and almost absent on other species; siphonal canals ornamented with numerous fine spiral cords and threads; aperture proportionally large, oval in shape, smooth on the interior; protoconchs proportionally large, bulbous and rounded, composed of 1 ½ whorls.

Type Species: *Laevisycon laevis* (Petuch, 1982) (originally "*Pyruella laevis*), Unit 4 of the Fruitville Member, Tamiami Formation of southern Florida, late Piacenzian Age of the Pliocene (Figure 1.13A).

Other Species in *Laevisycon*: an unnamed species from the Buckingham Member of the Tamiami Formation, early Piacenzian (or possibly late Zanclean) Pliocene of southern Florida; *Laevisycon demistriatum* (Petuch, 1982) (Figure 1.14B), Pinecrest Member of the Tamiami Formation, Piacenzian Pliocene; *Laevisycon turbinalis* (Petuch, 1982) (Figure 1.14A), Unit 3 of the Fruitville Member, Tamiami Formation, late Piacenzian Pliocene; *Laevisycon planulatum* (Dall, 1890) (Figure 1.13C), Fort Denaud Member of the Caloosahatchee Formation, Gelasian Pleistocene; *Laevisycon soror* (Petuch, 1994) (Figure 1.14C), Fort Denaud Member of the Caloosahatchee Formation, Gelasian Pleistocene; an unnamed species from the Ayers Landing Member of the Caloosahatchee Formation, late Gelasian Pleistocene.

Geologic Range: *Laevisycon* first appears in the late Zanclean-early Piacenzian Pliocene of southern Florida, where it is found in the Buckingham Member of the Tamiami Formation. The genus ranges into the early Pleistocene, where it is represented by three species in the Gelasian Caloosahatchee Formation. *Laevisycon* becomes extinct at the end of the Gelasian Age.

Etymology: Named as a combination of "laevus", "smooth" and "sycon", "fig".

Discussion: The named members of this new genus were originally described as species of *Pyruella* (Petuch, 1982; 1994), primarily because of their similar shell shape and size. That genus is now known to comprise only shells with heavy spiral sculpture on the body whorls and spires and on the interior of the aperture, charcters that are absent in *Laevisycon*. The geologic range of *Pyruella* is also far more expansive than that of *Laevisycon*, with heavily-ribbed *Pyruella* species being found in the Messinian Miocene (*P. blountense*) and extending right through the entire Pliocene until the Calabrian Pleistocene (*P. tomeui*). *Laevisycon*, on the other hand, ranges only from the early Pliocene (late Zanclean-early Piacenzian Ages) to the early

Pleistocene (late Gelasian Age). The genus *Pyruella* is also geographically far more wide-ranging than *Laevisycon*, being found in Plio-Pleistocene fossil beds extending from Virginia south to Florida and into the northeastern Gulf of Mexico (Florida Panhandle). Throughout the entire geochronologic range of *Laevisycon*, however, the new genus has always been confined to southern Florida. There, *Laevisycon* was associated with tropical estuarine environments (such as those in the Myakka Lagoon System and Miccosukee Island of the Okeechobean Sea; see Petuch, 2004) and may have represented a brackish water offshoot of the geologically-older *Pyruella*.

The Genus *Sycofulgur* Marks, 1950

Morphologically, the genus *Sycofulgur* closely resembles *Coronafulgur* Petuch, 2004 (discussed earlier), but differs in having much larger, broader, and much more inflated shells that consistently have wider, deeper, and better-developed sutural channels. Only five species are known, all of which are confined to the Miocene fossil beds of New Jersey, Delaware, Maryland, and northern Virginia (the area of the Miocene Salisbury Sea; Petuch, 2004; Petuch and Drolshagen, 2010). The genus is geochronologically short-lived, with the oldest-known species, *Sycofulgur scalaspirus* (Conrad, 1843), first appearing in the Langhian Age Calvert and Kirkwood Formations of Maryland, New Jersey, and Delaware and the youngest-known species, *Sycofulgur asheri* (Petuch, 1988), occurring in the mid-Tortonian Age Chancellor Point Sandstone layer of the St. Mary's Formation. The genus apparently becomes extinct by the mid-Tortonian, as the genus is absent from the Messinian Age Eastover Formation of Virginia. Interestingly, the genus *Coronafulgur*, which occurs together with *Sycofulgur* in the Salisbury Sea throughout the Langhian, Serravallian, and Tortonian Ages of the Miocene, has a longer geologic lifespan, as it persisted into the late Messinian Age in Virginia and Florida, almost 3 million years after *Sycofulgur* had disappeared.

Two of the *Sycofulgur* species grew to very large sizes, often exceeding 200 mm in length; the large and inflated *Sycofulgur choptankensis* (Petuch, 1993) from the Drumcliff Member of the Choptank Formation and *Sycofulgur rugosum* (Conrad, 1843) from the Windmill Point Member of the St. Mary's Formation (Figure 1.15A). Both of these species were the largest gastropods ever found in the Maryland Miocene and were, undoubtedly, the top molluscan predators in the Salisbury Sea during the Serravallian and Tortonian Ages. The late Serravallian *Sycofulgur martini* Petuch and Drolshagen, 2010 (from the Cove Point Member of the St. Mary's Formation; Figure 1.15B), although similar to its younger descendant *S. rugosum*, is a much smaller and broader shell with less-developed and smaller knobs along the shoulder angle. This sculptural pattern returns in the last-living species, *S. asheri*, which has a smooth shoulder carina that is devoid of any knobs or spines. Two representative species of *Sycofulgur* are shown here on Figure 1.15 and a list of the described species is given on Appendix 1 at the end of this book. The senior author originally placed all of these species in the genus *Busycotypus* (Petuch, 1988; 2004; Petuch and Drolshagen, 2010), but these should now be removed from that genus and placed in Marks' *Sycofulgur*.

Oligocene Busyconid Species Radiations

After the appearance of the primitive busyconid genus, *Spinifulgur*, in the early Oligocene (Rupelian Age), the first busyconid species radiation took place in central and northern Florida

and southern Georgia (the Choctaw Sea area; see Petuch, 2004). Here, during the Chattian Age, the original *Spinifulgur spiniger* and *S. nodulatum* lineages began to evolve into two different species complexes; one centered around the flat-spired and spiny-shouldered *S. stellatum* (Dall, 1890); and one centered around the heavily-knobbed *S. tampaensis* (Dall, 1890) and *S. perizonatum* (Dall, 1890). Of these late Oligocene *Spinifulgur* species, *S. tampaensis* and *S. perizonatum*, both appear to have evolved from the older, highly-ornate, and high-spired *S. gemmulatum* Petuch, 1997, which occurred in the extensive coral reef systems of the Flint River Embayment and Orange Island Reef Tract of the Choctaw Sea (preserved in the Suwannee and Flint River Formations; see Petuch, 2004: 57-67, figure 13). The flat-spired, slightly canaliculate *S. stellatum* appears to be a direct descendant of the older, similar-appearing *S. proterum* (Gardner, 1944) from the Flint River Formation of southern Georgia. These three coral reef-associated species gave rise to the early Miocene species complexes seen in the Chipola Formation of northern Florida. The busyconid species radiations of the **Oligocene Mississippi Embayment and Choctaw Sea** include:

Early Rupelian Age
Spinifulgur spiniger (Vicksburg Group)
Spinifulgur nodulatum (Vicksburg Group)
Late Rupelian Age
Spinifulgur gemmulatum (Suwannee Formation)
Spinifulgur proterum (Flint River Formation)
Chattian Age
Spinifulgur onslowensis (Belgrade Formation)
Spinifulgur perizonatum (Tampa Member, Arcadia Formation)
Spinifulgur stellatum (Tampa Member, Arcadia Formation)
Spinifulgur tampaensis (Tampa Member, Arcadia Formation)

By the end of the Chattian Age, the *Spinifulgur stellatum* lineage began to diverge from the main *Spinifulgur* line and became the progenitor of the subfamily Busycontypinae. At the same time, the *Spinifulgur perizonatum* - *S. tampaensis* lineage became the progenitor of the subfamily Busyconinae. The outlying *S. onslowensis* from North Carolina retained the shell morphology of the classic *Spinifulgur spiniger* line and was, essentially, a contemporaneous relict of the older Oligocene lineages. This pattern of two subfamilial complexes and a contemporaneous relictual complex persisted well into the Burdigalian Miocene.

Miocene Busyconid Species Radiations

The ancestral *Spinifulgur* stock was dying out by the beginning of the Miocene and separate new species complexes were appearing in northern Florida (Choctaw Sea) and in the Chesapeake Bay area (Salisbury Sea) (Petuch, 2004). In the Miocene beds of northern Florida, the first true *Busycon* species were beginning to dominate the shallow water ecosystems and quicky grew to large sizes. In the lower beds of the Chipola Formation, the first *Busycon* species, the small *B. burnsi* Dall, 1890 (Figure 3.8B) and the large *Busycon diegelae* Petuch, 2004 (Figure 3.8A), are common components of the lagoonal and estuarine facies and they were some of the top molluscan predators of their time. These, in turn, gave rise to the large, pear-shaped *Busycon radix* Gardner, 1944 during the Langhian Age (Oak Grove Formation) and later to the even

larger *Busycon montforti* Aldrich, 1909 during the Serravallian Age (Shoal River Formation). These large *Busycon* taxa, which were directly ancestral to the species radiations of the Floridian Pliocene and Pleistocene, co-occurred with several species of the smaller shells of the genus *Turrifulgur*. The busyconids of the early, middle, and late **Miocene Choctaw Sea** included:

Species Restricted to Northern Florida
Burdigalian Age
Spinifulgur armiger (Chipola Formation)
Spinifulgur epispiniger (Chipola Formation)
Busycon burnsi (Chipola Formation)
Busycon diegelae (Chipola Formation)
Pyruella sicyoides (Chipola Formation)
Langhian Age
Busycon radix (Oak Grove Formation)
Turrifulgur atractoides (Oak Grove Formation)
Turrifulgur foerstei (Oak Grove Formation)
Serravallian Age
Busycon montforti (Shoal River Formation)
Turrifulgur aldrichi (Shoal River Formation)
Turrifulgur dasum (Shoal River Formation)
Tortonian and Messinian Ages
Pyruella blountense (Red Bay Formation)
Coronafulgur propecoronatum (Red Bay Formation)

The Miocene Choctaw Sea busyconid faunas were dominated by the subfamily Busyconinae, particularly the genera *Busycon* and *Turrifulgur*. At the same time that these northern Floridian faunas were evolving, the busyconids of the Salisbury Sea of New Jersey, Delaware, Maryland, and Virginia (the core area of the Transmarian Molluscan Faunal Province; see Petuch, 2004; Petuch and Drolshagen, 2010) were forming large complexes of species in the subfamily Busycotypinae, primarily in the endemic Transmarian genus *Sycofulgur* and also in *Coronafulgur*. These busyotypine taxa occurred together with a large complex of species in the subfamily Busyconinae, primarily in the endemic Transmarian genus *Sycopsis* and the widespread Miocene genus *Turrifulgur*. The Busyconidae of the early, middle, and late **Miocene Salisbury Sea** and **Transmarian Province** included:

Species Restricted to Maryland, Delaware, New Jersey, and Virginia
Langhian Age
Sycopsis unnamed species (Calvert Formation)
Turrifulgur marylandicum (Calvert Formation)
Turrifulgur prunicola (Calvert Formation)
Coronafulgur calvertensis (Calvert Formation)
Sycofulgur scalaspirus (Calvert and Kirkwood Formations)
Serravallian Age
Sycopsis lindae (Choptank Formation)
Sycopsis carinatum (Cove Point Member, St. Mary's Formation)
Turrifulgur covepointensis (Cove Point Member, St. Mary's Formation)

Coronafulgur chesapeakensis (Cove Point Member, St. Mary's Formation)
Sycofulgur choptankensis (Choptank Formation)
Sycofulgur martini (Cove Point Member, St. Mary's Formation)

Tortonian Age

Sycopsis tuberculatum (Windmill Point Member, St. Mary's Formation)
Turrifulgur fusiforme (Windmill Point Member, St. Mary's Formation)
Turrifulgur turriculus (Chancellor Point Sandstone, St. Mary's Formation)
Coronafulgur coronatum (Windmill Point Member, St. Mary's Formation)
Sycofulgur rugosum (Windmill Point Member, St. Mary's Formation)
Sycofulgur asheri (Chancellor Point Sandstone, St. Mary's Formation)

Messinian Age

Coronafulgur kendrewi (Cobham Bay Member, Eastover Formation)

As can be seen from these lists, a major molluscan extinction event took place at the end of the Messinian Miocene, and this resulted in the complete disappearance of the genera *Turrifulgur*, *Sycopsis*, *Coronafulgur*, and *Sycofulgur* from the fossil record. This abrupt extinction of all the Transmarian busyconid taxa most probably resulted from the worldwide climatic degeneration caused by the impact of a giant asteroid at Kara-Kul, Tajikistan (for details, see Petuch, 2012: 967-981). Immediately following this severe extinction event and worldwide cooling, the sinistral ("left-handed") genus *Sinistrofulgur* appears for the first time in the early Zanclean Age of the Pliocene. This sinistrality in the Busyconidae may have been due to a coiling-direction mutation in a normally-dextral busyconine, induced by the extreme environmental stresses and climatic degeneration during the late Messinian-early Zanclean interval. Interestingly enough, the left-handed cone shell genus *Contraconus* also appears at this time and co-occurred with *Sinistrofulgur* throughout the Pliocene and early Pleistocene (Petuch, 2004).

Pliocene Busyconid Species Radiations

After the terminal Messinian extinction, Florida and the Gulf of Mexico region appear to have served as a refugium for the family Busyconidae. Here, the few surviving busyconids underwent rapid pulses of evolution, resulting in the first appearance of several new genera in both the Busyconinae and Busycotypinae. These included the left-handed coiling genus *Sinistrofulgur*, the elongated, flat-spired genera *Lindafulgur* and *Busycoarctum* (all in the subfamily Busyconinae) and the channel-sutured genera *Busycotypus*, *Brachysycon*, and *Fulguropsis* and the dwarf whelk genus *Laevisycon* (all in the subfamily Busycotypinae). These newly-evolved, post-Miocene genera coexisted with two well-established relictual genera, *Busycon* and *Pyruella*, both of which were the sole survivors of the Messinian extinction. Of special interest during the late Zanclean Pliocene was the sudden appearance of the left-handed genus *Sinistrofulgur* in the Okeechobean Sea of southern Florida. Obviously deriving from the right-handed genus *Busycon*, this new sinistral group first appears in the basal beds of the Tamiami Formation in southern Florida (*Sinistrofulgur hollisteri*) and appears to have resulted from a macromutation of one of the early Zanclean descendants of the Miocene *Busycon montforti* species complex.

Unlike the Miocene species radiations, which were concentrated in two different areas (Maryland and Florida), the Pliocene busyconid species complexes were far more homogeneous wide-ranging, with many species ranging from Virginia south to Florida and the northeastern

Gulf of Mexico (the core area of the Caloosahatchian Molluscan Faunal Province; see Petuch, 2004; 2013). Having evolved in Florida, these genera now moved northward up the Eastern Seaboard to populate the coastal areas that were left devoid of busyconids due to the Messinian lower temperatures and extreme sea level drop (Petuch, 2012; Petuch and Drolshagen, 2010). By the late Zanclean Age of the Pliocene, a modern-appearing busyconid fauna had become established from Virginia and North Carolina all the way south to the Florida Panhandle. The Busyconidae of the early and late **Pliocene Caloosahatchian Molluscan Province** included:

Restricted to Eastern Mexico—Messinian Age (Possibly Early Zanclean Age)
Lindafulgur alencasterae (Agueguexquite Formation of Veracruz State, Mexico)

Late Zanclean and early Piacenzian Ages
Busycon alumense (basal beds of the Jackson Bluff Formation)
Busycon filosum (Duplin Formation and Buckingham Member, Tamiami Formation)
Busycon pachyus (Buckingham Member, Tamiami Formation)
Sinistrofulgur grabaui (Buckingham Member, Tamiami Formation)
Sinistrofulgur hollisteri (Buckingham Member, Tamiami Formation)
Lindafulgur lindajoyceae (Buckingham Member, Tamiami Formation)
Busycoarctum tudiculatum (basal beds of the Jackson Bluff Formation and the Buckingham Member of the Tamiami Formation)
Busycotypus libertiense (lower beds of the Jackson Bluff Formation and the Buckingham Member of the Tamiami Formation)
Brachysycon preopeincile (lower beds of the Jackson Bluff Formation and Buckingham Member of the Tamiami Formation)
Fulguropsis aepynotum (lower beds of the Jackson Bluff Formation)
Fulguropsis carolinensis (Duplin Formation and Buckingham Member of the Tamiami Formation)
Pyruella harasewychi (Buckingham Member, Tamiami Formation)
Pyruella waltfrancei (Buckingham Member, Tamiami Formation)
Laevisycon unnamed species (Buckingham Member, Tamiami Formation)

Middle Piacenzian Age
Busycon maximus (Duplin and Yorktown Formations)
Busycon titan (Golden Gate Member, Tamiami Formation)
Sinistrofulgur contrarium (Yorktown, Duplin, and Tamiami Formations)
Sinistrofulgur robesonense (Duplin, Bear Bluff, and Tamiami Formations)
Lindafulgur miamiensis (Golden Gate Member, Tamiami Formation)
Busycoarctum superbus (Golden Gate Member, Tamiami Formation)
Busycoarctum tropicalis (Pinecrest Member, Tamiami Formation)
Busycotypus bicoronatum (Pinecrest Member, Unit 7, Tamiami Formation)
Busycotypus incile (Yorktown and Duplin Formations)
Busycotypus mansfieldi (upper beds of the Jackson Bluff Formation and the Pinecrest Member of the Tamiami Formation)
Brachysycon kissimmeensis (Pinecrest Member, Kissimmee Facies of the Tamiami Formation)
Fulguropsis excavatum (Pinecrest Member of the Tamiami Formation, Duplin Formation, and Yorktown Formation)

Fulguropsis radula (Golden Gate Member of the Tamiami Formation)
Pyruella carraheri (Pinecrest Member, Kissimmee facies, of the Tamiami Formation)
Pyruella miccosukee (Pinecrest Member, Unit 8, Tamiami Formation)
Pyruella osceola (Pinecrest Member, Unit 8, Tamiami Formation)
Pyruella rugosicostata (Pinecrest Member, Unit 7, Tamiami Formation)
Pyruella sarasotaensis (Pinecrest Member, Unit 5, Tamiami Formation)
Pyruella streami (Pinecrest Member, Unit 9, Tamiami Formation)
Laevisycon demistriatum (Pinecrest Member, Unit 7, Tamiami Formation)

Late Piacenzian Age

Busycon auroraensis (Chowan River Formation and Fruitville Member, Tamiami Formation)
Sinistrofulgur adversarium (Chowan River Formation and Fruitville Member, Tamiami Formation)
Sinistrofulgur unnamed species (Fruitville Member, Unit 3 of the Tamiami Formation)
Busycotypus concinnum (Chowan River Formation and Fruitville Member of the Tamiami Formation)
Brachysycon canaliferum (Chowan River Formation and Fruitville Member of the Tamiami Formation)
Fulguropsis pyriformis (Chowan River Formation and Fruitville Member of the Tamiami Formation)
Pyruella basingerensis (Fruitville Member, Kissimmee Facies, Tamiami Formation)
Pyruella federicoae (Fruitville Member, Unit 3 of the Tamiami Formation)
Pyruella schmidti (Fruitville Member, Unit 4 of the Tamiami Formation)
Laevisycon laevis (Fruitville Member, Unit 4 of the Tamiami Formation)
Laevisycon turbinalis (Fruitville Member, Unit 3 of the Tamiami Formation)

With 44 described species in eight different genera being present during the Zanclean and Piacenzian Ages, the Pliocene Epoch encompassed the largest busyconid fauna that ever evolved in the entire history of the family. During this time, warm tropical and subtropical conditions extended all the way northward to Virginia and this mild marine climate allowed for the development of many different types of marine communities and ecosystems. This was particularly true in southern Florida, where the immense coral reef structure of the Everglades Pseudoatoll had reached its peak of development during the Piacenzian Age (see Petuch, 2004; Petuch and Roberts, 2007 for maps of the Everglades Pseudoatoll and ecological and oceanographic data). The rich lagoonal habitats of the Pseudoatoll supported a large endemic species radiation of the genus *Pyruella* (with at least 12 different species).

Pleistocene Busyconid Species Radiations

With the exception of the genus *Lindafulgur*, which apparently moved into deep water and disappeared from the near-shore fossil record, all the genera that were present during the Piacenzian Age of the late Pliocene persisted on into the Gelasian Age of the early Pleistocene. This original busyconid fauna, composed of survivors from the Pliocene, subsequently underwent three separate speciation and extinction events during the 2 million year time span of the Pleistocene. The largest extinction took place at the end of the Gelasian Age (1.8 million years BP), when the genera *Brachysycon* and *Laevisycon* became extinct and the genus *Busycoarctum* disappears from the fossil record by, again, moving into deeper water habitats

(where it still resides today). A second catastrophic event took place at the end of the Calabrian Age (1.8 millon-780,000 years BP) that resulted in the extinction of the genus *Pyruella*. All geological units in the Eastern United States that were deposited during the subsequent Ionian Age (780,000-126,000 years BP) and Tarantian Age (126,000-12,000 years BP) contain only four busyconid genera; *Busycon*, *Sinistrofulgur*, *Busycotypus*, and *Fulguropsis*. This reduced busyconid fauna persisted into the Holocene and set the stage for the evolution of our modern fauna. The Busyconidae of the early and late **Pleistocene Eastern United States** include:

Early Gelasian Age

Busycon duerri (Fort Denaud Member, Caloosahatchee Formation)
Busycon gilmorei (James City and Waccamaw Formations)
Sinistrofulgur caloosahatcheensis (Fort Denaud Member, Caloosahatchee Formation)
Sinistrofulgur labelleensis (Bee Branch Member, Caloosahatchee Formation)
Sinistrofulgur palmbeachensis (Fort Denaud Member, Caloosahatchee Formation)
Sinistrofulgur pamlico (James City and Waccamaw Formations)
Busycoarctum rapum (Fort Denaud Member, Caloosahatchee Formation)
Brachysycon amoenum (James City and Nashua Formations)
Fulguropsis elongatus (Bee Branch Member, Caloosahatchee Formation)
Fulguropsis floridanum (Fort Denaud Member, Calooshatchee Formation)
Pyruella eismonti (Fort Denaud Member, Caloosahatchee Formation)
Laevisycon planulatum (Fort Denaud Member, Caloosahatchee Formation)
Laevisycon soror (Fort Denaud Member, Calooshatchee Formation)

Late Gelasian Age

Busycon rucksorum (Rucks Pit Member, Nashua Formation)
Sinistrofulgur yeehaw (Rucks Pit Member, Nashua Formation)
Busycoarctum unnamed species (Ayers Landing Member, Caloosahatchee Formation)
Busycotypus scotti (Rucks Pit Member, Nashua Formation)
Fulguropsis griffini (Ayers Landing Member, Caloosahatchee Formation)
Pyruella ovoidea (Ayers Landing Member, Caloosahatchee Formation)
Laevisycon unnamed species (Ayers Landing Member, Caloosahatchee Formation)

Calabrian Age

Busycon unnamed species (Holey Land Member, Bermont Formation)
Sinistrofulgur holeylandicum (Holey Land Member, Bermont Formation)
Fulguropsis capelettii (Holey Land Member, Bermont Formation)
Fulguropsis feldmanni (Holey Land Member, Bermont Formation)
Pyruella tomeui (Holey Land Member, Bermont Formation)

Ionian Age

Sinistrofulgur roseae (Belle Glade Member, Bermont Formation)
Fulguropsis evergladesensis (Belle Glade Member, Bermont Formation)

Tarantian Age

Busycon carica (Cape May, Sunderland, Socastee, Flanner's Beach, Norfolk Formations, and in the Recent)
Busycon carica eliceans (unnamed late Pleistocene beds in South Carolina and eastern Florida and in the Recent)
Sinistrofulgur perversum okeechobeensis (Okaloacoochee Member, Fort Thompson Formation)

Sinistrofulgur sinistrum (Coffee Mill Hammock Member of the Fort Thompson Formation, Miami Formation, Anastasia Formation, and in the Recent)
Sinistrofulgur laeostomum (Cape May, Sunderland, Socastee, Flanner's Beach, and Norfolk Formations, and in the Recent)
Busycotypus canaliculatus (Cape May, Sunderland, Socastee, Flanner's Beach, and Norfolk Formations, unnamed latest Pleistocene beds in northeastern Florida, and in the Recent)
Fulguropsis pyruloides pahayokee (Okaloacoochee Member, Fort Thompson Formation)

During the early Pleistocene, large sand and mud lagoon systems formed all along the Eastern United States, from Chesapeake Bay south to eastern Florida (Petuch, 2004). These linear coastal features were the result of the deposition of immense amounts of sediments by continental glaciers that covered the northern areas of North America at that time. One of the largest of these coastal estuarine areas was the Nashua Lagoon System, which extended from southern Georgia to the Fort Pierce area of eastern Florida (see Petuch and Roberts, 2007). Sheltered, quiet coastal lagoon systems like this provided the ideal habitats for several species of busyconids, which often occurred in large aggregations (Figure 2.2). Whelk accumulations such as this are typically encountered in the Nashua Formation of eastern Florida, which was deposited within the main axis of the Nashua Lagoon System. These early Pleistocene Nashua assemblages were dominated by the genera *Busycotypus*, *Busycon*, *Sinistrofulgur*, and *Brachysycon* but some older Pliocene lagoonal deposits were dominated by the genera *Lindafulgur*, *Busycon*, *Sinistrofulgur*, and *Busycoarctum* (Buckingham Member, Tamiami Formation) or by *Pyruella*, *Laevisycon*, and *Sinistrofulgur* (Unit 4 Fruitville Member, Tamiami Formation).

Iconography of Extinct Species in the Families Echinofulguridae and Busyconidae

The following figures illustrate examples of some of the more prominent and typical extinct genera and species of the ancestral family Echinofulguridae (subfamilies Protobusycininae, Levifusinae, and Echinofulgurinae) and the descendant family Busyconidae (subfamilies Busyconinae and Busycotypinae).

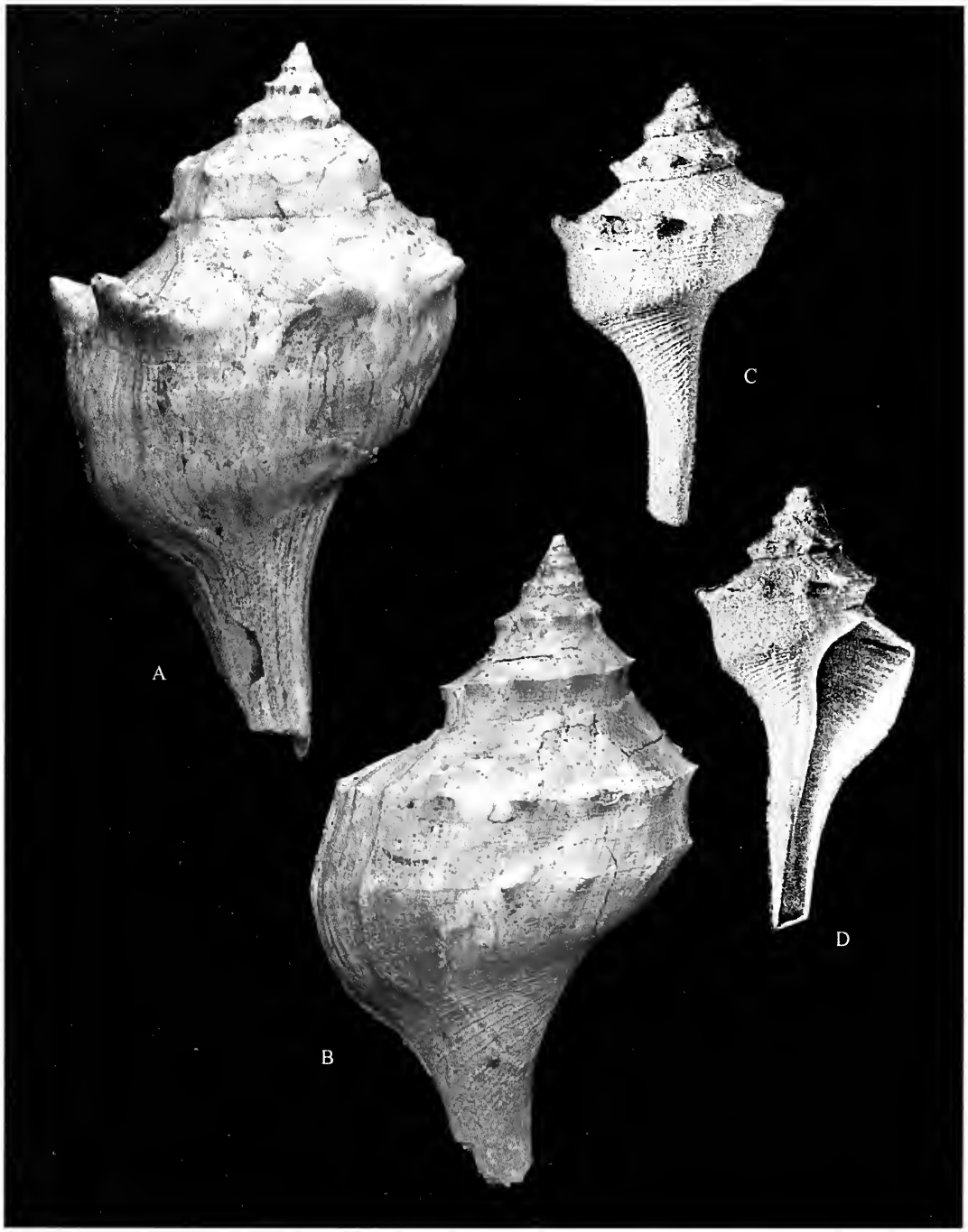


Figure 1.1 The Family Echinofulguridae: Ancestor of the Family Busyconidae.
A= *Levifusus branneri* (Harris, 1894). Length 83 mm, Moody's Branch Formation, Jackson Creek at Jackson, Mississippi. Jackson Stage, late Eocene. Largest species of *Levifusus*.
B= *Levifusus trabeatus* (Conrad, 1833). Length 54 mm, Gosport Formation at Claiborne Bluff, Claiborne, Alabama. Claiborne Stage, middle Eocene. Now recognized as the type species of the genus *Levifusus* Conrad, 1865 (the type genus of the new subfamily Levifusinae).
C, D= *Archefulgur fulguriparens* (Maury, 1909). Holotype, length 25 mm, from the Moodys Branch Formation at Montgomery, Louisiana. Jackson Stage, late Eocene (taken from Harris and Palmer, 1946: plate 49, figures 7 and 8). Type of the new genus *Archefulgur*.
These species of *Levifusus* and *Archefulgur* are representative of the Subfamily Levifusinae (new subfamily), Family Echinofulguridae (new family).

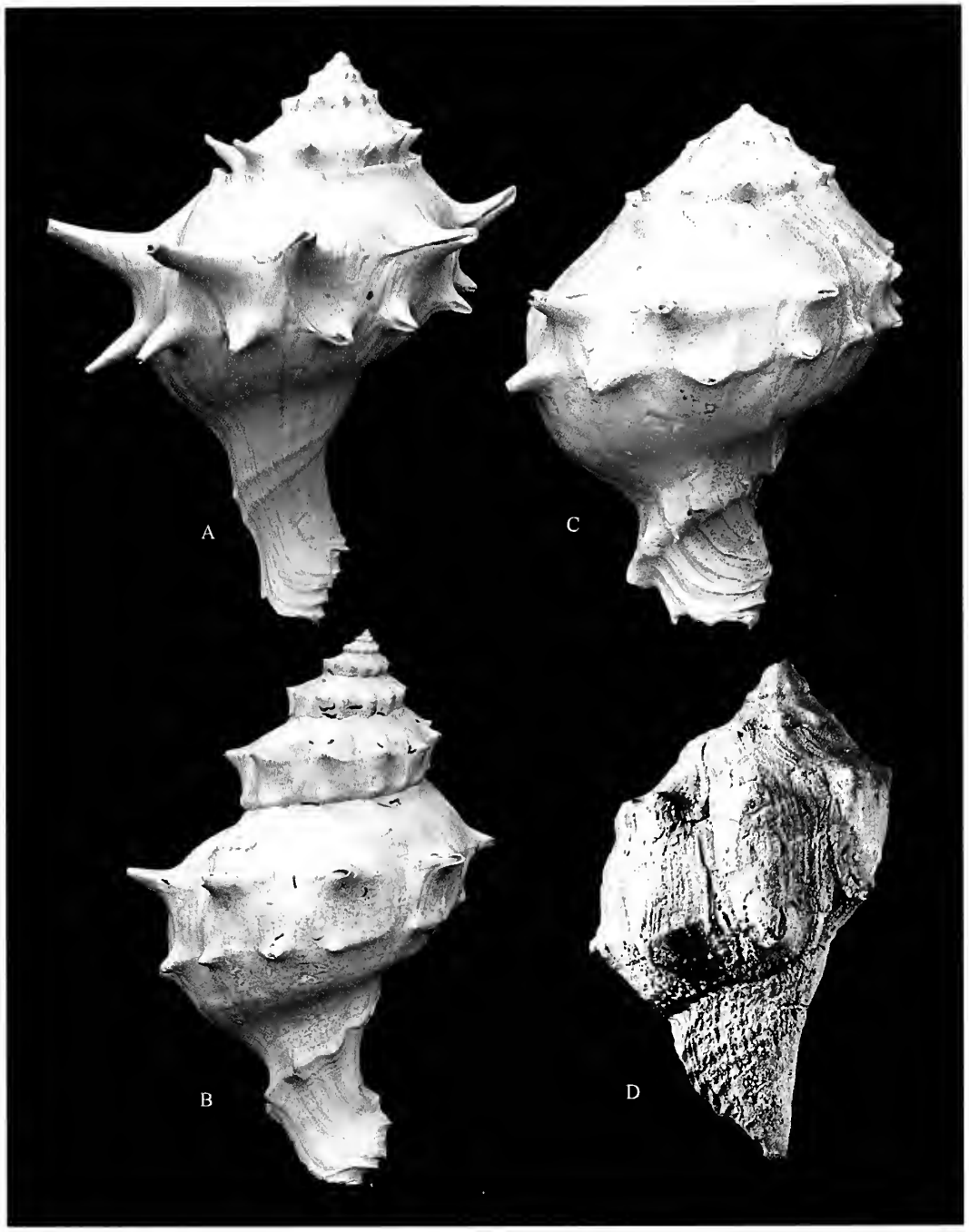


Figure 1.2 Representative Species of the Echinofulgurinae and Protobusyconinae, Family Echinofulguridae.
A= *Echinofulgur echinatum* (Dall, 1890), length 104 mm, Fort Denaud Member, Caloosahatchee Formation from the Miami Canal excavation, western Palm Beach County, Florida. Gelasian Age of the early Pleistocene. Subfamily Echinofulgurinae Petuch, 1994.
B= *Echinofulgur dalli* Petuch, 1994, length 100 mm, Pinecrest Member, Tamiami Formation from Unit 7 in the APAC Pit, Sarasota, Florida. Piacenzian Age of the Pliocene. Subfamily Echinofulgurinae Petuch, 1994.
C= *Echinofulgur cannoni* Petuch, 1994, length 74 mm, Buckingham Member of the Tamiami Formation from Unit 10 in the Quality Aggregates Pit #6, Sarasota, Florida. Early Piacenzian (late Zanclean?) Age of the Pliocene; oldest known species of the genus *Echinofulgur*. Subfamily Echinofulgurinae Petuch, 1994.
D= *Protobusycon binodosum* Sohl, 1964, length 63 mm, Ripley Formation, Pontotoc County, Mississippi. Early Maestrichtian Cretaceous (taken from Sohl, 1964: plate 24, figure 23). Subfamily Protobusyconinae (new subfamily).

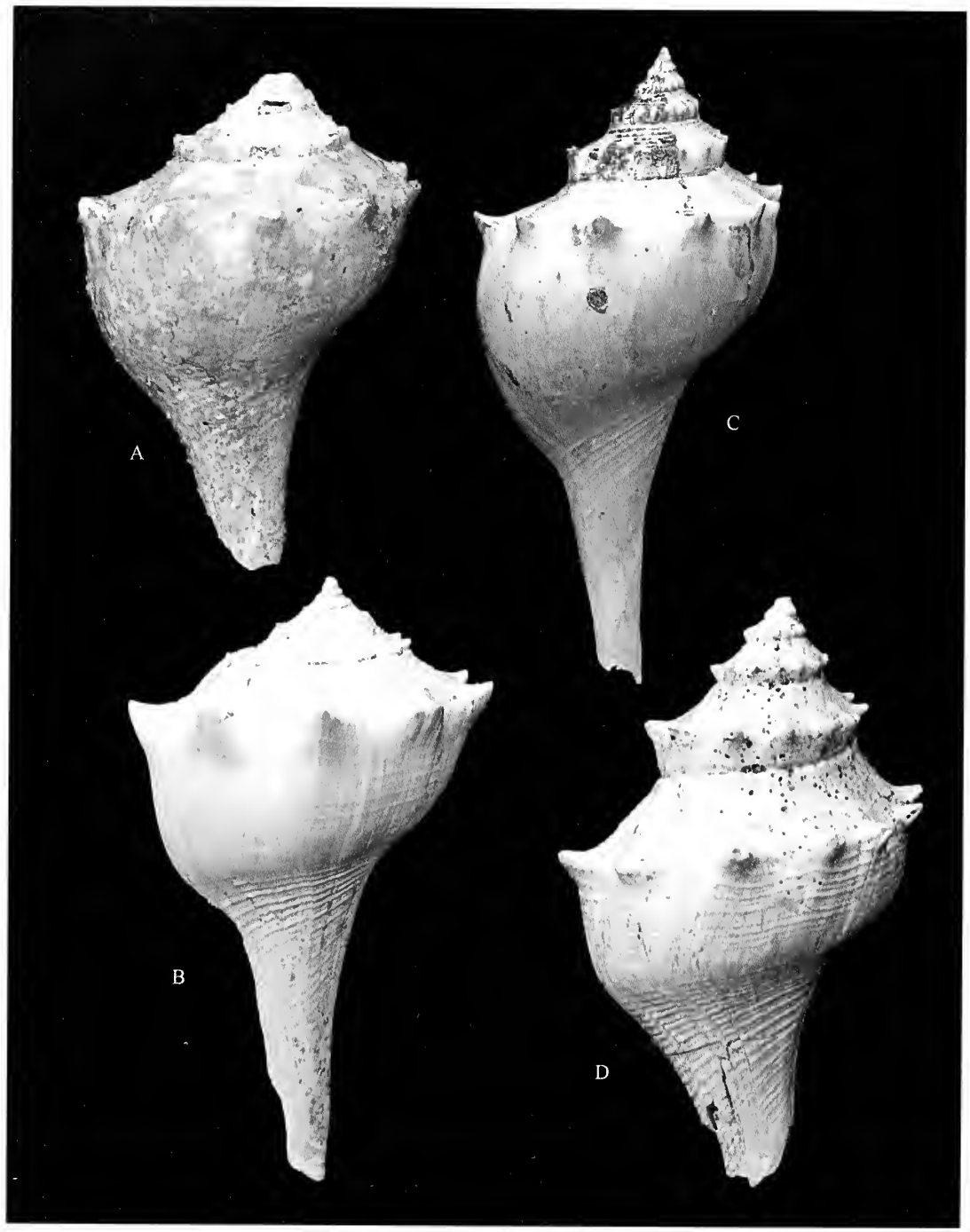


Figure 1.3 Representative Species of the Extinct Genus *Spinifulgur* Petuch, 1994, Subfamily Busyconinae, Family Busyconidae.

A= *Spinifulgur onslowensis* (Kellum, 1926), length 28 mm, Belgrade Formation at Haywood Landing, North Carolina. Chattian Age of the late Oligocene.

B= *Spinifulgur armiger* Petuch, 2004, length 39 mm, Chipola Formation along the Chipola River, rural Calhoun County, Florida. Burdigalian Age of the early Miocene.

C= *Spinifulgur epispiniger* (Gardner, 1944), length 69 mm, Chipola Formation at Farley Creek, rural Calhoun County, Florida. Burdigalian Age of the early Miocene.

D= *Spinifulgur spiniger* (Conrad, 1848), length 39 mm, Byram Formation, Vicksburg Group at Vicksburg, Mississippi. Vicksburg Stage of the middle Oligocene. Type Species of the extinct genus *Spinifulgur* Petuch, 1994. The genus *Spinifulgur* ranged from the early Oligocene (Rupelian Age) to the early Miocene (Burdigalian Age).

Figure 1.4 Representative Species of the Extinct Genus *Sycopsis* Conrad, 1867, Subfamily Busyconinae, Family Busyconidae.

A= *Sycopsis tuberculatum* (Conrad, 1839), length 60 mm, Windmill Point Member, St. Mary's Formation at Chancellor Point, St Mary's River, Maryland. Tortonian Age of the Miocene. Type species of the extinct genus *Sycopsis* Conrad, 1867.

B= *Sycopsis lindae* Petuch, 1988, length 73 mm, Drumcliff Member, Choptank Formation at Drumcliff, Patuxent River, St. Mary's County, Maryland. Serravallian Age of the middle Miocene.

The genus *Sycopsis* ranged from the early Miocene (Burdigalian Age) to the late Miocene (Tortonian Age).

C= *Sycopsis carinatum* (Conrad, 1862), length 74 mm, Cove Point Member, St. Mary's Formation at Little Cove Point, Calvert Cliffs, Maryland. Early Tortonian Age of the late Miocene.

Figure 1.5 Representative Species of the Extinct Genus *Turrifulgur* Petuch, 1988, Subfamily Busyconinae, Family Busyconidae.

A= *Turrifulgur fusiforme* (Conrad, 1839), length 64 mm, Windmill Point Member, St. Mary's Formation at Chancellor Point, St. Mary's River, Maryland. Tortonian Age of the Miocene. Type species of the extinct genus *Turrifulgur* Petuch, 1988.

B= *Turrifulgur covepointensis* Petuch, 2004, length 60 mm, Cove Point Member, St. Mary's Formation at Little Cove Point, Calvert Cliffs, Maryland. Early Tortonian Age of the late Miocene.

C= *Turrifulgur turriculus* Petuch, 1988, length 43 mm, Chancellor Point Sandstone Unit, St. Mary's Formation at Chancellor Point, St. Mary's River, Maryland. Middle Tortonian Age of the late Miocene.

The genus *Turrifulgur* ranged from the late Oligocene (Chattian Age) to the late Miocene (Tortonian Age).

Figure 1.6 Representative Species of the Extinct Genera *Coronafulgur* Petuch, 2004, Subfamily Busycotypinae, Family Busyconidae.

A= *Coronafulgur coronatum* (Conrad, 1839), length 127 mm, Windmill Point Member, St. Mary's Formation at Chancellor Point, St. Mary's River, Maryland. Tortonian Age of the late Miocene. Type species of the extinct genus *Coronafulgur* Petuch, 2004. The genus ranged from the early Miocene (Burdigalian Age) to the late Miocene (Messinian Age).

B= *Coronafulgur chesapeakensis* (Petuch, 1988), length 91 mm, Cove Point Member, St. Mary's Formation at Little Cove Point, Calvert Cliffs, Maryland. Early Tortonian Age of the late Miocene.

C= *Coronafulgur kendrewi* Petuch, 2004, length 123 mm, Cobham Bay Member, Eastover Formation along the Rappahannock River near Urbanna, Virginia. Messinian Age of the late Miocene.

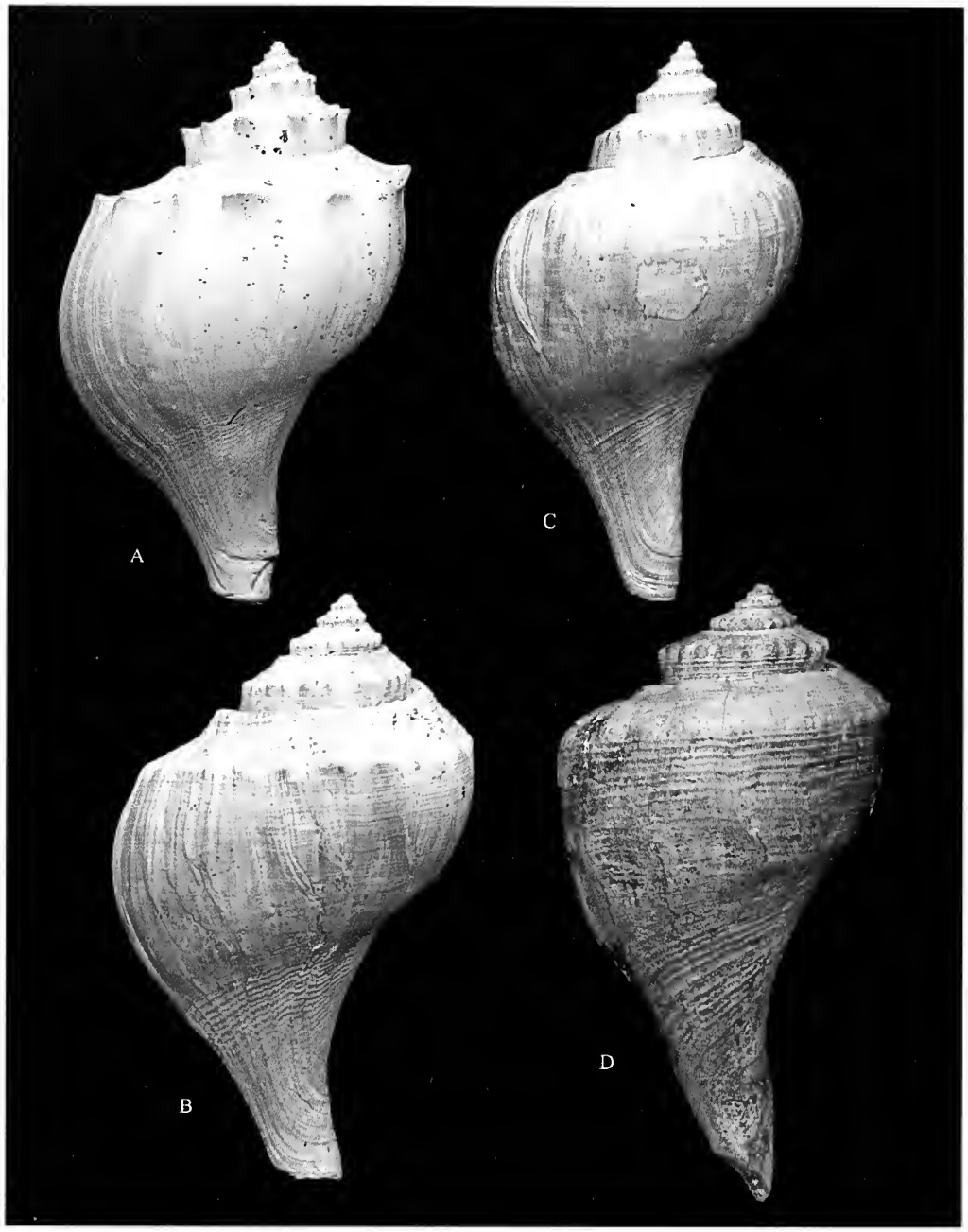


Figure 1.7 Representative Species of the Extinct Genus *Brachysycon* Petuch, 1994, Subfamily Busycotypinae, Family Busyconidae.

A= *Brachysycon amoenum* (Conrad, 1875), length 115 mm, Rucks Pit Member, Nashua Formation at Fort Drum, Okeechobee County, Florida. Gelasian Age of the Pleistocene. Type species of the extinct genus *Brachysycon* Petuch, 1994. The genus ranged from the early Pliocene (Piacenzian Age) to the early Pleistocene (Gelasian Age).

B= *Brachysycon canaliferum* (Conrad, 1862), length 105 mm, Edenhouse Member of the Chowan River Formation in the Lee Creek Phosphate Mine, Aurora, Beaufort County, North Carolina. Late Piacenzian Age of the late Pliocene.

C= *Brachysycon kissimmeensis* (Petuch, 1994), length 111 mm, Pinecrest Member (Kissimmee River facies), Tamiami Formation in the Rucks Pit, Fort Drum, Okeechobee County, Florida. Middle Piacenzian Age of the late Pliocene.

D= *Brachysycon propeincile* (Mansfield, 1930), length 68 mm, lower beds of the Jackson Bluff Formation at Alum Bluff, Liberty County, Florida, on the Apalachicola River. Early Piacenzian Age of the Pliocene.

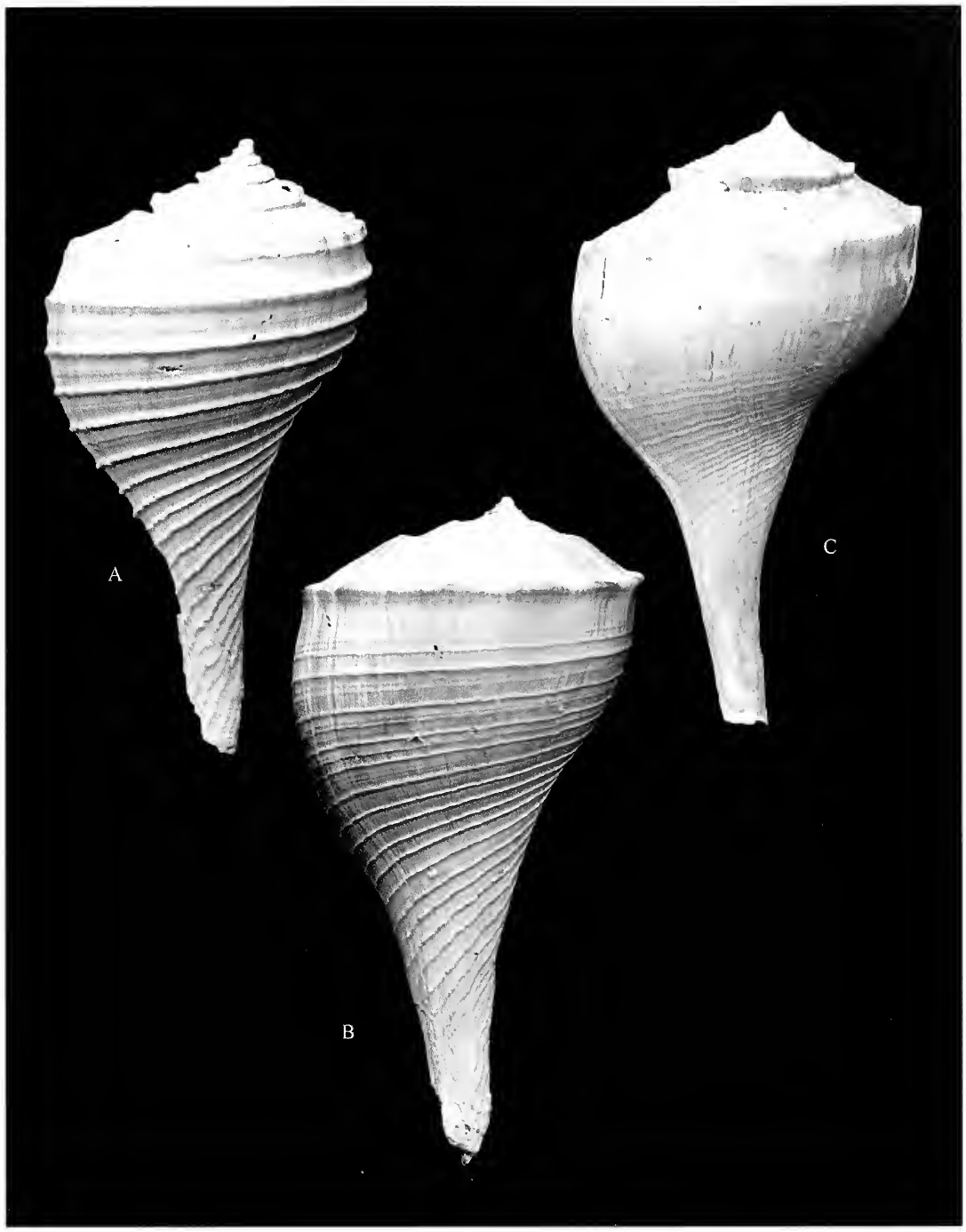


Figure 1.8 Representative Species of the Extinct Genus *Pyruella* Petuch, 1982, Subfamily Busycotypinae, Family Busyconidae.

A= *Pyruella rugosicostata* Petuch, 1982, length 53 mm, Pinecrest Member, Tamiami Formation from Unit 7 in the APAC Pit, Sarasota, Florida. Middle Piacenzian Age of the late Pliocene.

B= *Pyruella harasewychi* Petuch, 1982, length 91 mm, Buckingham Member, Tamiami Formation at Sarasota, Florida. Late Zanclean and early Piacenzian Ages of the Pliocene. Type species of the extinct genus *Pyruella* Petuch, 1982. The genus ranged from the late Miocene (Messinian Age), throughout the Pliocene, and to the early Pleistocene (Calabrian Age).

C= *Pyruella sicyoides* (Gardner, 1944), length 50 mm, Chipola Formation at Tenmile Creek, rural Calhoun County, Florida. Burdigalian Age of the early Miocene. Oldest known species of the genus *Pyruella* and the Subfamily Busycotypinae.

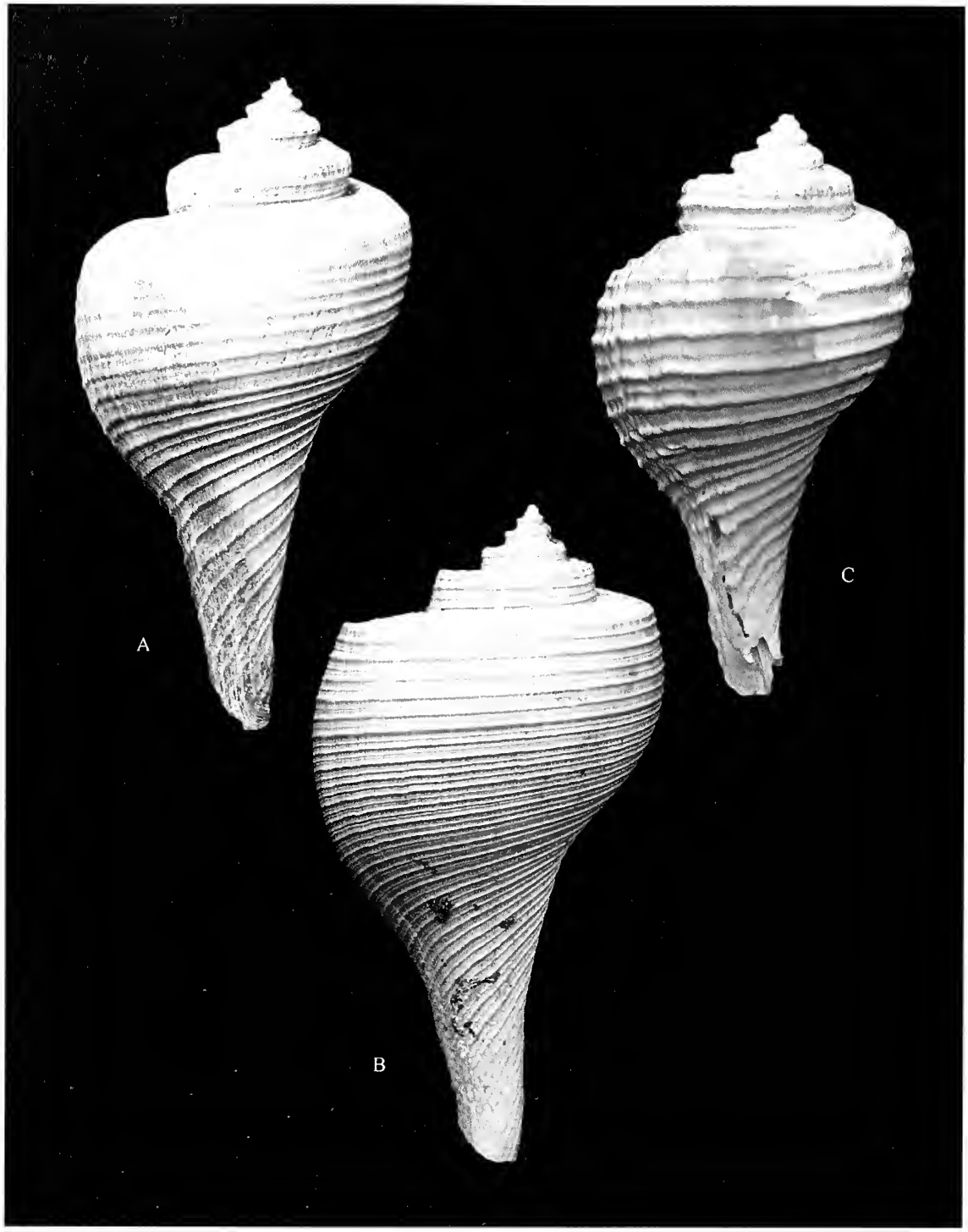


Figure 1.9 Representative Species of the Extinct Genus *Pyruella* Petuch, 1982, Subfamily Busycotypinae, Family Busyconidae.

A= *Pyruella schmidti* Petuch, 1994, length 55 mm, Fruitville Member (lower bed), Tamiami Formation from Unit 4 in the APAC Pit, Sarasota, Florida. Late Piacenzian Age of the late Pliocene.

B= *Pyruella tomeui* Petuch, 2004, length 82 mm, Holey Land Member, Bermont Formation from Palm Beach Aggregates Pit #9, Loxahatchee, Florida. Calabrian Age of the early Pleistocene.

C= *Pyruella waltfrancei* Petuch, 1994, length 60 mm, Buckingham Member, Tamiami Formation from Unit 10 in the APAC Pit, Sarasota, Florida. Late Zanclean and early Piacenzian Ages of the Pliocene.

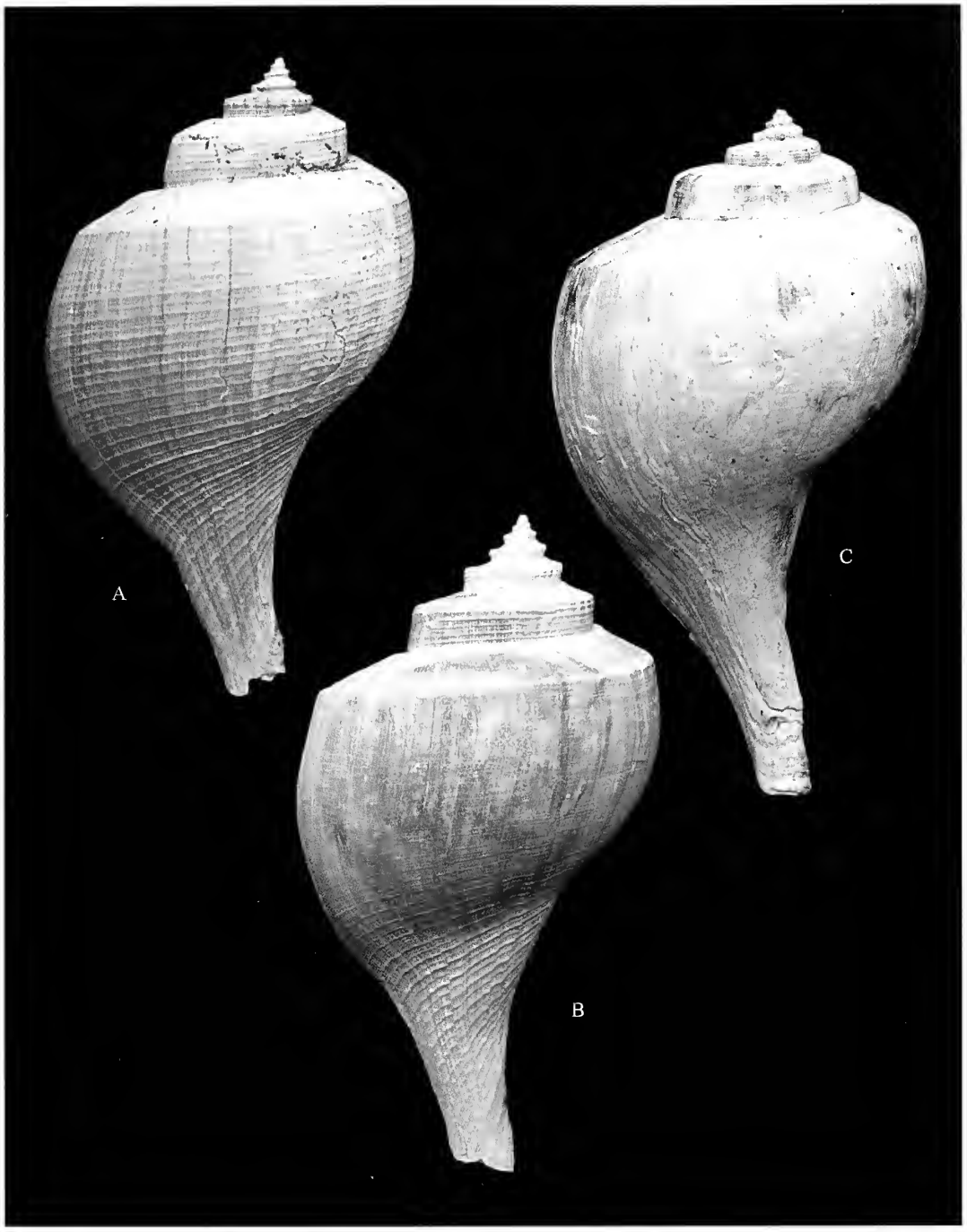


Figure 1.10 Representative Species of the Extinct Genus *Pyruella* Petuch, 1982, Subfamily Busycotypinae, Family Busyconidae.

A= *Pyruella eismonti* Petuch, 1994, length 115 mm, found in the Bergeron Star Pit, south of South Bay, Palm Beach County, Florida. Fort Denaud Member of the Caloosahatchee Formation, Gelasian Age of the early Pleistocene.

B= *Pyruella basingerensis* Petuch, 1994, length 92 mm, from the Kissimmee River excavation south of Fort Basinger, Highlands County, Florida. Fruitville Member (Kissimmee facies), Tamiami Formation. Late Piacenzian Age of the Pliocene.

C= *Pyruella bladenense* (Gardner, 1948), length 142 mm, found in a construction quarry at Shallotte, Brunswick County, North Carolina. Waccamaw Formation, Gelasian Age of the early Pleistocene. Also found in the contemporaneous Nashua Formation of Florida.

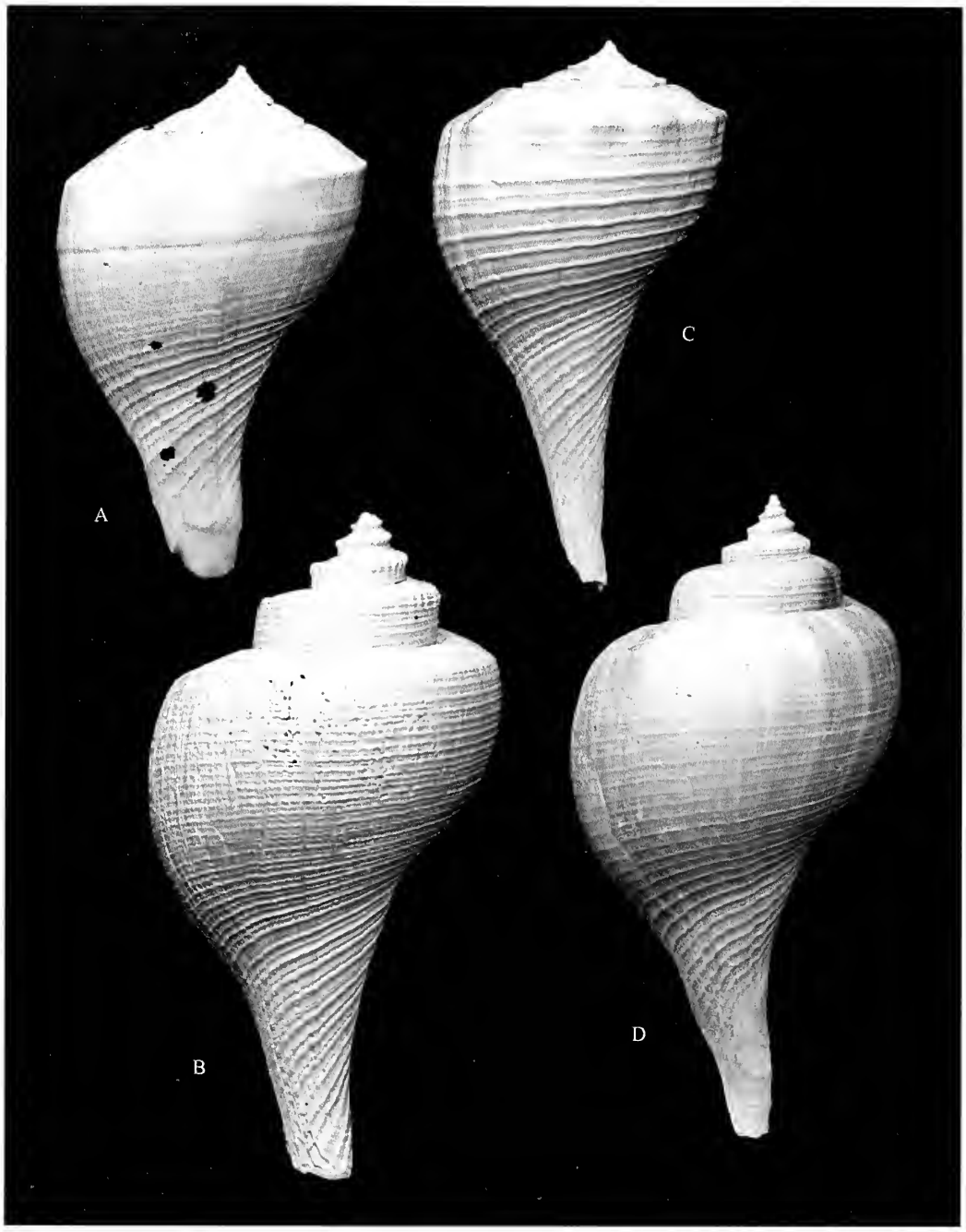


Figure 1.11 Representative Species of the Extinct Genus *Pyruella* Petuch, 1982, Subfamily Busycotypinae, Family Busiconidae.

A= *Pyruella streami* Petuch, 1994, length 56 mm, from Unit 9 in the APAC Pit, Sarasota, Sarasota County, Florida. Pinecrest Member of the Tamiami Formation, Piacenzian Age of the Pliocene.

B= *Pyruella carraheri* Petuch, 1994, length 63 mm, from the Kissimmee River excavation south of Fort Basinger, Highlands County, Florida. Pinecrest Member (Kissimmee facies) of the Tamiami Formation. Piacenzian Age of the Pliocene.

C= *Pyruella miccosukee* Petuch, 1994, length 55 mm, from Unit 8 in the APAC Pit, Sarasota, Sarasota County, Florida. Pinecrest Member of the Tamiami Formation, Piacenzian Age of the Pliocene.

D= *Pyruella ovoidea* Petuch, 1994, length 114 mm, from the Bergeron Star Pit, south of South Bay, Palm Beach County, Florida. Ayers Landing Member of the Caloosahatchee Formation, late Gelasian Age of the early Pleistocene.

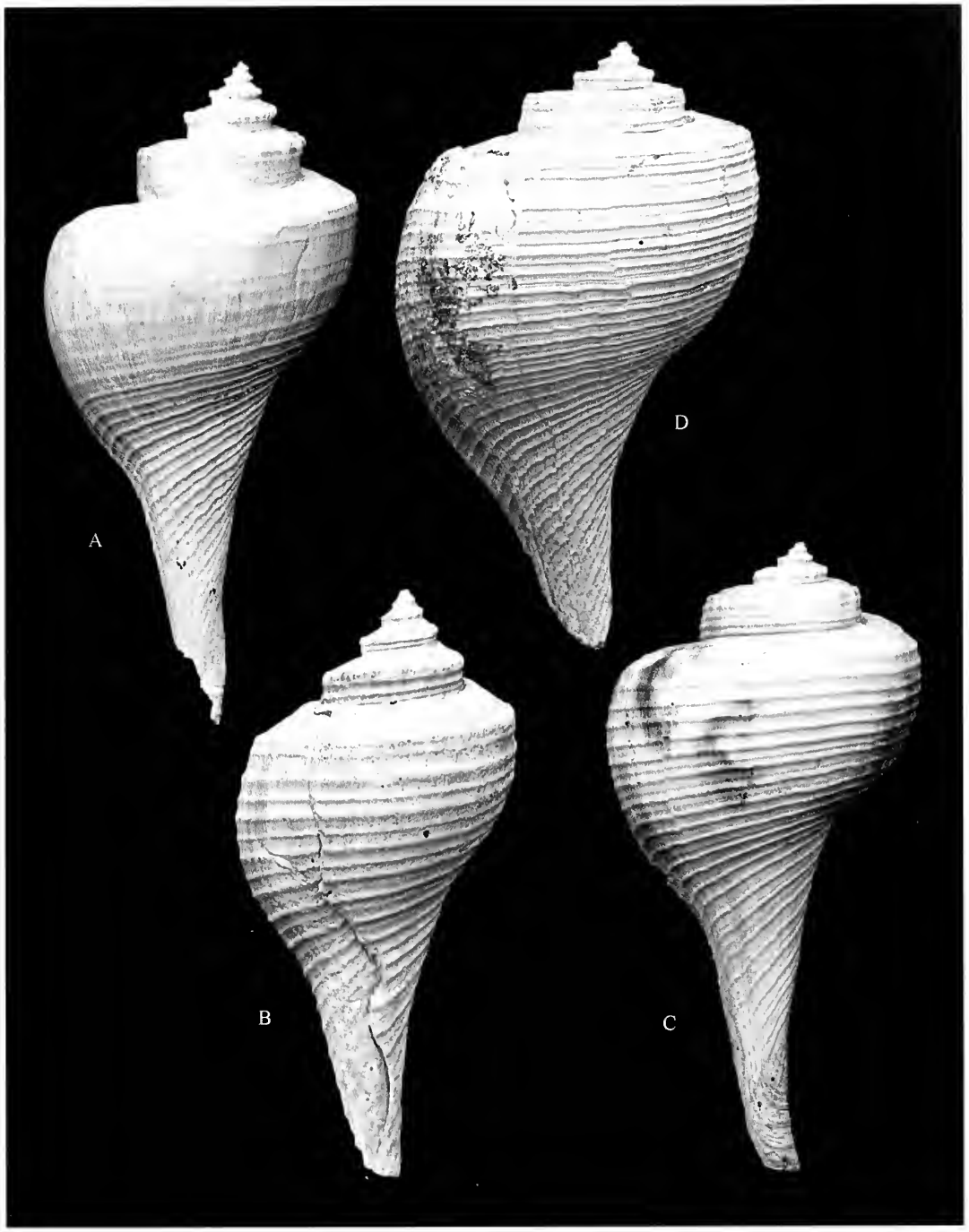


Figure 1.12 Representative Species of the Extinct Genus *Pyruella* Petuch, 1982, Subfamily Busycotypinae, Family Busyconidae.

A= *Pyruella sarasotaensis* Petuch, 1982, length 71 mm, from Unit 5 in the APAC Pit, Sarasota, Sarasota County, Florida. Fruitville Member (Unit 2) of the Tamiami Formation, late Piacenzian Age of the Pliocene.

B= *Pyruella seminole* Petuch, 1982, length 70 mm, from Unit 8 in the Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Pinecrest Member of the Tamiami Formation, Piacenzian Age of the Pliocene.

C= *Pyruella federicoae* Petuch, 1994, length 78 mm, from Unit 3 in the Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Fruitville Member (Unit 3) of the Tamiami Formation, late Piacenzian Age of the Pliocene.

D= *Pyruella osceola* Petuch, 1982, length 112 mm, from the Bird Road housing excavation, Miami, Dade County, Florida. Golden Gate Member (lower beds) of the Tamiami Formation. Piacenzian Age of the Pliocene.

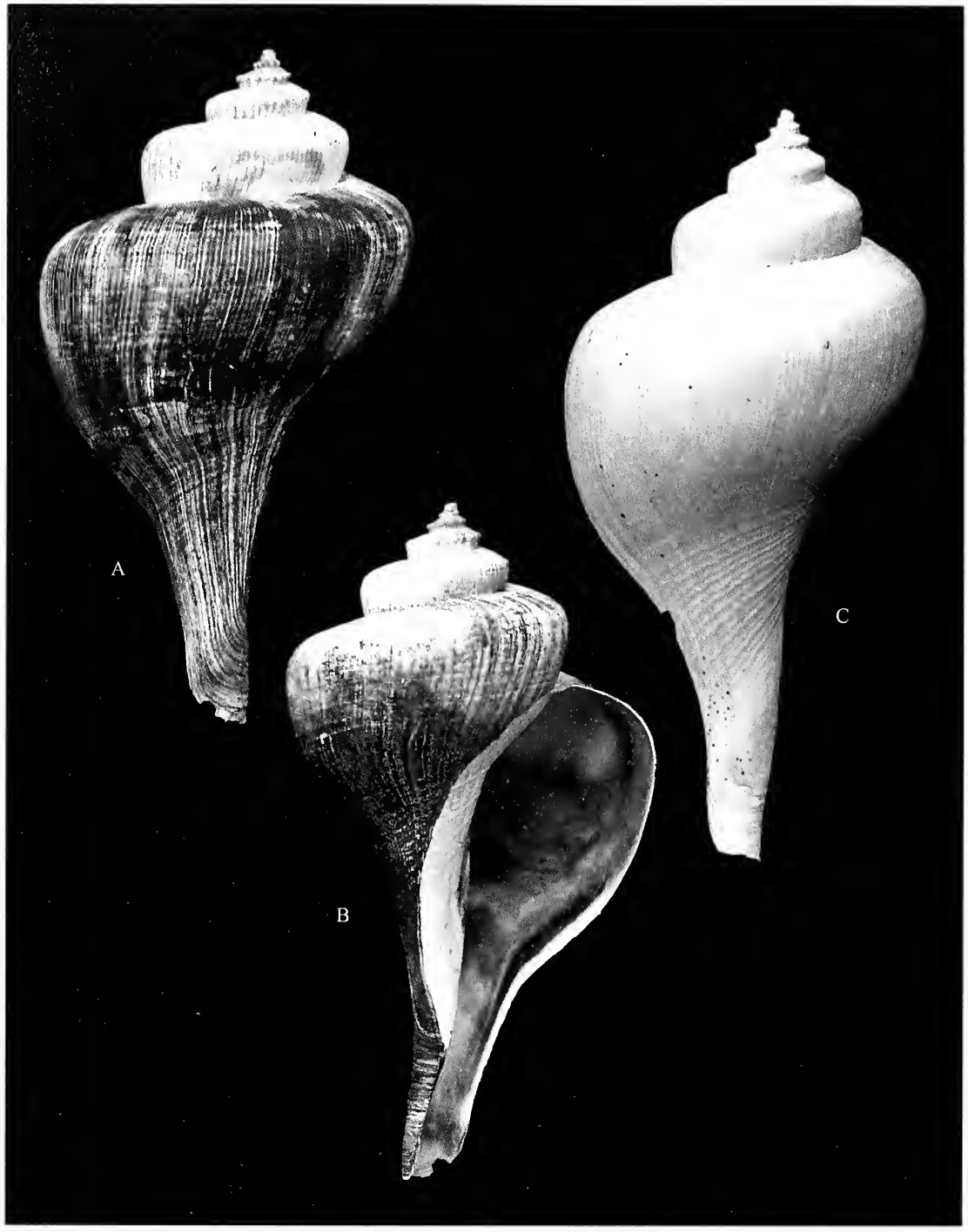


Figure 1.13 Representative Species of the Extinct Genus *Laevisycon* Petuch, Myers, and Berschauer, Subfamily Busycotypinae, Family Busyconidae.
A, B= *Laevisycon laevis* (Petuch, 1982), length 59 mm, Fruitville Member (lower bed), Tamiami Formation from Unit 4 in the APAC Pit, Sarasota, Florida. Early Piacenzian Age of the late Pliocene. Type species of the extinct genus *Laevisycon* Petuch, Myers, and Berschauer, new genus. The genus ranged from the Pliocene (late Zanclean and early Piacenzian Ages) to the early Pleistocene (Gelasian Age).
C= *Laevisycon planulatum* (Dall, 1890), length 65 mm, Fort Denaud Member, Caloosahatchee Formation from the Miami Canal excavation, 20 km south of Lake Harbor, Palm Beach County, Florida. Gelasian Age of the early Pleistocene.

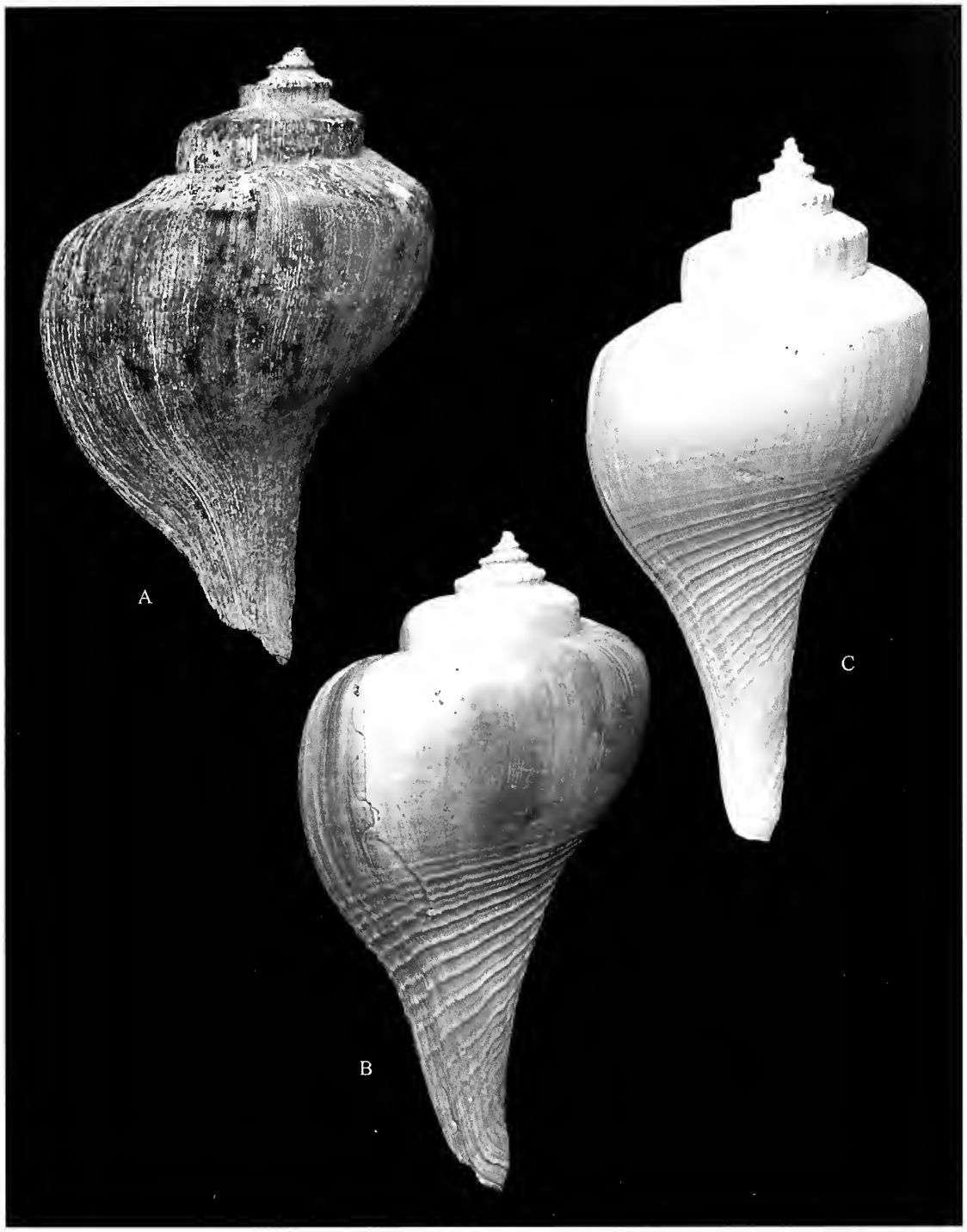


Figure 1.14 Representative Species of the Extinct Genus *Laevisycon* Petuch, Myers, and Berschauer, Subfamily Busycotypinae, Family Busyconidae.
A= *Laevisycon turbinalis* (Petuch, 1982), length 55 mm, Fruitville Member (upper beds), Tamiami Formation from Unit 3 in the APAC Pit, Sarasota, Florida. Late Piacenzian Age of the Pliocene.
B= *Laevisycon demistriatum* (Petuch, 1982), length 60 mm, from Unit 7 in the APAC Pit, Sarasota, Sarasota County, Florida. Pinecrest member of the Tamiami Formation, Piacenzian Age of the Pliocene.
C= *Laevisycon soror* (Petuch, 1994), length 72 mm, from the Miami Canal excavation, south of South Bay, Palm Beach County, Florida. Fort Denaud Member of the Caloosahatchee Formation, Gelasian Age of the early Pleistocene.

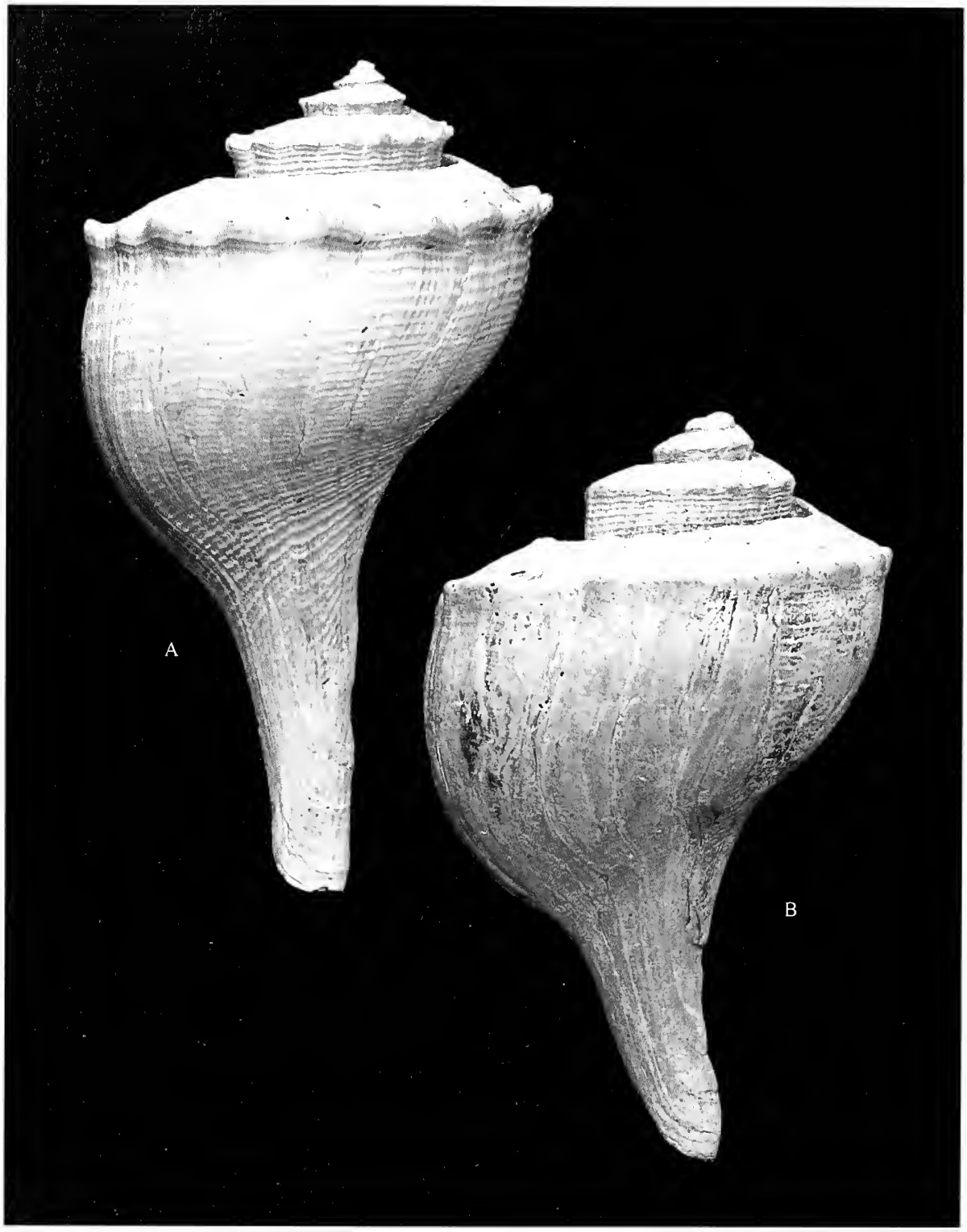


Figure 1.15 The Extinct Genus *Sycofulgur* Marks, 1950, Subfamily Busycotypinae, Family Busyconidae.
A= *Sycofulgur rugosum* (Conrad, 1843), length 93 mm, Windmill Point Member, St. Mary's Formation from Chancellor Point, St, Mary's River, Maryland. Type species of the extinct genus *Sycofulgur* Marks, 1950. The genus ranged from the early Miocene (Burdigalian Age) to the late Miocene (Tortonian Age).
B= *Sycofulgur martini* (Petuch and Drolshagen, 2009), length 116 mm, Cove Point Member, St. Mary's Formation from Little Cove Point, Calvert Cliffs, Maryland. Early Tortonian Age of the late Miocene.

CHAPTER TWO

Ecology of the Busyconidae

Belonging to the buccinoidean clade of the advanced gastropods, which is composed entirely of carnivores, the Busyconidae has evolved to be a group of voracious predators that specializes in feeding on bivalve mollusks. This predation on clams, scallops, and oysters dates back to at least the Miocene (Dietl, 2004) and may date even farther back in time, to the Cretaceous and Eocene and the ancestral subfamilies Protobusyconinae and Levifusinae of the Echinofulguridae. The busycon whelks, themselves, serve as food items for a variety of fishes, particularly elasmobranchs such as stingrays (especially the Southern Ray *Dasyatis australis*), skates, and Nurse Sharks. Small adult and juvenile whelks also fall victim to a variety of molluscicorous crustaceans, such as Stone Crabs (*Menippe mercenaria*), Box Crabs (*Calappa* spp.), and Spiny Lobsters (*Panulirus argus*). In Florida and along the Yucatan Peninsula of Mexico, small busyconids are also attacked and devoured by active, fast-moving melongenid gastropods such as the five subspecies of *Melongena (Rexmela) corona* (Florida) and *Melongena (Rexmela) bispinosa* (Yucatan). If a busycon whelk can survive all of these types of heavy predation and make it to adulthood, then the animal has reached a "size refuge"; when it has become as large, or larger, than its predators and has become essentially impregnable.

Feeding Strategies

Typically, busyconids envelop their prey with their powerful muscular foot and then use the edge of the shell lip to either chip or pry open the bivalve victim. As pointed out by both Kent (1983) and Dietl (2004), large slow-moving genera such as *Busycon* and *Sinistrofulgur* feed on large, thick clams such as the venerid *Mercenaria* and the arcticid *Arctica* (from Cape Cod to North Carolina only), while smaller, fast-moving whelks of the genus *Fulguropsis* feed on smaller, thin-shelled species such as tellinids, semelids, and mactrids. From field studies in northwestern Florida (Kent, 1983), it was observed that the Pear Whelk *Fulguropsis pyruloides* had a proportionally very large foot and was an active, fast-moving feeder, often chasing down and enveloping swimming prey such as the bay scallop *Argopecten irradians taylorae*. On the other hand, ponderous adult specimens of *Sinistrofulgur sinistrum* were found to be completely out-competed by the much swifter *Fulguropsis*, forcing them to specialize in feeding on large thick-shelled, immobile venerid clams such as *Mercenaria campechiensis*.

Of the two separate feeding strategies evolved by the busyconids, the "edge-chipping" method (see Dietl, 2004) is, by far, the most bizarre and unusual. Employed by the genera *Busycon* and *Sinistrofulgur* (and possibly also by the genera *Lindafulgur* and *Busycoarctum*), this method involves holding the clam prey steadily in a precise area of the foot, and then repeatedly pounding the blade-like edge of the shell outer lip onto the commissure of the two valves of the victim. The senior author has observed large *Sinistrofulgur* specimens patiently and rhythmically pounding away at the shell edges of *Mercenaria* clams for over four hours, which ultimately resulted in a small hole being opened along the edge of the commissure (examples shown here on Figure 2.1). Once the defense system of the bivalve shells was breached, the Left-Handed Whelk inserted its long, tooth-filled proboscis into the hole and rasped out chunks of living flesh

from the hapless venerid clam prey. After an hour or so, the entire *Mercenaria* clam was devoured and its empty shell discarded. This type of edge-chipping, although restricted to the subfamily Busyconinae ever since the early Pliocene, had evolved separately in the busycotypine genus *Sycofulgur* during the late Miocene (Dietl, 2004). All of these edge-chipping genera have a

Figure 2.1 Examples of Edge Chipping Predation by *Sinistrofulgur sinistrum*.
A= *Mercenaria campechiensis* (Gmelin, 1791); this large venerid clam prefers quiet intertidal sand flats and ranges from North Carolina, around both coasts of Florida and the Florida Keys, and throughout the entire Gulf of Mexico as far as Cabo Catoche on the Yucatan Peninsula. Throughout its geographical range, *Mercenaria campechiensis* is often the principal food source for large *Sinistrofulgur* species.
B= View of the commissure of *Mercenaria campechiensis*, showing the edge chipping caused by the repeated hammering of the shell lip edge of *Sinistrofulgur sinistrum*. This 90 mm wide specimen was collected on Rabbit Key in the Ten Thousand Islands, Collier County, Florida. Here, whelk predation was very heavy and the beaches were heaped with large numbers of chipped individuals (see Figure 2.6).
C= *Mercenaria hartae* Petuch, 2013; this newly-discovered smaller venerid clam is endemic to the coastal lagoons of southeastern Florida, where it occurs along with the more common and widespread *Mercenaria campechiensis*. Both species are subject to heavy edge chipping predation by large specimens of *Sinistrofulgur sinistrum*.
D= View of the commissure of *Mercenaria hartae*, showing the edge chipping caused by the shell lip pounding of a large *Sinistrofulgur sinistrum*. This 77 mm wide specimen was collected in the Lake Worth Lagoon, at Pine Point, Singer Island, Palm Beach County, Florida.

record of their predation preserved on their shells; every time they feed, the continuous pounding leaves small chips and breaks along the central, blade-like part of their lip. Over time as the shell grows, these form a wide central band of closely-packed healed fractures and scars around the middle of the body whorl.

The genus *Fulguropsis* (the Pear Whelks) are active hunters and feed exclusively on small, thin-shelled bivalves, primarily in the families Semelidae, Tellinidae, Mactridae, and Lucinidae, but will also feed on small venerid clams like *Chione elevata*, *Chione cancellata*, and *Chione mazyckii* and also scallops in the genus *Argopecten*. Unlike *Sinistrofulgur* and *Busycon*, *Fulguropsis* species hold their prey with their foot and then slowly force the blade-like edge of their outer lip between the closed commissure. As the whelk applies continuous pressure, the bivalve steadily weakens to the point that the *Fulguropsis* can create a gap between the valves. Once the valves are spread apart, the whelk can insert its long, worm-like proboscis into the interior of the bivalve body cavity and tear out large chunks of flesh from the living victim. This method of feeding, referred to as "edge wedging" (Dietl, 2004), seems to be the older of the two predation methods, dating back to the genus *Spinifulgur* in the Oligocene and possibly employed by the ancestral family Echinofulguridae and the subfamilies Protobusyconinae, Levifusinae, and Echinofulgurinae. The Channeled Whelk, *Busycotypus canaliculatus*, also uses edge-wedging as a predation method, forcing apart the valves of large, thin-shelled clams such as *Spisula*, *Mactrotoma*, and *Dosinia*. Judging from the lack of fine healed scars on the shell mid-body, all of the smaller whelk genera that lived during the Miocene, such as *Spinifulgur*, *Sycopsis*, *Turrifulgur*, and *Pyruella* (also Pliocene and Pleistocene), must have employed edge-wedging as their method of predation. The only edge-chippers from the late Miocene were the larger genera *Sycofulgur* (restricted to the Salisbury Sea) and *Busycon* (restricted to the Choctaw Sea).

Habitat Preferences

As apex predators within their ecosystems, the busyconids are tightly-bound to habitats that offer the greatest potential food resources. Because of this, the 17 whelk species and subspecies have followed their bivalve prey into an extraordinarily-wide range of habitats, including, intertidal mud flats and oyster banks in estuaries, deep quiet lagoons behind barrier islands, nearshore sea grass beds, deeper water offshore clam and scallop beds, and even coral and worm shell reefs. Based on the molluscan assemblages preserved in the Eastern American fossil record (Petuch, 2004), busycon whelks have preferred these types of coastal and near-shore habitats since at least the early Miocene. The following is an overview of the main types of habitats and environments preferred by the Busyconidae, along with the primary prey items found in each resident ecosystem.

Salt water creeks and estuaries contain the vast majority of shallow intertidal habitats found along the eastern United States, the northern Gulf of Mexico, and the Texas coast. With the exception of the southeastern Florida coast, the Florida Keys, the Ten Thousand Islands, and southwestern Florida coast, all the other estuarine environments are dominated by vast meadows of the tall Cordgrass (*Spartina alterniflora*) (Figure 2.2). The mud flats and tidal creeks found in these grassy marshlands often house immense beds of the venerid clam genus *Mercenaria*, and these are the principal food resource for several species of *Busycon* and *Sinistrofulgur*. The

biogeographical ranges of these two large and heavy busyconine genera correlate exactly with the distribution of *Spartina* marshlands and *Spartina*-edged coastal lagoons.

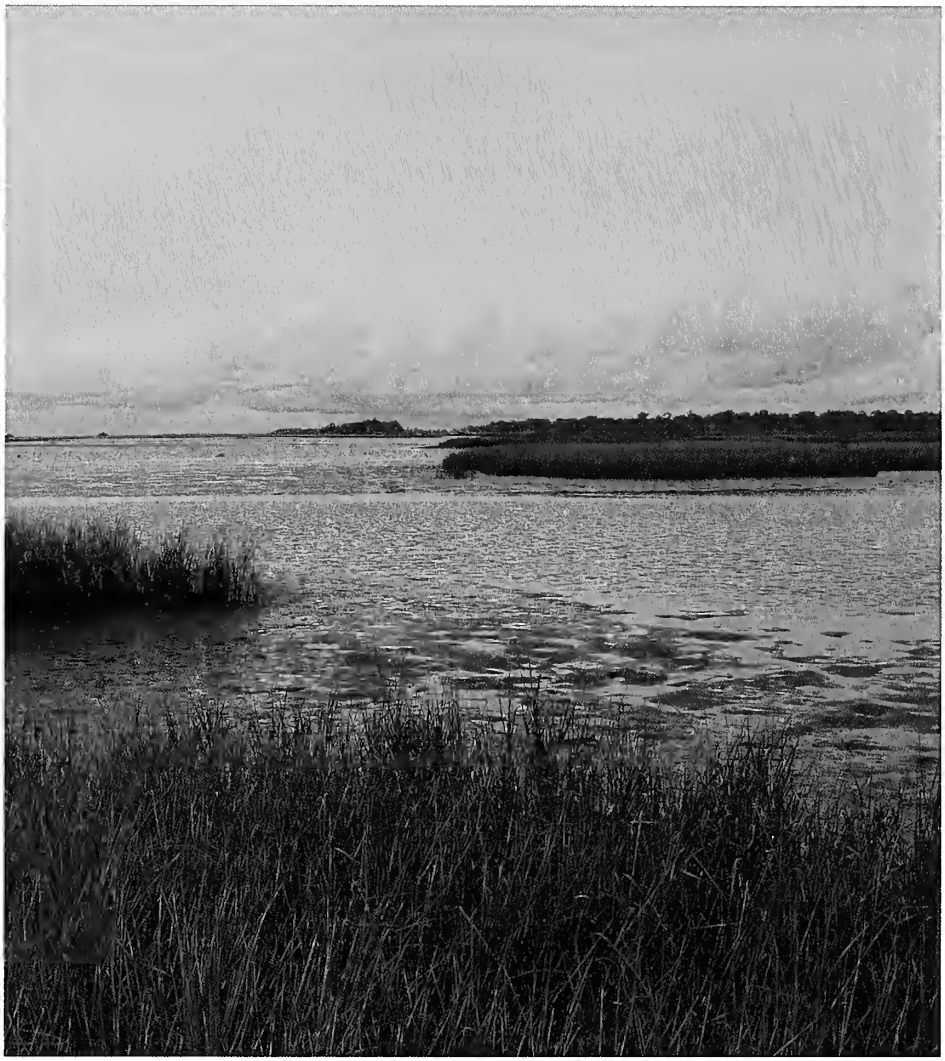


Figure 2.2 View of a *Spartina alterniflora* (Cordgrass) salt marsh, at dusk, within an estuary near Cedar Key, Levy County, Florida. Cordgrass marshes like this one extend along the entire eastern coast of the United States, from Maine to Texas, but are best developed in coastal lagoons and estuaries extending from Cape Cod south to northeastern Florida, and in the Gulf of Mexico from Cedar Key, Florida to Laguna Madre, Texas. In the area extending from Cape Cod to Cape Canaveral, the large busyconid, *Busycon carica*, is the dominant intertidal clam-eating predator and often occurs in large numbers. Along the South Carolina and Georgia coasts, these types of estuarine environments support large aggregations of the smaller whelk, *Busycon carica eliceans*. South of there, from Fort Pierce, Florida, throughout the Florida Keys, and along western Florida, *Busycon carica* and *Busycon carica eliceans* are absent and are replaced, as the dominant molluscivorous predators, by the large Left-Handed Whelk, *Sinistrofulgur sinistrum*. In similar Cordgrass marshes within the coastal lagoons of Texas, *Sinistrofulgur sinistrum* is absent and is replaced by the equally-large and voracious *Sinistrofulgur pulleyi*. These tidal creeks provide the habitat for dense aggregations of the shallowly-buried venerid clam *Mercenaria*. This genus of venerid clams is the principal food source for large intertidal busyconids, and comprises four species and one subspecies: *M. mercenaria* (ranging from Cape Cod to Cape Hatteras); *M. mercenaria notata* (ranging from Cape Hatteras to Fort Pierce, Florida); *M. hartae* (restricted to the St. Lucie River estuary, Lake Worth, and Palm Beach coastal lagoons, southeastern Florida); *M. campechiensis* (ranging from Cape Hatteras, around the Florida Keys, and the entire Gulf of Mexico); and *M. texana* (restricted to the coastal lagoons of Texas).

Within the Cordgrass marshes that extend from Cape Cod south to Cape Hatteras, the purple-edged *Mercenaria mercenaria* (Linnaeus, 1758) is the main prey item for *Busycon carica*. From Virginia south to the Indian River Lagoon, Florida, the smaller, brown-patterned *Mercenaria mercenaria notata* (Say, 1822) occurs on these marshlands in such abundance that it is commercially harvested. From Cape Hatteras, North Carolina south to the Indian River Lagoon, the large *Mercenaria campechiensis* (Gmelin, 1791) co-occurs with *M. mercenaria notata* and the two sympatric species are among the main prey items for *Busycon carica* (Cape Hatteras to Cape Canaveral), *Busycon carica eliceans* (South Carolina to northern Florida), and *Sinistrofulgur sinistrum* (Cape Canaveral to the Indian River Lagoon). Along western Florida and the northeastern Gulf of Mexico, from Tampa northward to the Mississippi River Delta, only *Mercenaria campechiensis* occurs in the *Spartina* marshes and only one large busyconid, *Sinistrofulgur sinistrum*, is its main predator. The Cordgrass marshlands of the Texas coastal lagoons host two sympatric *Mercenaria* species; the wide-ranging *Mercenaria campechiensis* and the smaller Texas endemic *Mercenaria texana* (Dall, 1902). Both of these venerids are among the principal food resources for the Texas endemic busyconid, *Sinistrofulgur pulleyi*.

Large aggregations of the oyster *Crassostrea virginica* (Gmelin, 1791) frequently form reef-like biohermal structures within estuaries all along the Eastern Seaboard and Gulf of Mexico. These can develop either in tidal creeks near *Spartina* marshes or, in more tropical areas such as the Florida Keys and Ten Thousand Islands, near Red Mangrove forests (Figure 2.3). From Cape Cod south to Virginia, these oyster reefs are essentially a monoculture of only one species. In a more complex biohermal structure, from Virginia south to the Florida Keys and Gulf of Mexico, a second oyster species, *Ostreola equestris* (Say, 1834), lives closely together with *Crassostrea virginica*. From Palm Beach, the Florida Keys, and the Ten Thousand Islands of Florida, a third species of oyster, *Crassostrea rhizophorae* (Guilding, 1828) (the Mangrove Oyster), often grows in large aggregations on oyster banks that are in close proximity to Red Mangrove forests. Large specimens of the Left-Handed Whelk, *Sinistrofulgur sinistrum* (Figure 2.4), are frequently encountered on these intertidal banks, where they can be found feeding on small, thin-shelled juvenile oysters.

Quiet, deeper water lagoons (2-20 m depths) occur all along the coasts of Eastern North America and the Gulf of Mexico, where they form behind narrow barrier islands or chains of small islands. Typically, these coastal lagoons contain large areas of open sand sea floors and often house immense aggregations of shallow infaunal bivalves. In the northern end of the range of the family Busyconidae, in the Virginian Molluscan Faunal Province (discussed later in this chapter), these sand substrates harbor shoals of the large mactrid bivalve *Spisula (Hemimactra) solidissima* (Dillwyn, 1817), and these support large populations of the Channeled Whelk *Busycotypus canaliculatus* and the left-handed Whelk *Sinistrofulgur laeostomum*. South of Cape Hatteras and into the Gulf of Mexico, these deeper lagoons house large aggregations of the mactrid bivalves *Spisula (Hemimactra) similis* (Say, 1822) and *Mactrotoma fragilis* (Gmelin, 1791) and these serve as a main food resource for the small, thin-shelled busyconid genus *Fulguropsis*. In some quiet lagoonal areas, such as those along the Ten Thousand Islands of southwestern Florida (Figure 2.5), *Mactrotoma fragilis* occurs along with shoals of the bright pink tellinid, *Eurytellina lineata* (Turton, 1819) and these support large populations of the small Pear Whelk, *Fulguropsis pyruloides*. In lagoons where the pink tellins dominate the benthic infauna, specimens of *Fulguropsis pyruloides* have been found that have taken on a bright

orange or pinkish-tan shell color, a probable result of their diet. Within the coastal lagoons along the northern Texas coast, these same bivalve species are among the main food resources for the

Figure 2.3 View of an oyster bank and island, made up primarily of the oysters *Crassostrea virginica* and *Ostreola equestris* and the Red Mangrove Tree (*Rhizophora mangle*), in Chokoloskee Bay, Ten Thousand Islands, Collier County, Florida. This type of intertidal habitat often supports large numbers of the Left-Handed Whelk, *Sinistrofulgur sinistrum*.

Figure 2.4 Close-up view of a living specimen of *Sinistrofulgur sinistrum* (Hollister, 1958), found crawling on a crushed oyster shell substrate near a large oyster bank off Cedar Key, Levy County, Florida. Note the distinctive solid black animal and the lighter-colored base of the foot.

Figure 2.5 View of Lumber Key, Ten Thousand Islands, Collier County, Florida, showing the wide beach adjacent to a deep coastal lagoon. The sandy seafloor of this lagoon supports large beds of sponges, ramose colonies of the bryozoan ectoproct *Schizoporella*, and aggregations of bivalves such as the mactrid *Mactrotoma fragilis*, the tellinid *Eurytellina lineata*, and the venerid *Macrocallista nimbosa*. This lagoonal environment also housed rare and distinctive bright orange specimens of the Pear Whelk *Fulguropsis pyruloides* (see Figure 7.10 in Chapter 7 of this book).

Galveston Pear Whelk, *Fulguropsis plagosum galvestonensis*. Many of the bivalve-rich coastal lagoons, especially those along western Florida, also house immense aggregations of the Left-Handed Whelk, *Sinistrofulgur sinistrum*, and dead specimens of these large busyconids often accumulate in piles on the adjacent beaches (Figure 2.6).

From Cape Hatteras southward into the Gulf of Mexico, intertidal areas adjacent to deep coastal lagoons often support extensive meadows of Shoalgrass (*Halodule wrightii*), which frequently extend for kilometers across exposed mudflats (Figure 2.7). These organic-rich sediments and beds of delicate sea grass house a large fauna of small, shallow-burrowing bivalves such as the venerid *Chione elevata* (Say, 1822), the mactrids *Mulinia lateralis* (Say, 1822) and *Mactrotoma fragilis* (Gmelin, 1791), the tellinids *Macoma cerina* (C.B. Adams, 1845), and *Macoma constricta* (Bruguiere, 1792), and the lucinids *Parvilucina costata* (d'Orbigny, 1842) and *Divaricella dentata* (Wood, 1815) (see Petuch, 2014 for details on the *Halodule*-based molluscan community). These wide-ranging Shoalgrass-associated bivalves, which are found throughout the entire Carolinian Molluscan Province, are the principal food resources for Pear Whelks of the genus *Fulguropsis*. From Cape Hatteras south to Palm Beach County, Florida, the coarsely-sculptured Rachel Carson's Pear Whelk, *Fulguropsis rachelcarsonae*, is the principal predator on small bivalves in the *Halodule* meadows. Along the western coast of Florida, from the Ten Thousand Islands north to Escambia Bay, and also along the Alabama and Mississippi coasts, this niche is occupied by the smooth-shelled Pear Whelk *Fulguropsis pyruloides* (Figure 2.8). In Shoalgrass beds along the Texas coast, particularly in quiet, protected bays behind barrier islands, the large angled-shouldered Texas Pear Whelk, *Fulguropsis texanus*, is the main small bivalve predator in the intertidal areas.

One of the more unusual habitats that is occupied by busyconids is the hard-bottom sponge "reef" (bioherm) environment of the Central and Lower Florida Keys and the shallow water areas around the Dry Tortugas. Here, the eroded limestone of the late Pleistocene Miami Formation forms a solid underpinning for the entire area. On this carbonate rock sea floor, immense numbers of sponges become attached and often grow to large sizes, forming reeflike biohermal structures (Figure 2.9). A thin layer of coarse carbonate sand, around 5 to10 cm thick and mostly composed of coralline algal fragments, covers the Miami limestone between the sponge bioherms and offers a substrate for the development of large clumps of the Finger Corals *Porites divaricata* and *Porites furcata* and the Rose Coral *Manicina areolata.* These corals and sponges occur together with the large Purple Sea Anemone *Condylactis giganteus* and dense growths of dasycladacean coralline algae such as *Halimeda* and *Penicillus* in a rich and diverse ecosystem that is unique to the Florida Keys. The coarse carbonate sand also houses an interesting fauna of small bivalves, such as the tellinid *Scissula similis* (Sowerby I, 1806) and the glycymerid *Tucetona pectinata* (Gmelin, 1791), and these are among the principal prey items of the endemic, heavily-sculptured Florida Keys Pear Whelk, *Fulguropsis keysensis* (originally described as a subspecies of the Yucatan *F. spiratum*, but now considered distinct). The heavy spiral cords and ribs on the body whorl of this small busyconid, the most heavily-sculptured of all the Pear Whelks, strengthen the shell and provide an added protection from the mollusk-eating Stone Crabs (*Menippe mercenaria*) and Box Crabs (*Calappa* sp.) that are so abundant on the sponge reefs. Besides *Fulguropsis keysensis*, these hard-bottom sponge bioherm environments also house a large number of other endemic Florida Keys mollusks, such as the cone shell *Gradiconus mazzolii* Petuch and Sargent, 2011, the bubble shell *Bulla frankovichi*

Petuch and Sargent, 2011, the nassariids *Uzita websteri* Petuch and Sargent, 2011 and *Uzita swearingeni* Petuch and Myers, 2014, and the drilliid *Neodrillia blacki* Petuch, 2004.

Figure 2.6 View of the beach on Rabbit Key, Ten Thousand Islands, Collier County, Florida, showing one of the immense accumulations of dead *Sinistrofulgur sinistrum* that can be found on the southern coast of the island. Such dense accumulations as this are very typical of the outer Ten Thousand Islands and give mute testament to the abundance of Left-Handed Whelks along southwestern Florida. Interspersed between the whelk shells are numerous large valves of the venerid clam *Mercenaria campechiensis*, and these served as the principal prey items for the voracious busyconids.

Figure 2.7 View of a mud flat and Red Mangrove forest, at low tide, near Pine Point, Singer Island, in Lake Worth Lagoon, Palm Beach County, Florida. This organic-rich mud flat, which is covered with thick beds of Shoal Grass (*Halodule wrightii*) and aggregations of the small batillariid gastropod *Batillaria minima*, supports a large and diverse bivalve fauna, including the venerid *Chione elevata*, the mactrid *Mulinia lateralis*, the tellinid *Macoma cerina*, the semelid *Semele donovani*, and the psammobiid *Heterodonax bimaculatus*. These small, thin-shelled bivalves are the principal prey items of the Pear Whelk *Fulguropsis rachelcarsonae*. The large venerid *Mercenaria hartae*, which is endemic to southeastern Florida, also occurs here and serves as one of the main food resources for a local population of the Left-Handed Whelk *Sinistrofulgur sinistrum*.

Figure 2.8 Close-up view of a bed of *Halodule wrightii* (Shoal Grass) growing off Rabbit Key, Ten Thousand Islands, Florida, showing a partially buried large specimen of the Pear Whelk *Fulguropsis pyruloides*. Along western Florida, this distinctive busyconid is always associated with Shoal Grass or with vermetid worm gastropod reefs.

Figure 2.9 View of a typical "sponge reef" from off Middle Torch Key, Lower Florida Keys, Florida. Here, a large Vase Sponge (*Ircinia campana*) can be seen growing among dense aggregations of smaller sponges, corals, and calcareous algae. This type of environment, punctuated with small open patches of calcareous sand, is the ideal habitat for the ornate, heavily-sculptured Pear Whelk *Fulguropsis keysensis* (see Chapter 7). This sponge-associated whelk feeds upon small, shallowly-burrowing bivalves such as the tellinid *Scissula similis*, the lucinid *Ctena orbiculata*, and the glycymerid *Tucetona pectinata*. (Photograph by Ron Bopp)

Biogeography of the Busyconidae

As shown in Chapter 1, the family Busyconidae evolved within the Mississippi River Valley ("Mississippi Sea") and spread southward into the Gulf of Mexico, as that region dried out during the Oligocene. From there, the family later migrated northward up the eastern coast of the United States at least as far as Cape Cod, Massachusetts. Throughout its entire evolutionary history, the Busyconidae remained restricted to the eastern coasts of the United States and Mexico and never dispersed into the tropical areas farther to the south or into the frigid waters of the Boreal Region to the north. Based on these dispersal patterns, the family seems to be physiologically adapted only to temperate, warm-temperate, and subtropical water areas. By being restricted to low-diversity temperate-water ecosystems, the busyconids have few, or no, molluscan competitors and can dominate the infaunal trophic structure as apex predators on bivalves.

The 17 species and subspecies of living busyconids are distributed within two marine molluscan faunal provinces; the temperate-water **Virginian Molluscan Province** (ranging from Cape Cod, Massachusetts to Cape Hatteras, North Carolina) and the warm-temperate and subtropical **Carolinian Molluscan Province** (ranging from Cape Hatteras, North Carolina south to the Florida Keys, around the Florida Peninsula to the entire Gulf of Mexico as far as Cabo Catoche, Yucatan Peninsula, Mexico) (Figure 2.10). Of the two busycon-containing provinces, the Carolinian is the largest and most complex, comprising five separate subprovinces and one transitional zone; the **Georgian Subprovince** (Cape Hatteras south to east central Florida), the **Palm Beach Provinciatone** (a transition zone ranging from near Fort Pierce, Florida to Dania Beach, Florida), the **Floridian Subprovince** (Miami and Biscayne Bay, the Florida Keys, and the Dry Tortugas), the **Suwannean Subprovince** (the Ten Thousand Islands north to the Florida Panhandle and west to Alabama and the Mississippi River Delta), the **Texan Subprovince** (the Mississippi River Delta west along the Texas coast and south to near Veracruz, Mexico), and the **Yucatanean Subprovince** (Veracruz, Mexico to the Campeche Banks and the entire coast of the Yucatan Peninsula eastward to Cabo Catoche and Isla Contoy, Mexico) (see Petuch, 2013 for quantitative analyses of the five subprovinces of the Carolinian Province). The **Virginian Province** contains two subprovincial divisions: the **Montaukian Subprovince** (Cape Cod to Cape May, New Jersey) and the **Delawarean Subprovince** (Cape May to Cape Hatteras) (see Figure 2.10).

From Cape Cod south to southern New Jersey, the Virginian Province houses only two species of busyconids, the busyconine *Busycon carica* and the busycotypine *Busycotypus canaliculatus*. Due to the extremely cold winter temperatures and the marginal temperate water conditions, the molluscan fauna of the Montaukian Subprovince of the Virginian Province is very impoverished, often with fewer than two dozen bivalves and gastropods being found in any given community. Of these, the busycon whelks are the largest gastropods and are often among the only conspicuous mollusks. Farther south, from near Cape May, New Jersey to Cape Hatteras, North Carolina, water temperatures remain more temperate during the winter months and a third busyconid occurs along with the two cold-tolerant species; the large Left-Handed Whelk *Sinistrofulgur laeostomum* (often referred to as the "Snow Whelk"). The Pear Whelk genus *Fulguropsis*, so common in more southern climes, is not found north of Cape Hatteras and its absence is a good marker for the biogeographical boundaries of the Virginian Molluscan

Province. The presence of *Sinistrofulgur laeostomum* in the Delawarean Subprovince of the Virginian Province supports the designation of a separate subprovincial region for the area extending from Cape May to Cape Hatteras.

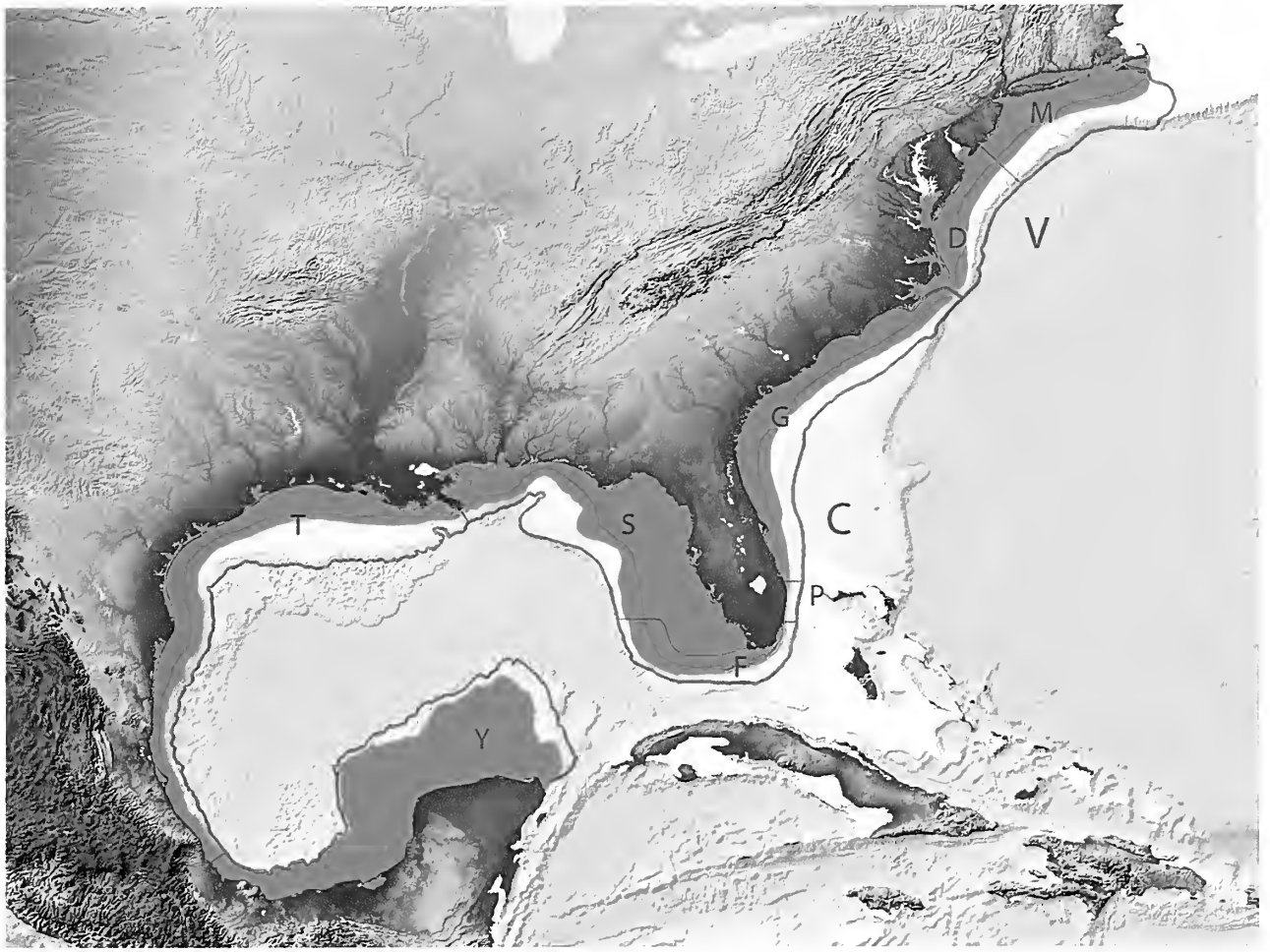


Figure 2.10 Map of Eastern North America and the Gulf of Mexico, showing the areal extents of the **Virginian Molluscan Province (V)** and **Carolinian Molluscan Province (C)**. The biogeographical subdivisions of the Virginian Province include: **M= Montaukian Subprovince**; **D= Delawarean Subprovince**. The biogeographical subdivisions of the Carolinian Province include: **G= Georgian Subprovince**; **P= Palm Beach Provinciatone**; **F= Floridian Subprovince**; **S= Suwannean Subprovince**; **T= Texan Subprovince**; **Y= Yucatanean Subprovince**. The Montaukian and Delawarean Subprovinces are here proposed informally, pending more detailed research. The family Busyconidae is restricted to the Virginian and Carolinian Provinces.

In the northern part of the Georgian Subprovince, extending from Cape Hatteras south to near Cape Canaveral, Florida, the three Virginian Province species (*Busycon carica*, *Sinistrofulgur laeostomum*, and *Busycotypus canaliculatus*) co-exist with a fourth busyconid, Rachel Carson's Pear Whelk, *Fulguropsis rachelcarsonae* (see Chapter 7 for the formal description of this new species). This sculptured whelk is endemic to the southeastern coast of the United States, from Cape Hatteras to Palm Beach, Florida, and is abundant in the coastal lagoons that characterize this region. In the northern section of the Georgian Subprovince, a fifth busyconid, *Busycon carica eliceans*, also occurs in these shallow coastal lagoons. Ranging from North Carolina to

southern Georgia, this distinctive subspecies may have begun to speciate during the late Pleistocene, when many of the coastal lagoons were isolated from each other by lowered sea levels. Since the end of the Pleistocene, *Busycon carica eliceans* has come back into contact with populations of typical *Busycon carica carica* and the two subspecies may be in the process of hybridization. This is particularly notable in the southern end of the range of *eliceans* in southernmost Georgia and northeasternmost Florida, where variants that combine features from both subspecies are commonly collected. A similar pattern of hybridization and morphological intergradation is also seen in the three subspecies of *Melongena (Rexmela) corona* that occur along eastern Florida (*M. corona sprucecreekensis* in the north, *M. corona altispira* in the central area, and *M. corona winnerae* in the south). Like the *Busycon carica* subspecies, these three distinctive melongenids probably evolved by geographical isolation (allopatry) in disjunct coastal lagoon systems during the lowered sea levels of the late Pleistocene.

In the southern part of the Georgian Subprovince, extending from Cape Canaveral to southern Palm Beach County, the Virginian Province *Busycon carica* and *Busycotypus canaliculatus* disappear and the Snow Whelk, *Sinistrofulgur laeostomum* is replaced by the equally-large *Sinistrofulgur sinistrum*. In this faunal transition zone between the cooler northern waters and the subtropical conditions of the Florida Keys (the Palm Beach Provinciatone; see Petuch, 2013), only two busyconids are present; the large *Sinistrofulgur sinistrum* and the smaller *Fulguropsis rachelcarsonae*. Wise *et al.* (2004) recognize subtle genetic differences between the eastern and western Florida populations of *Sinistrofulgur sinistrum*, and the eastern Florida and Florida Keys populations may actually represent a new undescribed subspecies. In the Floridian Subprovince (Florida Keys area) to the south, *Fulguropsis rachelcarsonae* is replaced by the heavily-sculptured Keys endemic, *Fulguropsis keysensis*, which also occurs together with typical *Sinistrofulgur sinistrum*. Of all the biogeographical subdivisions of the Carolinian Province, the Palm Beach Provinciatone and Floridian Subprovince contain the fewest number of busyconid species, with only two being found in each area.

The Suwannean Subprovince, extending from the Ten Thousand Islands of southwestern Florida northward to the Florida Panhandle and the coasts of Alabama and Mississippi, contains the richest busyconid fauna found in the entire Carolinian Province. The large Left-Handed Whelk, *Sinistrofulgur sinistrum*, which occurs throughout the Palm Beach Provinciatone and Floridian Subprovince, also extends along western Florida and the northeastern Gulf coast. Here, it occurs along with the much smaller endemic Smooth Pear Whelk, *Fulguropsis pyruloides*. In addition, two offshore, deeper water species also occur within the Suwannean Subprovince; the Keeled Pear Whelk *Fulguropsis plagosus* and Lyons' Whelk, *Lindafulgur lyonsi*. The thin-shelled, bright orange and pink Lyons' Whelk is the deepest-dwelling busyconid, often occurring in depths of 250 m. At the edge of the continental shelf off western Florida, in depths of over 200 m, *Lindafulgur lyonsi* lives on coralline algal rubble sea floors and occurs with deep water species such as the Slit Shell *Perotrochus amabilis*, the muricids *Vokesimurex lindajoyceae* and *Chicoreus rachelcarsonae*, and the extremely elongated terebrid *Myurellina lindae* (see Petuch, 1987 and Petuch and Myers, 2014 for details on the composition of this deep water community). This is the only known marine ecosystem where a busyconid, belonging to a family that normally occurs in shallow water, lives together with a pleurotomariid slit shell, belonging to a family that normally occurs only in deep water. In the area north of the Dry Tortugas, at the extreme northern edge of the Floridian Subprovince, *Lindafulgur lyonsi* can be found in

shallower water depths of only 100 m. Here it occurs along with other Dry Tortugas coralline algal bank endemics such as fasciolariid *Cinctura tortugana* and the conid *Dauciconus aureonimbosus* (Petuch and Myers, 2014). The Keeled Pear Whelk, *Fulguropsis plagosus*, occurs closer to shore, in shallower water depths of only 50-100 m.

The Mississippi River Delta, with its immense fresh water effluent, acts as a physiological and biogeographical barrier to the busyconid species found within the Gulf of Mexico. This deltaic ecological barrier is considered to be the boundary between the Suwannean and Texan Subprovinces. Only two busyconids are known to extend around the fresh water and mud barrier, and these include the Galveston Pear Whelk, *Fulguropsis plagosus galvestonensis*, and the Texas Pear Whelk, *Fulguropsis texanum* (Hollister, 1958: 97-99). These two mud and brackish water-adapted whelks extend eastward only as far as the eastern side of the Delta, where they occur with *Fulguropsis pyruloides* and *Sinistrofulgur sinistrum*. The Texas Pear Whelk, *Fulguropsis texanus*, ranges westward along the entire coast of Texas, south to the western edge of the Yucatan Peninsula, while the Galveston Pear Whelk, *Fulguropsis plagosus galvestonensis*, ranges from Alabama westward to only just south of Galveston, Texas. Both *Fulguropsis* taxa are common faunal components of the shallow water coastal lagoons that are characteristic of the Texan Subprovince. These lagoonal ecosystems also house the endemic Pulley's Left Handed Whelk, *Sinistrofulgur pulleyi*, which has been officially designated as the Texas State Shell. The busyconid fauna of the southern Texas coastal lagoons mirrors that of the Floridian Subprovince, with each area containing only two species of whelks; a large left handed species, *Sinistrofulgur pulleyi*, and a smaller Pear Whelk species, *Fulguropsis texanus*, in southern Texas and a large left handed species, *Sinistrofulgur sinistrum*, and a smaller Pear Whelk species, *Fulguropsis keysensis*, in the Florida Keys. The Yucatanean Candelabra Whelk, *Lindafulgur candelabrum*, also extends into the deeper water areas of the southern part of the Texan Subprovince, where it is occasionally collected by shrimp boats off Port Isabel and southern Padre Island.

Of the five subprovinces of the Carolinian Molluscan Province, the Yucatanean Subprovince contains one of the richest busyconid faunas, with five species (two endemic) occurring along either the coastline or on offshore banks. As in the Georgian, Floridian, and Suwannean Subprovinces, a species pair composed of a large Left Handed Whelk and a smaller Pear Whelk also occurs in the Yucatanean coastal lagoons; in this case, the endemic species *Sinistrofulgur perversum* and *Fulguropsis spiratus*. Along the western edge of the offshore Campeche Banks and in the coastal lagoons from Veracruz to the Laguna del Carmen, the Texas Pear Whelk, *Fulguropsis texanus*, often occurs along with the Yucatan Pear Whelk, *Fulguropsis spiratus*. Deep water, highly-distorted specimens of *Sinistrofulgur perversum* are also found on the offshore Campeche Banks, where they occur together with the Candelabra Whelk, *Lindafulgur candelabrum*, the Yucatan endemic Turnip Whelk, *Busycoarctum coarctatum*, and the Pear Whelks *Fulguropsis spiratus* and *Fulguropsis texanus*. The four primary Yucatanean Subprovince index species, *Sinistrofulgur perversum*, *Lindafulgur candelabrum*, *Busycoarctum coarctatum*, and *Fulguropsis spiratus*, range all the way to Isla Contoy and Contoy Light and that area represents the extreme easternmost edge of the Yucatanean Subprovince and the boundary of the Carolinian Molluscan Province and the Caribbean Molluscan Provinces.

The living members of the family Busyconidae are arranged here by biogeography:

WESTERN ATLANTIC REGION

VIRGINIAN PROVINCE (Cape Cod, Massachusetts to Cape Hatteras, North Carolina)
Montaukian Subprovince (Informally proposed here; from Cape Cod to Cape May, New Jersey and named for Montauk Point, Long Island, New York)
Busycon carica (Gmelin, 1791)
Busycotypus canaliculatus (Linnaeus, 1758)
Delawarean Subprovince (Informally proposed here; from Cape May, New Jersey to Cape Hatteras, North Carolina and named for the State of Delaware and Delaware Bay)
Busycon carica (Gmelin, 1791)
Sinistrofulgur laeostomum (Kent, 1982)
Busycotypus canaliculatus (Linnaeus, 1758)

CAROLINIAN PROVINCE (Cape Hatteras to the Florida Keys, western Florida, and the entire Gulf of Mexico to Isla Contoy, Yucatan Peninsula of Mexico)
Georgian Subprovince (Cape Hatteras to Palm Beach County, Florida; see Petuch, 2013)
Busycon carica (Gmelin, 1791)
Busycon carica eliceans (Montfort, 1810) (the Carolinas to southern Georgia)
Sinistrofulgur laeostomum (Kent, 1982) (from Cape Hatteras to Cape Canaveral)
Sinistrofulgur sinistrum (Hollister, 1958) (from Cape Canaveral southward)
Busycotypus canaliculatus (Linnaeus, 1758) (Cape Hatteras to Cape Canaveral)
Fulguropsis rachelcarsonae Petuch, Myers, and Berschauer, new species
Palm Beach Provinciatone (Transition Zone) (Fort Pierce, Florida to Palm Beach, Florida; see Petuch, 2013)
Sinistrofulgur sinistrum (Hollister, 1958)
Fulguropsis rachelcarsonae Petuch, Myers, and Berschauer, new species
Floridian Subprovince (Palm Beach, Florida to Biscayne Bay, the Florida Keys, and the Dry Tortugas; see Petuch, 2013)
Sinistrofulgur sinistrum (Hollister, 1958)
Fulguropsis keysensis Petuch, 2013
Suwannean Subprovince (Ten Thousand Islands, Florida northward to the Florida Panhandle and west to the Mississippi River Delta; see Petuch, 2013)
Sinistrofulgur sinistrum (Hollister, 1958)
Lindafulgur lyonsi (Petuch, 1987)
Fulguropsis plagosus (Conrad, 1863)
Fulguropsis plagosus galvestonensis (Hollister, 1958) (Alabama and Mississippi only)
Fulguropsis pyruloides (Say, 1822)
Fulguropsis texanus (Hollister, 1958) (Alabama and Mississippi coasts only)
Texan Subprovince (Mississippi River Delta west and south to Veracruz, Mexico; see Petuch, 2013)
Sinistrofulgur pulleyi (Hollister, 1958)
Lindafulgur candelabrum (Lamarck, 1816) (Corpus Christi, Texas southward only)
Fulguropsis plagosus galvestonensis (Hollister, 1958)
Fulguropsis spiratus (Lamarck, 1816) (Corpus Christi, Texas southward only)
Fulguropsis texanus (Hollister, 1958)

Yucatanean Subprovince (Veracruz, Mexico, the Campeche Banks, and the entire Yucatan Peninsula as far east as Isla Contoy; see Petuch, 2013)
Sinistrofulgur perversum (Linnaeus, 1758)
Lindafulgur candelabrum (Lamarck, 1816)
Busycoarctum coarctatum (Sowerby I, 1825)
Fulguropsis spiratus (Lamarck, 1816)
Fulguropsis texanus (Hollister, 1958) (only from Veracruz to the western Campeche Banks)

Figure 2.11 View of a tidal creek in a typical Cordgrass (*Spartina alterniflora*) salt marsh near Cedar Key, Levy County, Florida. These types of *Spartina* marshes and organic-rich mudflats support large numbers of bivalved mollusks which, in turn, are the food resource for two species of busyconids; the large Left-Handed Whelk *Sinistrofulgur sinistrum* (Hollister, 1958) and the Pear Whelk *Fulguropsis pyruloides* (Say, 1822). Similar salt marshes along New York, New Jersey, and the Delmarva Peninsula typically support large populations of the Lightning Whelk, *Busycon carica* (Gmelin, 1791) and the Channeled Whelk, *Busycotypus canaliculatus* (Linnaeus, 1758).

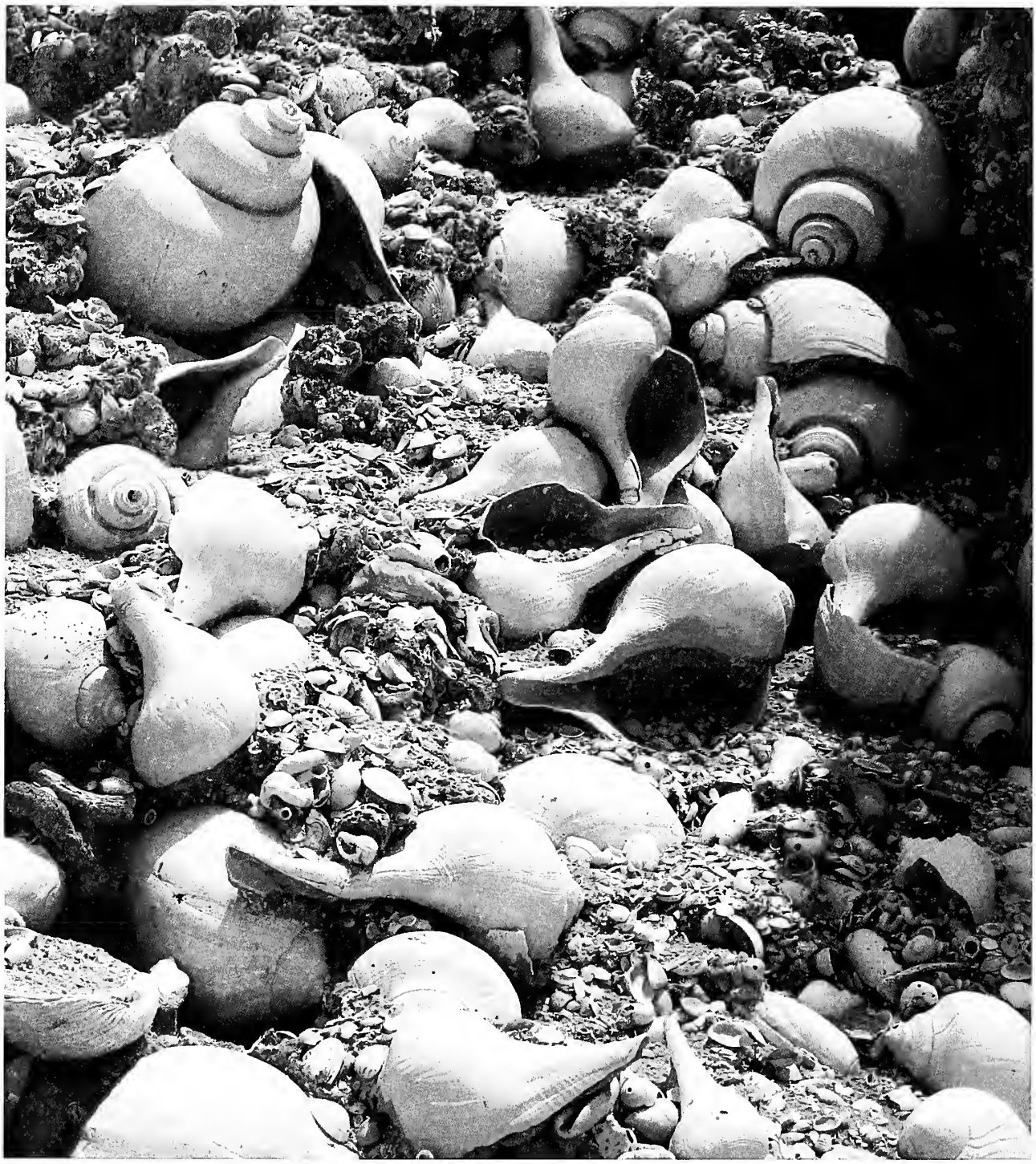


Figure 2.12 View of a large aggregation of fossil busyconid whelks within an outcrop of the Rucks Pit Member of the Nashua Formation in the Dickerson Aggregates Indrio Mine, Indrio Road, Fort Pierce, Florida. Four classic early Pleistocene Nashua Formation species can be seen to dominate the assemblage, including *Busycotypus scotti* Petuch, 1994 (the large shells with prominent channeled spires and the most abundant species), *Brachysycon amoenum* (Conrad, 1875), *Busycon rucksorum* Petuch, 1994, and *Sinistrofulgur yeehaw* Petuch, 1994. This fossil whelk bed was deposited within the Nashua Lagoon System of eastern Florida during the late Gelasian Pleistocene.

CHAPTER THREE

The Lightning Whelks: Genus *Busycon*

The genus *Busycon* Röding, 1798, the Lightning Whelks, represents the archetype for the family Busyconidae and the subfamily Busyconinae. The genus first appears in the early Miocene (Burdigalian Age) of Florida and was confined to that area until the early Pliocene (Zanclean Age), when *Busycon* spread northward into the Carolinas and Virginia. By the middle and late Pleistocene, the genus had spread even farther northward, being found in fossil beds in Maryland (Sunderland Formation) and New Jersey (Cape May Formation) (Petuch, 2004). These northern populations gave rise to the Recent *Busycon carica* and that species still occupies the range of its ancestral late Pleistocene forms. Although over 14 fossil *Busycon* species are known (Miocene to Pleistocene), only one species and one subspecies have survived into the Recent; *B. carica* and its southern subspecies *B. carica eliceans*. The named fossil species are listed on Appendix 1 at the end of this book and most are illustrated in the iconography at the end of this chapter.

Family Busyconidae
Subfamily Busyconinae
Genus *Busycon* Röding, 1798

***Busycon carica* (Gmelin, 1791)**
(Figures 3.1 - 3.4)

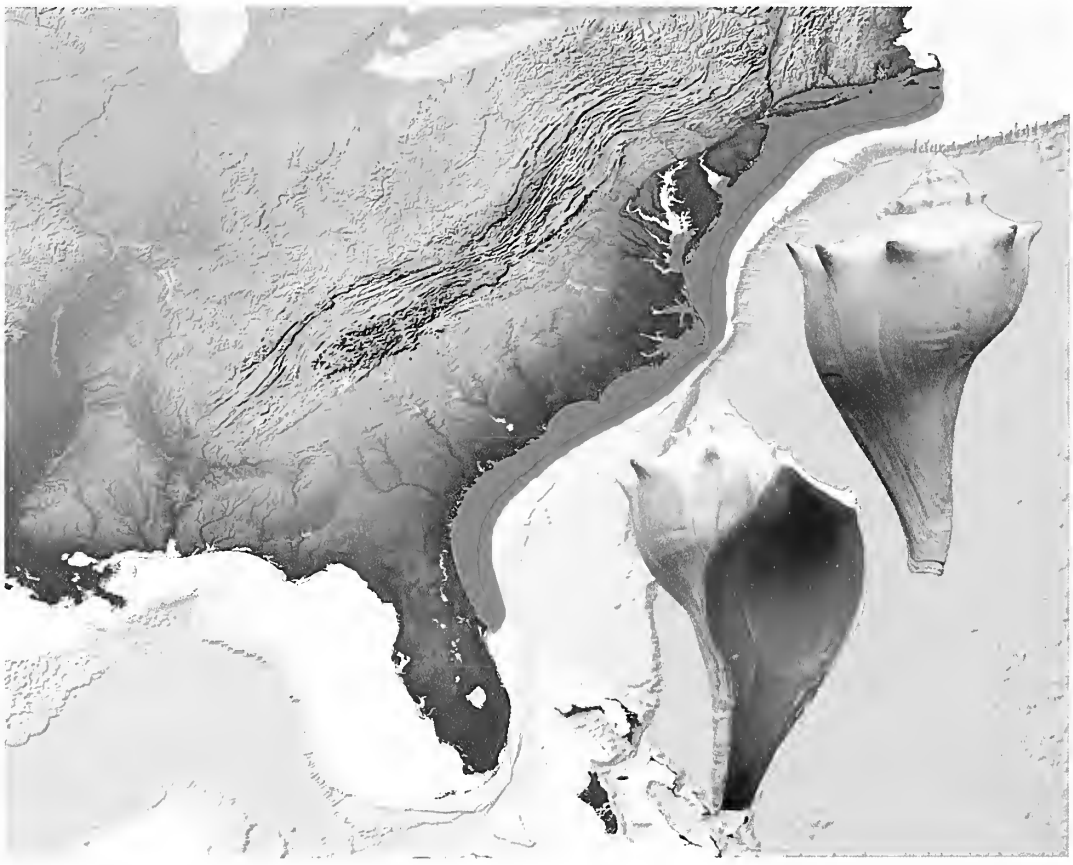
Synonymy:
Murex carica Gmelin, 1791
Busycon muricatum Röding, 1798
Pyrula carica Lamarck, 1816
Fulgur carica Conrad, 1853
Busycon (Busycon) aruanum Hollister, 1958 not Linnaeus, 1758
Busycon carica (Gmelin) Petuch, 2013

Description: The classic Lightning Whelk is a dextral (right-handed), medium-to-large sized shell with an elongated, fusiform or pyriform shape; spire is generally high and protracted, subpyramidal in shape, with sloping spire whorls; siphonal canal is proportionally long, roughly one-half the length of the body whorl; shoulder is distinctly angled and is ornamented with large, evenly-spaced sharp knobs; body whorl and spire have a smooth and silky texture and are ornamented with very numerous fine spiral threads; siphonal canal sculptured with numerous large and coarse spiral cords; aperture wide and flaring, most often a bright red-orange or deep red color, but some specimens having purple, yellow-orange, or brown apertures; shell color generally pale cream tan with numerous closely-packed irregular dark brown or purple-brown longitudinal flammules ("Lightning" markings); periostracum thin, rough-textured, tightly adherent.

Discussion: Although one of the more widely-distributed busyconids, *Busycon carica* shows little major variation over its biogeographical range in the Virginian and Carolinian Provinces.

Specimens from the Delawarean Subprovince of the Virginian Province tend to be larger than average and are the prime targets for the busycon whelk fisheries industry along southern New Jersey. Specimens from the southern part of the Georgian Subprovince of the Carolinian Province tend to be smaller and more elongated, often with proportionally higher spires. Northern specimens also tend to have fewer and proportionally-larger shoulder knobs, while southern specimens, especially those for Georgia and northeastern Florida, often have numerous very small shoulder knobs. All of these variations are illustrated in the iconogrpahy at the end of the chapter. Some evidence for sexual dimorphism also exists (Smith, 1902), where males are much smaller and more elongated than females, which tend to be larger and more inflated. These dimorphic patterns appear to be more common in southern populations, while shells of both sexes in northern populations are more similar in size.

Biogeographical Range: As shown on Map 1, *Busycon carica* ranges from Cape Cod, Massachusetts, south to central eastern Florida, near Cape Canaveral. In the Long Island Sound, Delaware Bay, and the lagoons and sounds behind Cape Hatteras (Pamlico Sound, Bogue Sound, Shackleford Island Lagoon, etc.), the Lightning Whelk occurs at intertidal depths and can be collected on sand flats at low tide. Farther south off the coast of northeastern Florida, *Busycon carica* prefers offshore deeper water and is frequently collected by scallop boats off Cape Canaveral.



Map 1. The biogeographical range of *Busycon carica* extends from Pleasant Bay, Cape Cod, Massachusetts to Cape Canaveral, Florida. The species is most abundant in the area extending from New Jersey south to northern South Carolina.

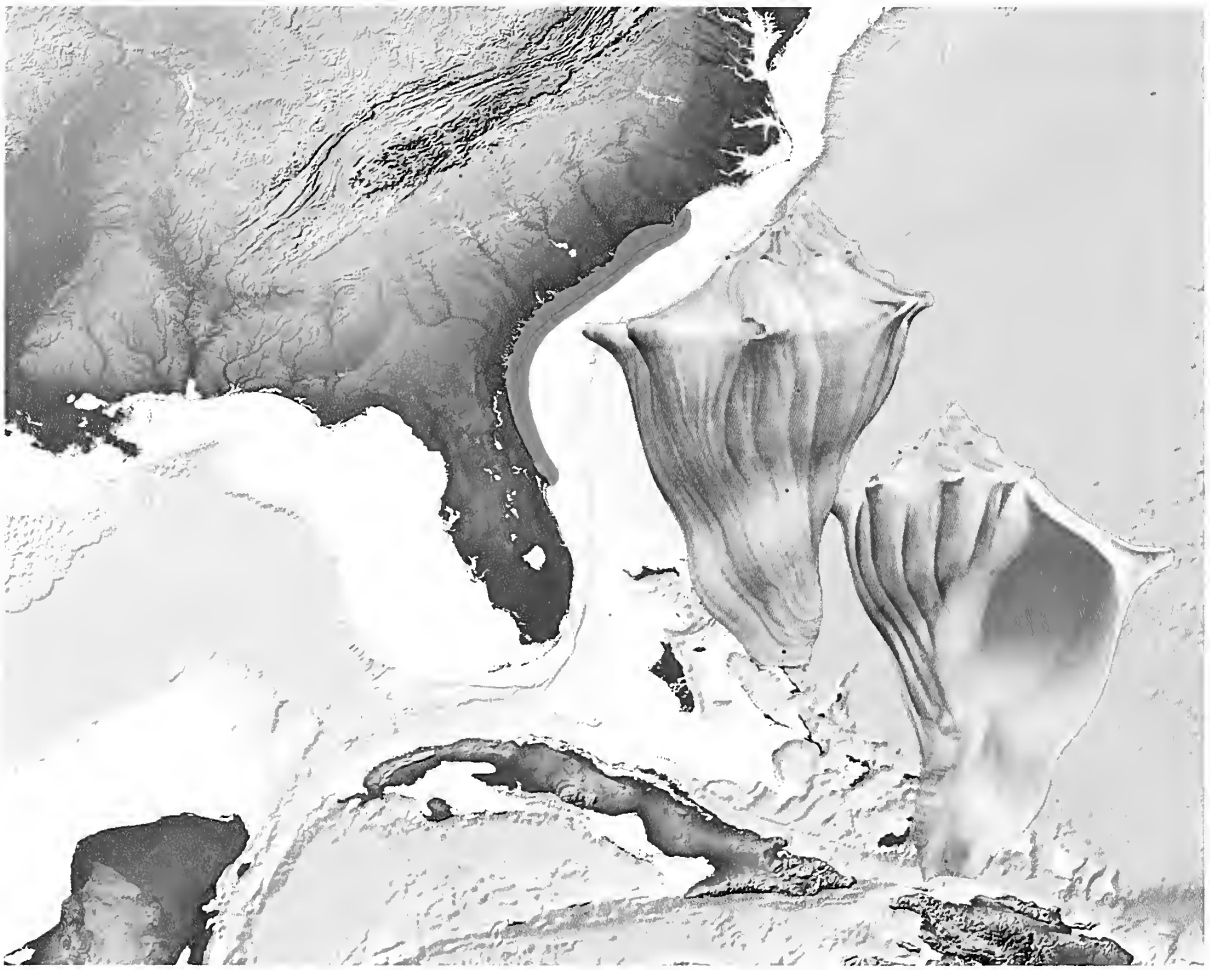
Busycon carica eliceans (Montfort, 1810) (Figures 3.5, 3.6, and 3.7)

Synonymy:
Fulgur eliceans Montfort, 1810
Pyrula perversa variety *dextra* Kiener, 1840
Busycon eliceans (Montfort) Conrad, 1867
Busycon (Busycon) eliceans (Montfort) Hollister, 1958
Busycon carica eliceans (Montfort) Petuch, 2013

Description: Shell with dextral (right-handed) coiling, proportionally very broad across shoulder, short, stocky and vase-shaped; shoulder angled, ornamented with only 5-8 very large, flattened spine-like knobs on body whorl; body whorl broad and inflated; siphonal canal wide, short, and stumpy, generally less than one-half the length of the body whorl, most often ornamented with a conspicuous, broad, tumid ridge; spire proportionally low, slightly stepped, broadly pyramidal; body whorl ornamented with very numerous fine spiral threads, producing a silky surface texture; siphonal canal ornamented with numerous large spiral cords, which become stronger and more noticeable on the raised tumid ridge; aperture wide and flaring, most often white or a pale yellow-cream color; shell colored a pale tan-grey or yellow-tan overlaid with numerous closely-packed, amorphous, brown or purple-brown longitudinal flammules; periostracum thin, rough, strongly adherent.

Discussion: As in the case of the previously-discussed nominate subspecies, *Busycon carica eliceans* shows little variation in shell color and shape over its biogeographical range. Most of the variations seem to involve the size and development of the tumid ridge on the siphonal canal, with some specimens having well-developed ridges and highly-distorted and twisted siphonal canals, while others have poorly-developed ridges and relatively straight siphonal canals.

Biogeographical Range: As shown on Map 2, *Busycon carica eliceans* ranges from near Wrightsville Beach, North Carolina south to near Cocoa Beach, Brevard County, Florida (Hollister, 1958). The subspecies is most frequently encountered along the South Carolina and Georgia coasts, where it is a common component of the intertidal lagoonal sandflats behind barrier islands. In some areas of South Carolina, *Busycon carica eliceans* occurs together with typical *Busycon carica*, and there appear to be no morphological intergrades. More in-depth genetic studies of these two busyconine taxa may show that they are, indeed, separate and distinct sibling species that split apart from each other during a time of isolation caused by late Pleistocene sea level drops.



Map 2. The biogeographical range of *Busycon carica eliceans* extends from near Wrightsville Beach, North Carolina south to near Cocoa Beach, Florida. The subspecies is most commonly encountered in the tidal creeks and estuaries of southern South Carolina and Georgia.

Iconography of Living and Fossil *Busycon* Species

The following sets of figures illustrate both typical specimens and variations of *Busycon carica* and *Busycon carica eliceans*. Several specimens of each subspecies are illustrated. Besides the living species and subspecies, most of the named fossil *Busycon* taxa are also illustrated.

Figure 3.1 *Busycon carica*, Type Species of the Genus *Busycon*.
A, B= *Busycon carica* (Gmelin, 1791), length 224 mm, in 1 m depth off Shackleford Island, Carteret County, North Carolina. This is a classic specimen with a bright red aperture. (p. 65)

Figure 3.2 *Busycon carica* Color Variant.
A, B= *Busycon carica* (Gmelin, 1791), length 213 mm, exposed at low tide off Shackleford Island, Carteret County, North Carolina. Variant with a yellow and brown aperture color. (p. 65)

Figure 3.3 *Busycon carica* High-Spired Variant.
A, B= *Busycon carica* (Gmelin, 1791), length 101 mm, exposed at low tide in a tidal creek off Fripp Island, Beaufort County, South Carolina. Variant with high, protracted spire. (p. 65)

Figure 3.4 *Busycon carica* Dwarf Variants.
A, B= *Busycon carica* (Gmelin, 1791), length 120 mm, on sand flats at low tide, off Amelia Island, Nassau County, Florida. Dwarf variant with numerous small shoulder knobs.
C= *Busycon carica* (Gmelin, 1791), length 94 mm, on sand flats at low tide, off Amelia Island, Nassau County, Florida. Dwarf variant with numerous small shoulder knobs; possibly a small male. (p. 65)

Figure 3.5 ***Busycon carica eliceans*, Typical Specimen.**
A, B= *Busycon carica eliceans* (Montfort, 1810), length 136 mm, in a tidal creek, exposed at low tide, off Sapelo Island, McIntosh County, Georgia. (p. 67)

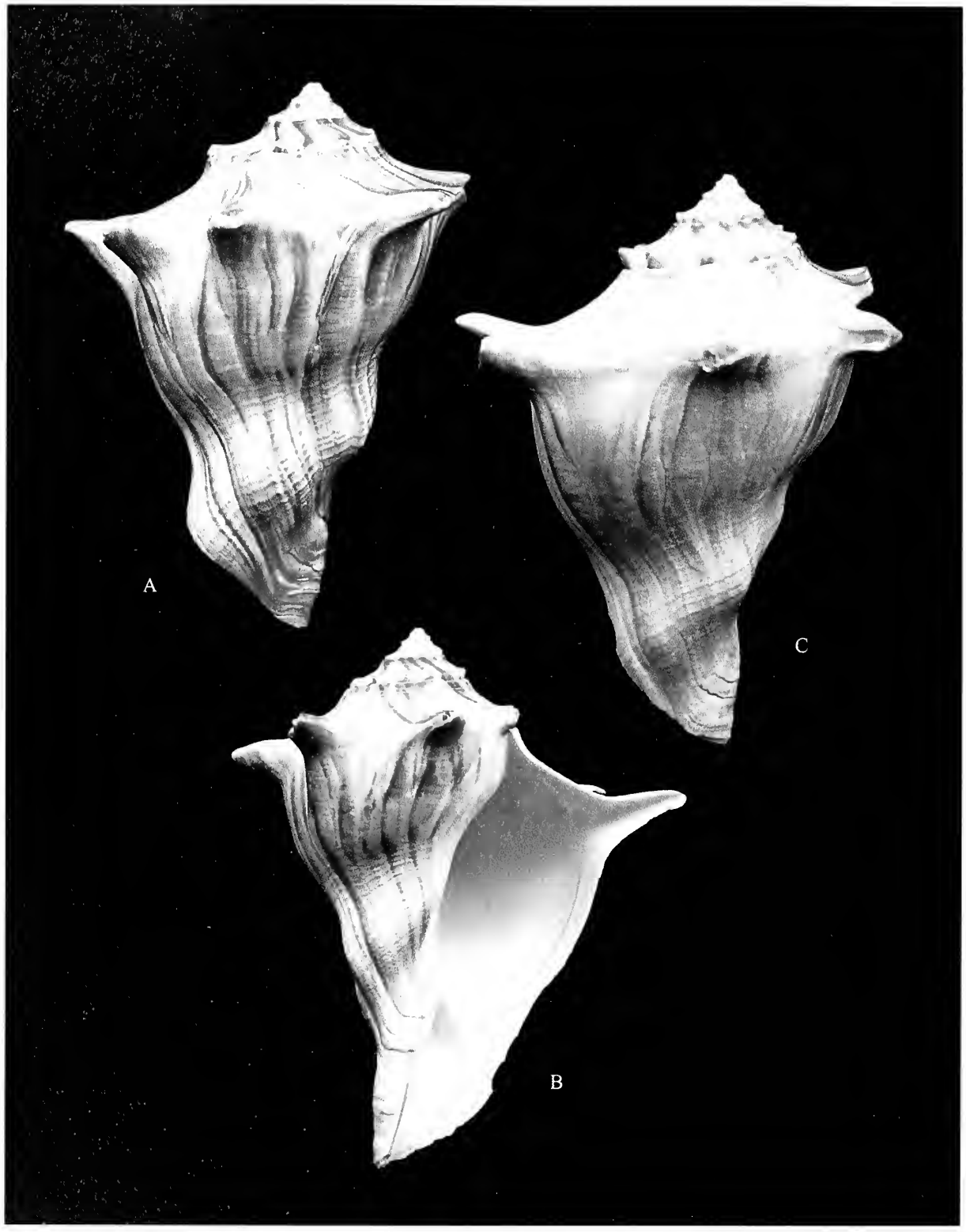


Figure 3.6 *Busycon carica eliceans* Variants with Tumid Ridges.
A= *Busycon carica eliceans* (Montfort, 1810), length 115 mm, exposed at low tide, on sand flats off southern Edisto Island, Colleton County, South Carolina. Variant with a pronounced tumid ridge on the siphonal canal.
B, C= *Busycon carica eliceans* (Montfort, 1810), length 99 mm, exposed at low tide, on sand flats off southern Edisto Island, Colleton County, South Carolina. Variant with a pronounced tumid ridge on the siphonal canal. (p. 67)

Figure 3.7 *Busycon carica eliceans* Variants.
A= *Busycon carica eliceans* (Montfort, 1810), length 113 mm, found dead in a tidal creek off St. Simons Island, Glynn County, Georgia. Variant with an extremely well-developed tumid ridge and extensive webbed flutings, reminiscent of the Pliocene fossil *Busycon filosum* (Figure 3.9).
B= *Busycon carica eliceans* (Montfort, 1810), length 97 mm, on sand bars along the Bear River, southern Ossabaw Island, Chatham County, Georgia. Variant with narrow siphonal canal.
C= *Busycon carica eliceans* (Montfort, 1810), length 80 mm, on sand bars along the Bear River, southern Ossabaw Island, Chatham County, Georgia. Variant with narrow siphonal canal. (p. 67)

Figure 3.8 Fossil *Busycon* Species.
A= *Busycon diegelae* Petuch, 2004, length 129 mm, confluence of Tenmile Creek and the Chipola River, Calhoun County, Florida; Chipola Formation, Burdigalian Age, Miocene.
B= *Busycon burnsi* Dall, 1890, length 59 mm, lower bed at Alum Bluff, Apalachicola River, Liberty County, Florida; upper beds of the Chipola Formation, Burdigalian Age, Miocene.
C= *Busycon diegelae* Petuch, 2004, length 42 mm, confluence of Tenmile Creek and the Chipola River, Calhoun County, Florida; Chipola Formation, Burdigalian Age, Miocene. Juvenile specimen for comparison with *Busycon burnsi*.

Figure 3.9 Fossil *Busycon* Species.
A= *Busycon filosum* Conrad, 1862, length 130 mm, from the Buckingham Member of the Tamiami Formation, Unit 10 in Quality Aggregates Pit #6, Sarasota, Florida; early Piacenzian Age, Pliocene. Also found in the contemporaneous Duplin Formation of the Carolinas. Note the well-developed weblike flutings on the enlarged tumid ridge of the siphonal canal.
B= *Busycon auroraensis* Petuch, 1994, length 151 mm, from the middle fossiliferous beds in the Lee Creek Mine, Aurora, Beaufort County, North Carolina; Edenhouse Member of the Chowan River Formation, late Piacenzian Age, Pliocene. Note the prominent spiral cords and threads on the body whorl and spire.
C= *Busycon filosum* Conrad, 1862, high-spired variety *tritonis* Conrad, 1863, length 198 mm, collected in Unit 10, Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Buckingham Member of the Tamiami Formation, early Piacenzian Age of the Pliocene. Also found in the contemporaneous Duplin Formation of the Carolinas.

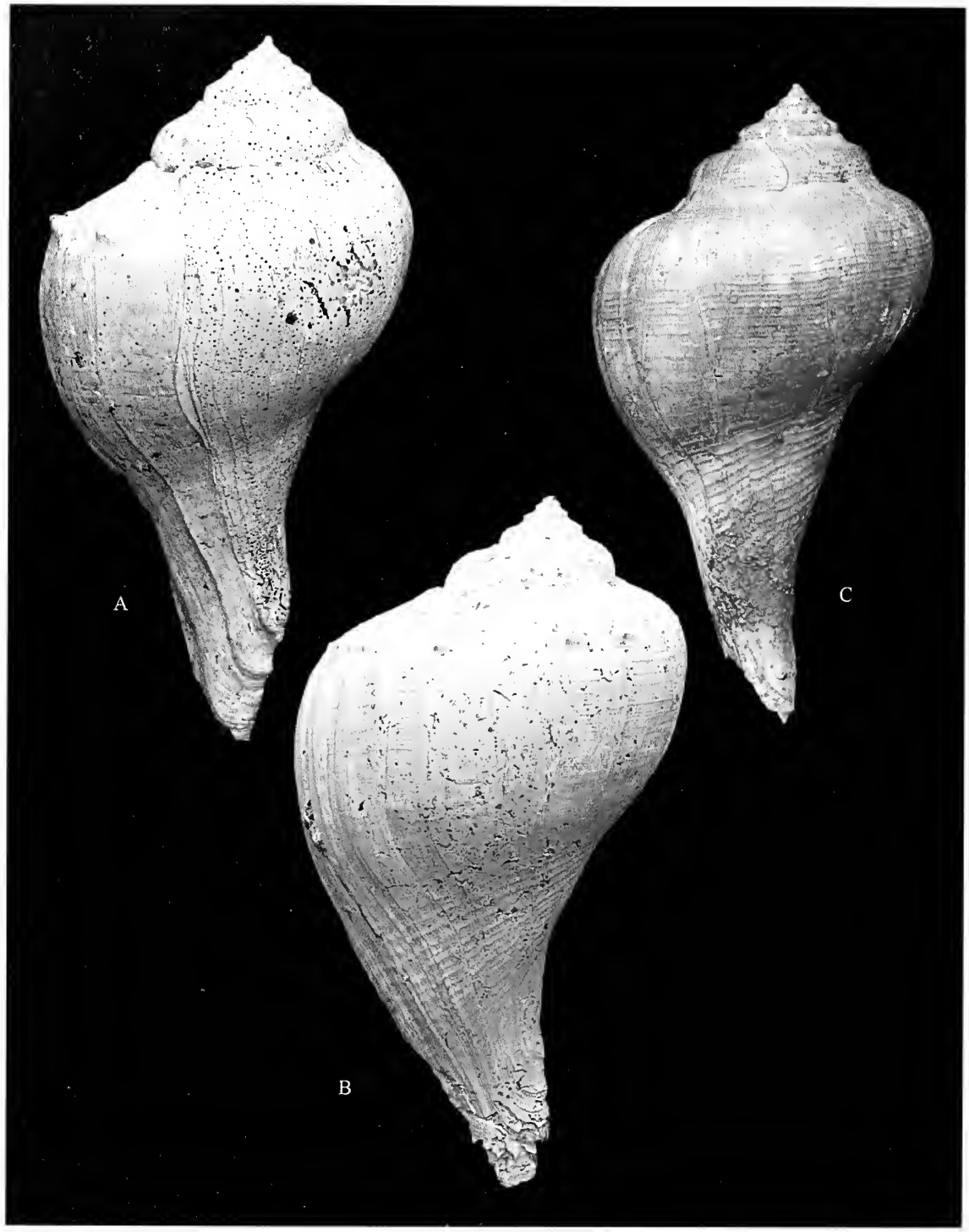


Figure 3.10 Fossil *Busycon* Species.
A= *Busycon maximus* (Conrad, 1839), length 151 mm, collected in the Lone Star Cement Company pit, Chuckatuck, Isle of Wight County, Virginia; Rushmere Member of the Yorktown Formation, early Piacenzian Age, Pliocene.
B= *Busycon duerri* Petuch, 1994, length 217 mm, from the Miami Canal excavation south of Lake Harbor, Palm Beach County, Florida; Fort Denaud Member of the Caloosahatchee Formation, Gelasian Age, early Pleistocene. Note the strong spiral cords on the spire, siphonal canal, and body whorl.
C= *Busycon alumensis* (Mansfield, 1930), length 75 mm, lower bed of the Jackson Bluff Formation at Alum Bluff, Liberty County, Florida, along the Apalachicola River; Piacenzian Age, Pliocene.

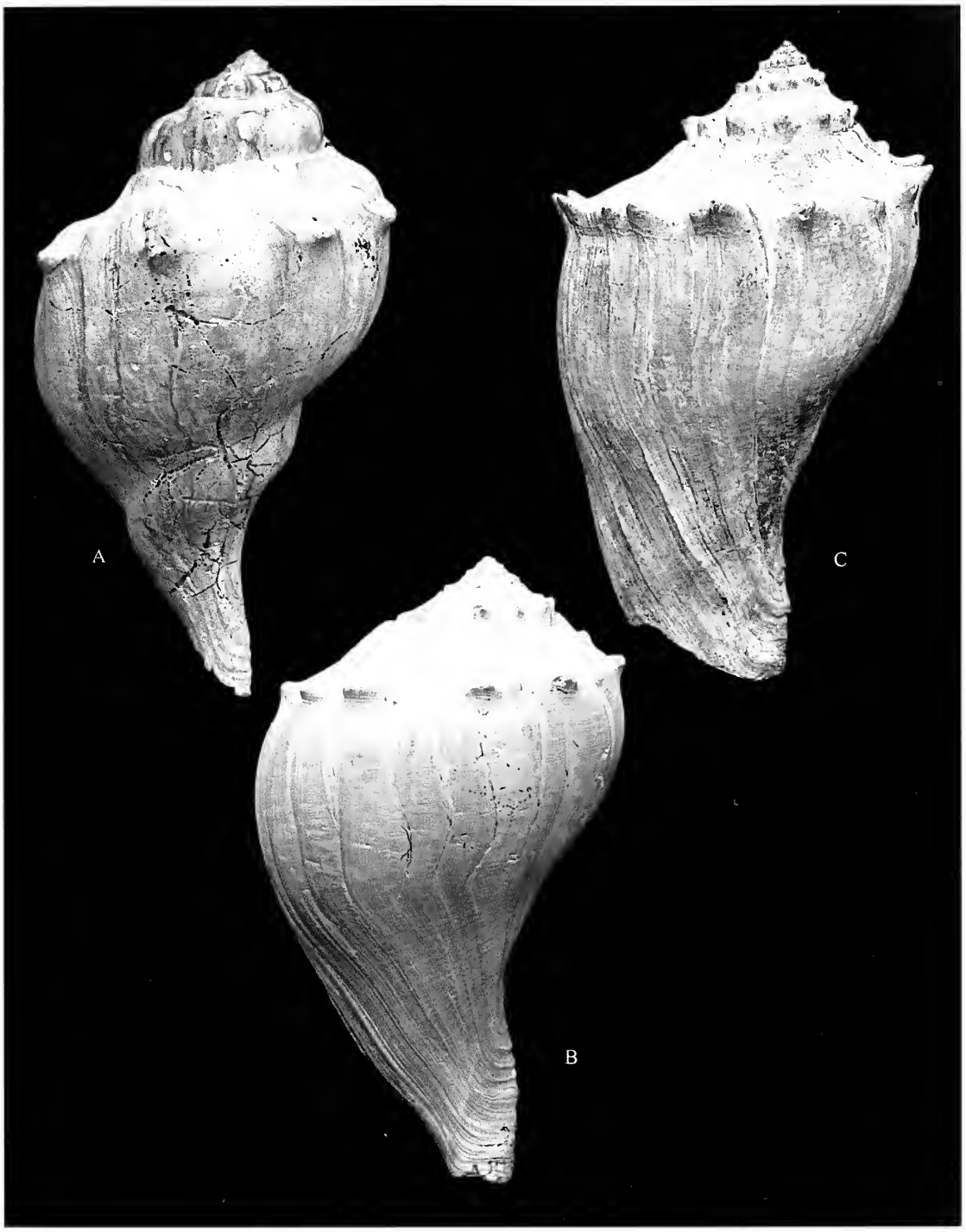


Figure 3.11 Fossil *Busycon* Species.
A= *Busycon pachyus* Petuch, 1994, length 152 mm, collected in Unit 10, Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Buckingham Member of the Tamiami Formation, early Piacenzian Age of the Pliocene.
B= *Busycon rucksorum* Petuch, 1994, length 215 mm, from the middle shell beds in the Rucks Pit, Fort Drum, Okeechobee County, Florida. Fort Drum Member of the Nashua Formation, Gelasian Age of the early Pleistocene. Note the strong spiral threads on the spire and body whorl.
C= *Busycon gilmorei* Petuch, 1994, length 165 mm, from the upper fossiliferous beds in the Lee Creek Mine, Aurora, Beaufort County, North Carolina; James City Formation, Gelasian Age, Pleistocene. Also found in the contemporaneous upper beds of the Waccamaw Formation of the Carolinas.

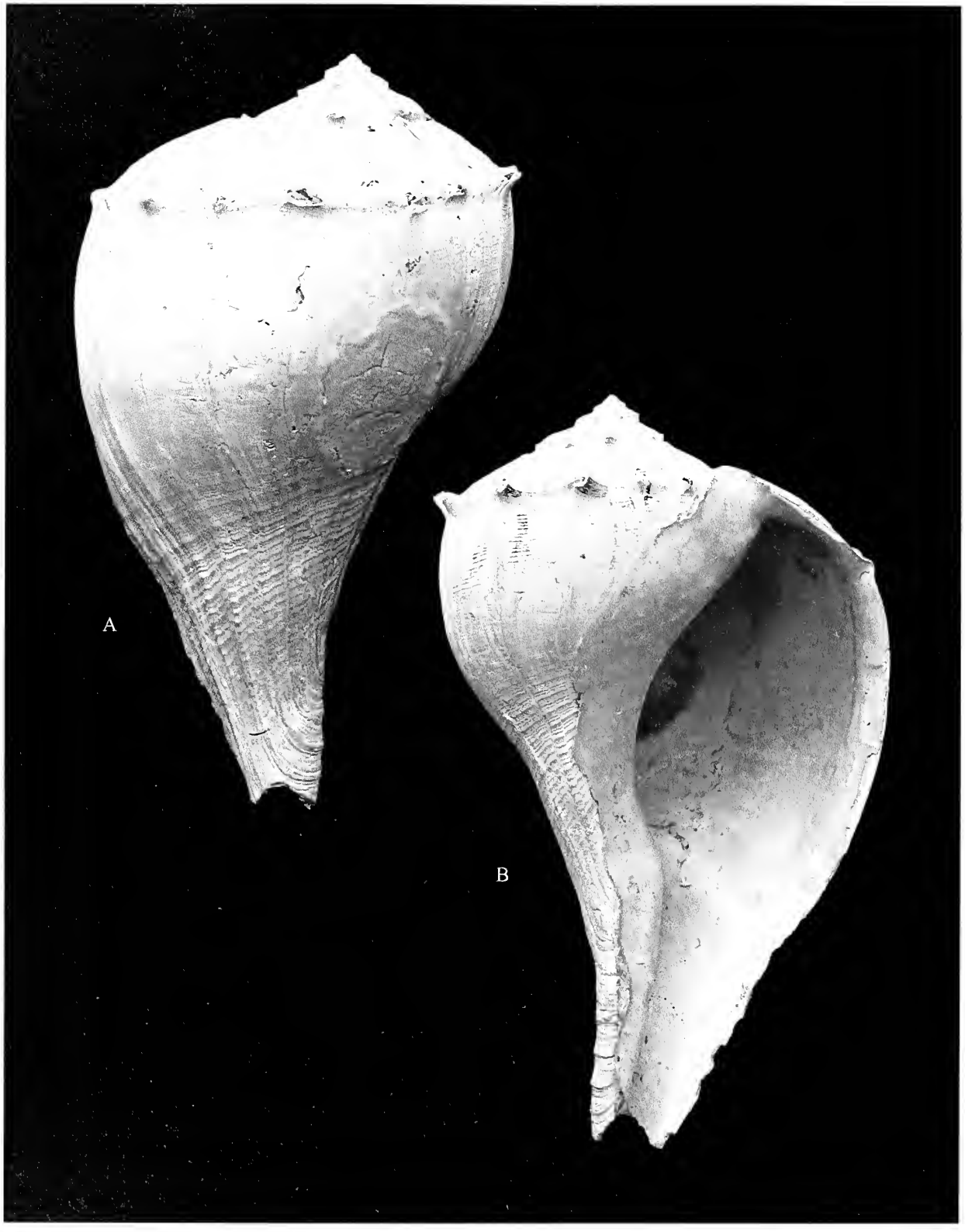


Figure 3.12 Largest-known *Busycon* Species.
A, B= *Busycon titan* Petuch, 1994, length 315 mm, collected at the Lakes of the Meadows housing excavation off Bird Road, Miami, Dade County, Florida. Golden Gate Member of the Tamiami Formation; Piacenzian Age, Pliocene. Known only from the fossil coral reef deposits of the Tamiami Formation of southern Florida.

CHAPTER FOUR

The Left-Handed Whelks: Genus *Sinistrofulgur*

This genus of large and ecologically-important busyconids is the only group of sinistral (counter-clockwise coiling) buccinoidean gastropods found in the Virginian and Carolinian Provinces. The first *Sinistrofulgur* species appear during the earliest Zanclean Age of the Pliocene, immediately after the mass extinction that took place at the end of the Messinian Age of the Miocene. No immediate predecessor busyconid is presently known and the genus may have evolved as a sinistral-coiling mutation of some still-undescribed *Busycon* from southern Florida. Since the Tortonian and Messinian Miocene deposits of southern Florida are highly leached by flowing groundwater, their aragonitic shell fossils have all dissolved away millions of years ago. This has left a huge hiatus in the fossil record of the genus *Busycon*, between the Serravallian Miocene *Busycon montforti* and the Zanclean Pliocene species such as *Busycon filosum*, *Busycon pachyus*, and *Busycon alumense*. One of the "missing links" during the Serravallian-to-Messinian interval was undoubtedly the ancestor of the entire genus *Sinistrofulgur*. By the late Zanclean and early Piacenzian Pliocene, *Sinistrofulgur* had already begun to undergo a species radiation, producing two large sympatric species, *Sinistrofulgur hollisteri* (probably the oldest of the two) and *Sinistrofulgur grabaui*, in the shallow tropical lagoons of the Okeechobean Sea.

The genus weathered all the severe extinction events that occurred during the late Pliocene, early Pleistocene, and late Pleistocene (Petuch, 1995; 2004), and always remained an abundant predator in virtually every shallow marine ecosystem from Virginia to Florida. Although 13 *Sinistrofulgur* species have been described from the eastern North American fossil record, only one or two species are ever found together in any single stratigraphic unit. Since the late Pleistocene, this pattern of low diversity has been reversed and the genus is now undergoing an explosive species radiation, resulting in four distinct taxa being distributed over the entire area of the Virginian and Carolinian Provinces. The named fossil species are listed in Appendix 1 at the end of this book and all of these are illustrated here in the iconography at the end of this chapter. The four living species are described here and illustrated in the following iconography. Although the taxon was originally described as a subgenus of *Busycon* (Hollister, 1958), we here consider it to be a distinct, full genus all to itself.

Family Busyconidae
Subfamily Busyconinae
Genus *Sinistrofulgur* Hollister, 1958

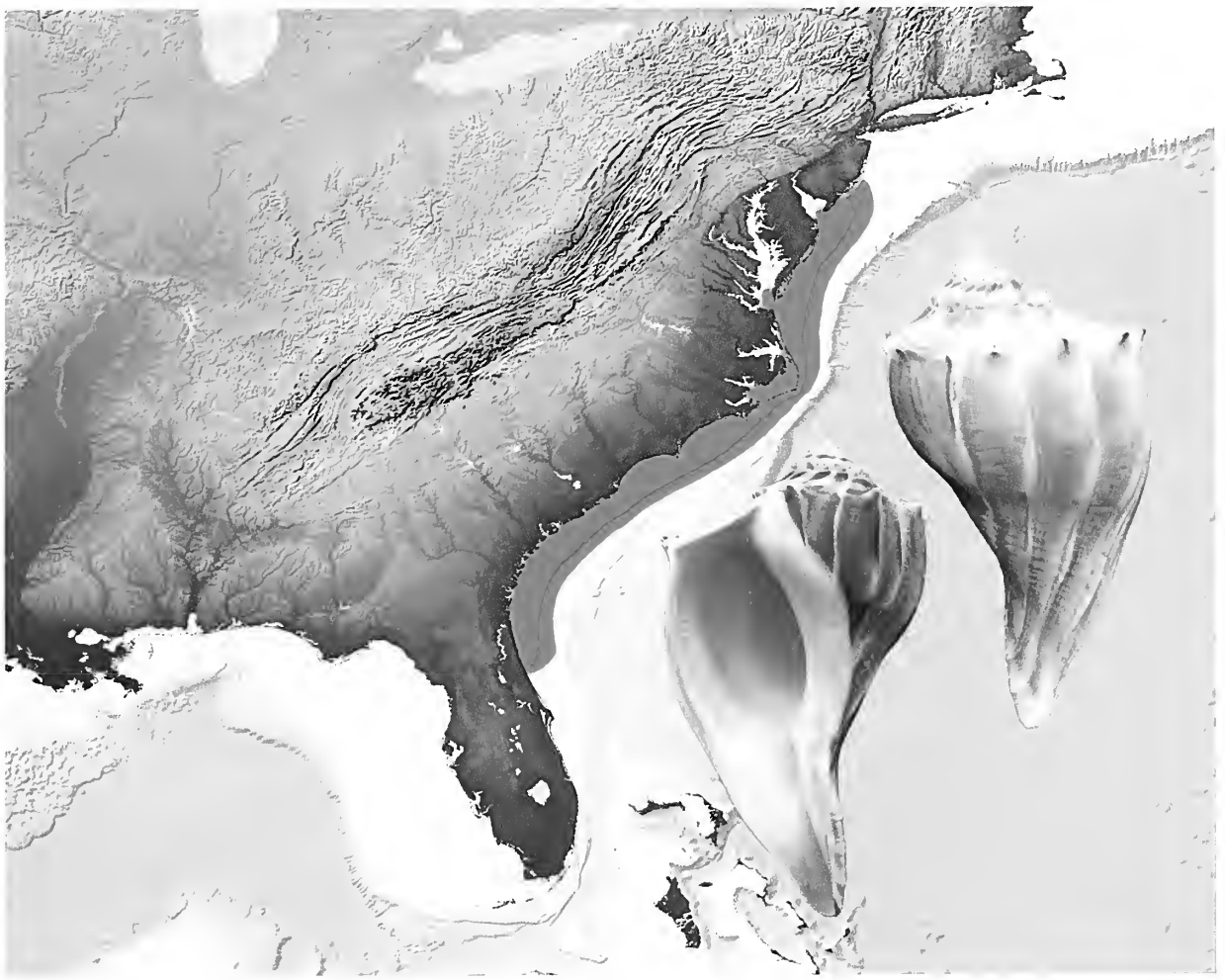
***Sinistrofulgur laeostomum* (Kent, 1982)**
(Figures 4.1, 4.2, and 4.3)

Synonymy:
Busycon carica (Gmelin) sinistral form, Abbott, 1974
Busycon (Sinistrofulgur) sinistrum Hollister, 1958 from North Carolina
Busycon laeostomum Kent, 1982
Sinistrofulgur laeostomum (Kent) Petuch, 2013

Description: This large left-handed (sinistral) species typically has an inflated, pyriform shell with rounded, almost bulging sides; the spire is elevated and scalariform, with distinctly sloping spire whorls; shoulder sharply angled, ornamented with large, evenly-spaced spine-like knobs, usually 10-12 per whorl; siphonal canal elongated and wide, roughly one-half the entire length of the body whorl; body whorl and spire whorls smooth, with a silky texture; siphonal canal ornamented with large, low spiral cords, which are especially prominent on specimens with tumid ridges; shell color somewhat variable, ranging from pure white to yellow-tan to pinkish-white with wide tan longitudinal flammules; aperture wide and flaring, pure white or pale cream-white within; periostracum thin, rough, and tightly adherent, gray-brown in color.

Discussion: Generally, *Sinistrofulgur laeostomum* resembles a left-handed version of *Busycon carica*, but with a white or cream-colored aperture. The most variable character is that of shell color, which varies from pure white ("Snow Whelk"), to pale salmon-orange, to pale tan or brown with darker brown longitudinal flammules. Specimens from southern populations, such as those in the Carolinas, Georgia, and northeastern Florida, tend to be darker in color, most often tan or light brown; specimens from off New Jersey are most often white or pale salmon-orange. The interior of the aperture on some specimens has numerous strong cords along the inner edge of the lip, while other specimens are completely smooth on the interior. The only other major shell variation is seen in the form of the wide siphonal canal, which can be straight and smooth or ornamented with a thick tumid ridge. Specimens from South Carolina and Georgia often have a strong tumid ridge, which can be highly sculptured with numerous prominent spiral cords.

Biogeographical Range: As seen on Map 3, *Sinistrofulgur laeostomum* is a widespread species, ranging from southern New Jersey (off Stone Harbor and Cape May) southward to Cape Canaveral, Florida, and inhabits both the Virginian and Carolinian Provinces. The Virginian Province specimens are larger, paler-colored, and more inflated than are the specimens from the Georgian Subprovince of the Carolinian Province, which are smaller, heavier, and darker.



Map 3. The biogeographical range of *Sinistrofulgur laeostomum* extends from New Jersey south to northeastern Florida, primarily in offshore waters.

Sinistrofulgur sinistrum (Hollister, 1958) (Figures 4.4 - 4.11)

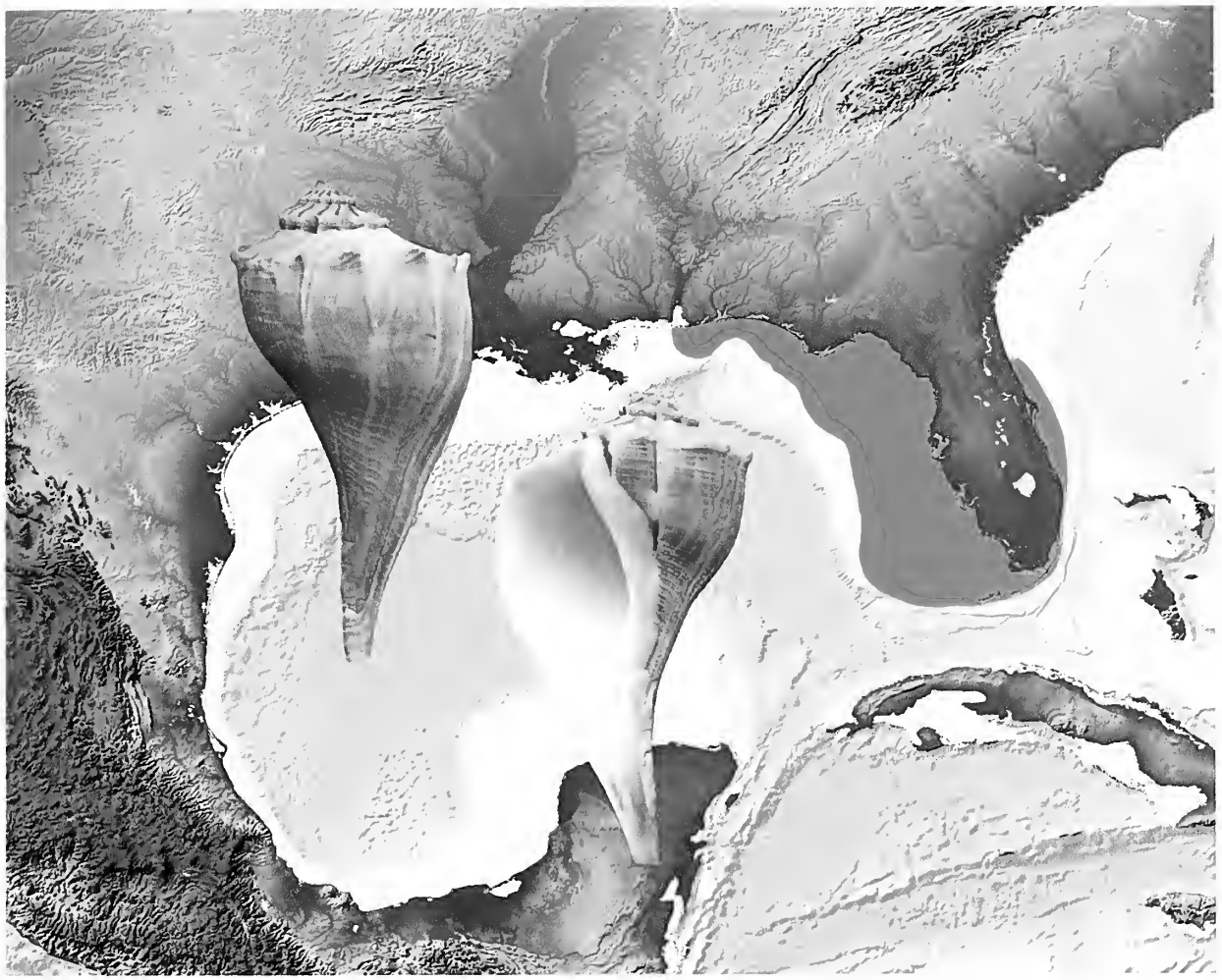
Synonymy:
Fulgur perversum (Linne) Dall, 1890
Busycon contrarium (Conrad) B. Smith, 1939
Busycon (Sinistrofulgur) sinistrum Hollister, 1958
Busycon (Sinistrofulgur) aspinosum Hollister, 1958
Busycon contrarium (Conrad) Abbott, 1974
Sinistrofulgur sinistrum (Hollister) Petuch, 1994

Description: This large sinistral (left-handed) species typically has an elongated, vase-shaped shell with relatively straight sides; the spire is elevated, protracted, stepped and scalariform, with flattened whorls that are only slightly sloping; shoulder sharply angled, ornamented with 12-16 large, prominent, rounded knobs; body whorl sculptured with numerous strong spiral cords and

ribs; central area of the body whorl with a wide band of reduced spiral sculpture that corresponds to a blade-like process on the outer lip; siphonal canal proportionally long and narrow, approximately one-half of total shell length, ornamented with numerous very strong and prominent spiral cords; aperture wide and flaring, often with numerous strong cords on the interior of the lip; aperture generally white, but may be pale orange, yellow, or purple-brown on interior; shell base color white, tan, or orange-tan, overlaid with regularly-spaced thin dark brown longitudinal flammules that correspond to the edges of previous apertural lips; periostracum thin, rough, tightly adherent, gray-brown in color.

Discussion: Of the four living species of Left-Handed Whelks, *Sinistrofulgur sinistrum* is, by far, the most variable morphologically. These great differences in shell shape and color reflect the wide range of habitats within which this species is capable of living. The height and form of the spire is probably the most variable character, ranging from high and protracted, with distinctly stepped whorls (Figure 4.5), to low and completely flattened (Figure 4.8). *Sinistrofulgur sinistrum* also exhibits the widest range of colors of all four of the Left-Handed Whelks, being pure white (Figure 4.6), solid bright orange (Figure 4.6), dark purplish-brown (Figure 4.7), or pale salmon-orange and pink (Figure 4.10, for deep water specimens from the Dry Tortugas). A variant with reduced or absent shoulder knobs (Figure 4.11) was named *Busycon (Sinistrofulgur) aspinosum* by Hollister (1958) and was considered to be a full species. Subsequent research has shown that this knobless whelk is no more than a rare variant of *S. sinistrum* and it appears most often in populations that live in quiet lagoons with fluctuating salinities. Many recent workers, particularly R.T. Abbott (1974), have incorrectly referred to this common sinistral busyconid as "*Busycon contrarium*". As pointed out by Hollister (1958), that species is a Pliocene fossil (from the Yorktown, Duplin, and Tamiami Formations) and a classic specimen of the real *Sinistrofulgur contrarium* is shown here on Figure 4.18.

Biogeographical Range: As seen on Map 4, *Sinistrofulgur sinistrum* is a widespread species, ranging from near Cape Canaveral, Florida, around the Florida Keys, up the western coast of Florida to the Florida Panhandle, and westward to the Mississippi River Mouth. This is the only busyconid species that actually occurs in three separate molluscan faunal subprovinces of the Carolinian Province; the Georgian Subprovince, the Floridian Subprovince, and the Suwannean Subprovince. M.G. Harasewych (Smithsonian Institution, personal communication) has suggested that the Georgian Subprovince populations may represent a separate subspecies of *S. sinistrum* and that this unnamed taxon acts as an intermediate between the northern *S. laeostomum* and the southern *S. sinistrum*. Specimens from the Florida Keys and adjacent areas are heavier and smaller than typical *sinistrum* and are also more heavily sculptured with strong spiral cords (Figure 4.9).



Map 4. The biogeographical range of *Sinistrofulgur sinistrum* extends from northeastern Florida, around southern Florida and the Florida Keys, along western Florida, and across the coasts of Alabama and Mississippi. The Mississippi River Delta, with its huge freshwater effluent, acts as a barrier to the dispersal of *Sinistrofulgur sinistrum* and the species does not range west of the delta.

Sinistrofulgur pulleyi (Hollister, 1958)
(Figures 4.12, 4.13, and 4.14)

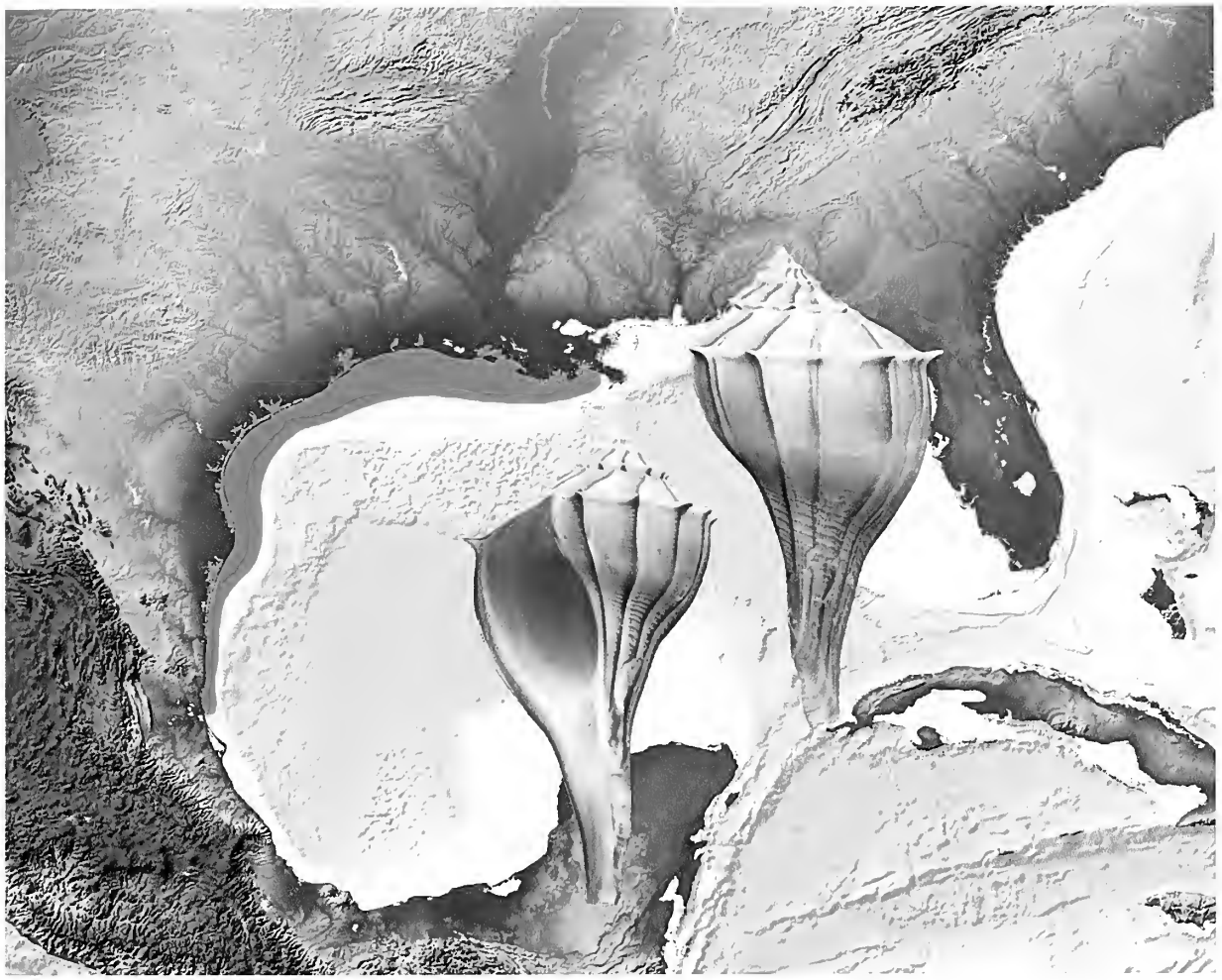
Synonymy:
Busycon (Sinstrofulgur) pulleyi Hollister, 1958
Busycon perversum pulleyi (Hollister) Abbott, 1974
Busycon pulleyi (Hollister) Tunnell, *et al.*, 2010
Sinistrofulgur pulleyi (Hollister) Petuch, 2013

Description: This distinctive sinistral (left-handed) species is generally smaller, thinner, and more delicate than typical specimens of *Sinistrofulgur sinistrum* and *S. laeostomum*, and has a less elongated and more vase-shaped shell; the shoulder is sharply-angled and ornamented with 14-18 long, thin, and sharp spine-like knobs, which are sharper, thinner, and more pointed than the shoulder knobs of *S. sinistrum*; spire stepped, protracted, much narrower than the other three

Sinistrofulgur species; siphonal canal long, straight, and proportionally narrow, approximately one half the length of the entire shell; body whorl smooth, with a silky texture, encircled with very fine, low spiral threads and small cords; siphonal canal heavily sculptured with numerous very strong spiral cords; aperture wide and flaring, ornamented with strong cords on the inside of the lip, generally colored a pale-to-dark yellow or yellow-orange on the interior; shell base color variable, ranging from pale yellow-tan to dark gray-tan, overlaid with numerous evenly-spaced dark purple-brown longitudinal lines that correspond to the previous edges of the outer lip; periostracum thin, rough, and tightly adherent, gray-brown in color.

Discussion: *Sinistrofulgur pulleyi*, the State Shell of Texas, differs greatly from its highly variable eastern relative, *S. sinistrum*, in being relatively invariant. Most specimens are of a yellow-tan color with dark purple-brown longitudinal lines, although some individuals may have a grayish or gray-tan base color; aged and senile individuals tend to be of a pure white color. Characteristically, all individuals have beautiful deep yellow or yellow-orange apertures. Some specimens, particularly those from shallow lagoonal areas in southern Texas (Figure 4.14), have relatively low spires, and superficially resemble sinistral specimens of the sympatric *Lindafulgur candelabrum*. Occasional specimens of *S. pulleyi*, particularly those from the southern part of its range, also can have a twisted siphonal canal and slightly resemble the more distorted *S. perversum* from the Yucatanean Subprovince to the south (Figure 4.15).

Biogeographical Range: As seen on Map 5, *Sinistrofulgur pulleyi* is completely confined to the Texan Subprovince of the Carolinian Province and ranges from the western side of the Mississippi River Delta southward to near Veracruz, Mexico.



Map 5. The biogeographical range of *Sinistrofulgur pulleyi* extends from the western coast of Louisiana (western side of the Mississippi River Delta), along the entire coast of Texas, south to near Veracruz, Veracruz State, Mexico.

Sinistrofulgur perversum (Linnaeus, 1758) (Figures 4.15, 4.16, and 4.17)

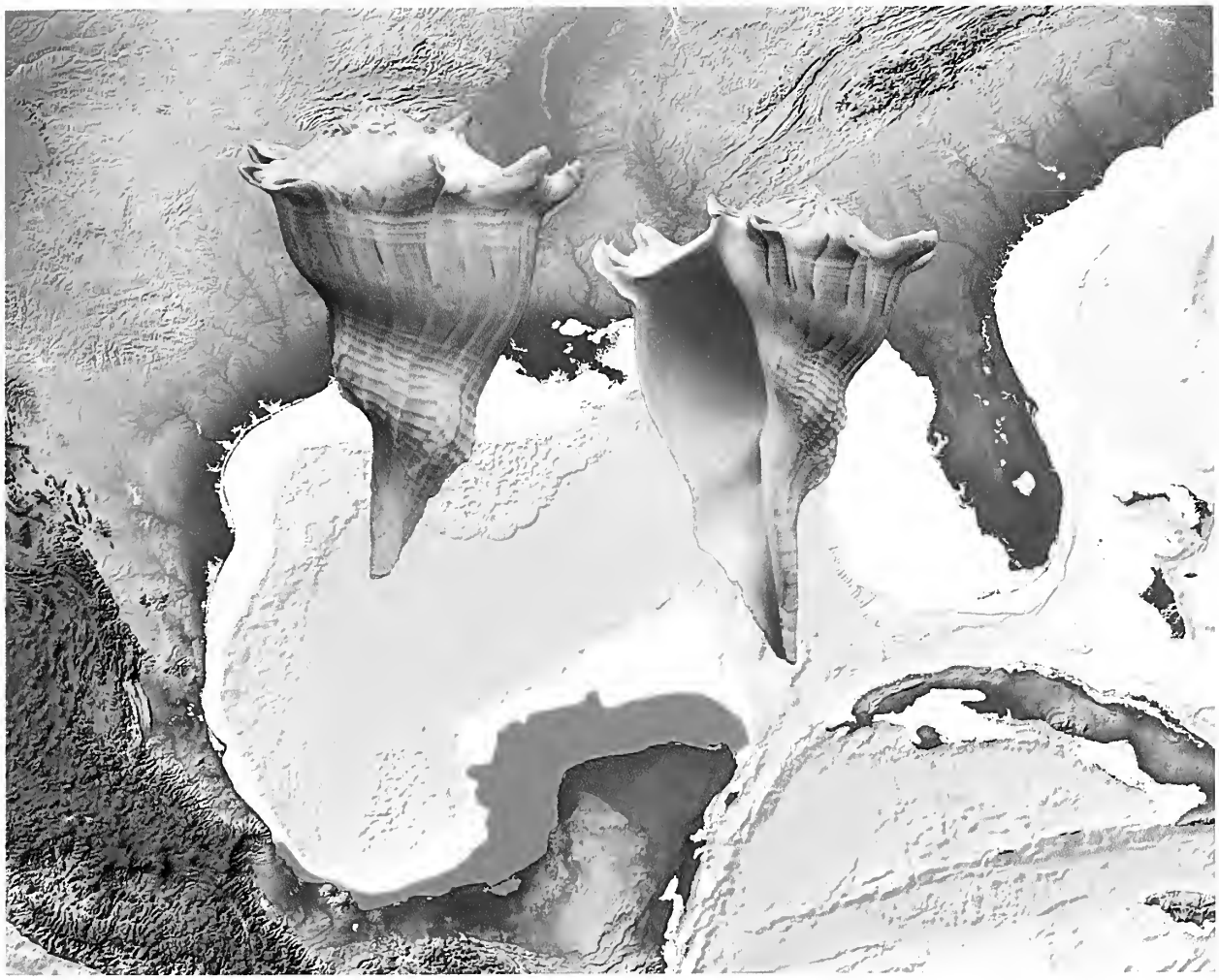
Synonymy:
Murex perversus Linnaeus, 1758
Pyrula kieneri Philippi, 1848 (right-handed mutations)
Fulgur gibbosum Conrad, 1853
Busycon perversum (Linnaeus) Smith, 1939
Busycon (Sinistrofulgur) perversum (Linne) Hollister, 1958
Busycon perversum (Linne) Abbott, 1974
Sinistrofulgur perversum (Linnaeus) Petuch, 2013

Description: Of the four living *Sinistrofulgur* species, *S. perversum* has the most distinctive and remarkable shell morphology; generally, these large sinistral busyconids have very wide, inflated, and broadly vase-shaped shells and low, almost flattened spires; the shoulder is sharply-angled and is ornamented with 7-15 extremely large, flattened, paddle-like knobs; the prominent

shoulder knobs are open and blade-like, and frequently curve upward (posteriorward) in a pronounced cup-like fashion; the vase-shaped body whorl flares posteriorward and is ornamented with very numerous strong spiral cords, giving the shell a rough texture; the flattened spire whorls are strongly sculptured with large spiral cords and threads; the siphonal canal is wide and broad and is roughly one-half the length of the body whorl; characteristically, an extremely large and prominent tumid ridge is present around the siphonal canal, producing a twisted and distorted appearance to the entire shell; the siphonal canal and the tumid ridge are ornamented with extremely heavy, almost scaly, spiral cords and ribs, further enhancing the distorted apprearance of the shell; on some specimens, the tumid ridge bears numerous large, wing-like flutings that extend beyond the outline of the siphonal canal; the shell base color is generally white, yellow, or pale salmon-orange, overlaid with large, evenly-spaced dark reddish-brown longitudinal lines; a single broad band of pale salmon-orange or white encircles the middle of the body whorl; aperture wide and flaring, with strong cords along the inner side of the lip, deep yellow-orange within the interior; periostracum thin, rough, and tightly adherent, gray-brown in color.

Discussion: With its distinctive vase-like shape, huge and flattened shoulder spines, fluted tumid ridge, and highly twisted siphonal canal, *Sinistrofulgur perversum* cannot be confused with any other Left-Handed Whelk. Offshore specimens from deeper water areas near the Campeche Banks are larger and much more distorted, often having well developed wing-like flutings and webbings along the tumid ridge of their siphonal canals, reminiscent of the Pliocene *Busycon filosum* (Figure 3.9, Chapter 3) and *Sinistrofulgur grabaui* Petuch, 1994 (Figure 4.20). Shallow water specimens from the coastal lagoons along the Yucatan Peninsula are generally smaller and more darkly colored, have straighter siphonal canals with less-developed tumid ridges, and have proportionally larger shoulder spines. A dwarf fossil subspecies, *Sinistrofulgur perversum okeechobeensis* Petuch, 1994 (shown here on Figure 4.19), is known from the late Pleistocene of southern Florida and indicates that the species may have been much more widely distributed during some of the warmer interglacial times during the Tarantian Age.

Biogeographical Range: As seen on the Map 6, *Sinistrofulgur perversum* is completely restricted to the Yucatanean Subprovince of the Carolinian Province, ranging from near Veracruz, Mexico, across the northern coast of the Yucatan Peninsula, the Campeche Banks, and the offshore Alacran, Arcas, and Arenas Reefs, to Isla Contoy, Quintana Roo State, Mexico. The species is found only in Mexico.



Map 6. The biogeographical range of *Sinistrofulgur perversum* is totally confined to Mexico, extending from near Veracruz, Veracruz State, across the Yucatan Peninsula and Campeche Bank, to Isla Contoy, Quintana Roo State.

Iconography of Living and Fossil *Sinistrofulgur* Species

The following sets of figures illustrate both typical specimens and variations of the four living species of *Sinistrofulgur*. Several specimens of each species are illustrated. Besides the living species, all of the named fossil *Sinistrofulgur* taxa are also illustrated here.

Figure 4.1 *Sinistrofulgur laeostomum*, Typical Specimen.
A, B= *Sinistrofulgur laeostomum* (Kent, 1982), length 178 mm, typical specimen, trawled by commercial fishermen from 20 m depth, off Cape May, Cape May County, New Jersey. (p. 82)

Figure 4.2 *Sinistrofulgur laeostomum*, Typical Specimens.
A= *Sinistrofulgur laeostomum* (Kent, 1982), length 195 mm, found on the beach after a heavy storm, Nags Head, Dare County, North Carolina. This specimen exhibits the pure white color of the "Snow Whelk" variety. Collected by Tammy Bailey Myers.
B= *Sinistrofulgur laeostomum* (Kent, 1982), length 172 mm, trawled by commercial fishermen from 20 m depth off Cape May, Cape May County, New Jersey. (p. 82)

Figure 4.3 *Sinistrofulgur laeostomum* Variant with Tumid Ridge.
A, B= *Sinistrofulgur laeostomum* (Kent, 1982), length 169 mm, trawled by scallop boats from 20 m depth off Edisto Island, Colleton County, South Carolina. Note the large, wide tumid ridge that has developed around the base of the siphonal canal. Characteristically, specimens from South Carolina also have numerous strong spiral cords on the tumid ridge. (p. 82)

Figure 4.4 *Sinistrofulgur sinistrum* Typical Specimen.
A, B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 215 mm, on sand flat at low tide, off Siesta Key, Sarasota County, Florida. (p. 83)

Figure 4.5 *Sinistrofulgur sinistrum* High-Spired Variants.
A, B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 137 mm, exposed at low tide on mud near oyster banks, Cedar Key, Levy County, Florida. Note the high, stepped spire and exceptionally colorful shell.
C, D= *Sinistrofulgur sinistrum* (Hollister, 1958), length 132 mm, exposed at low tide on mud and oyster banks, Cedar Key, Levy County, Florida. Note the high, stepped spire. (p. 83)

Figure 4.6 *Sinistrofulgur sinistrum* Color Variants.
A= *Sinistrofulgur sinistrum* (Hollister, 1958), length 140 mm, found on a sand bar at low tide, St. Petersburg Beach, Pinellas County, Florida. Pure white color form.
B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 174 mm, on a sand bar at low tide in Estero Bay, north of Bonita Springs, Lee County, Florida. Bright orange color form; note the deep orange color inside the aperture. (p. 83)

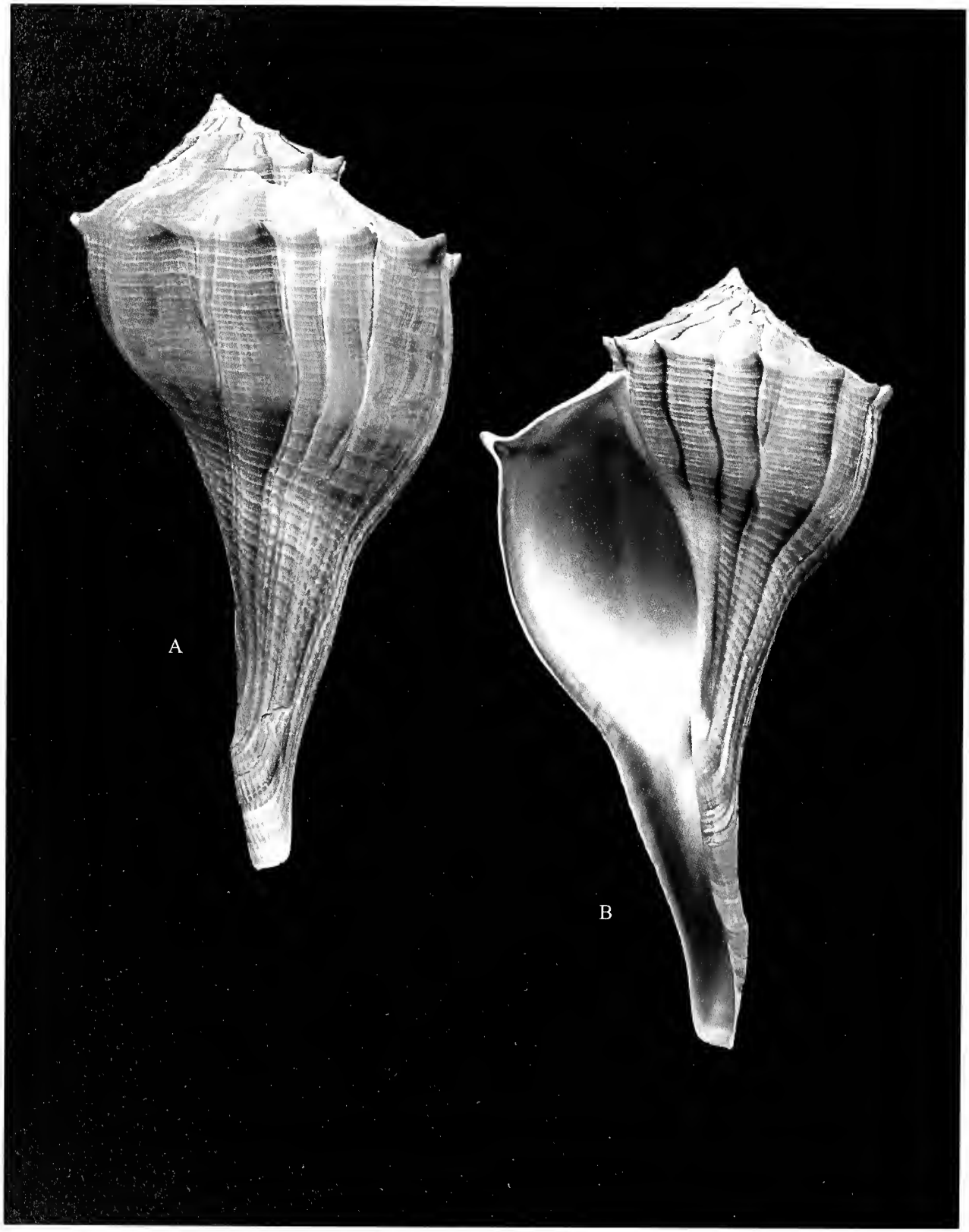


Figure 4.7 *Sinistrofulgur sinistrum* Dark Color Variant.
A, B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 157 mm, found at low tide in mud and oyster banks, Cedar Key, Levy County, Florida. Note the exceptionally dark shell color that is typical of shells from Cedar Key. (p. 83)

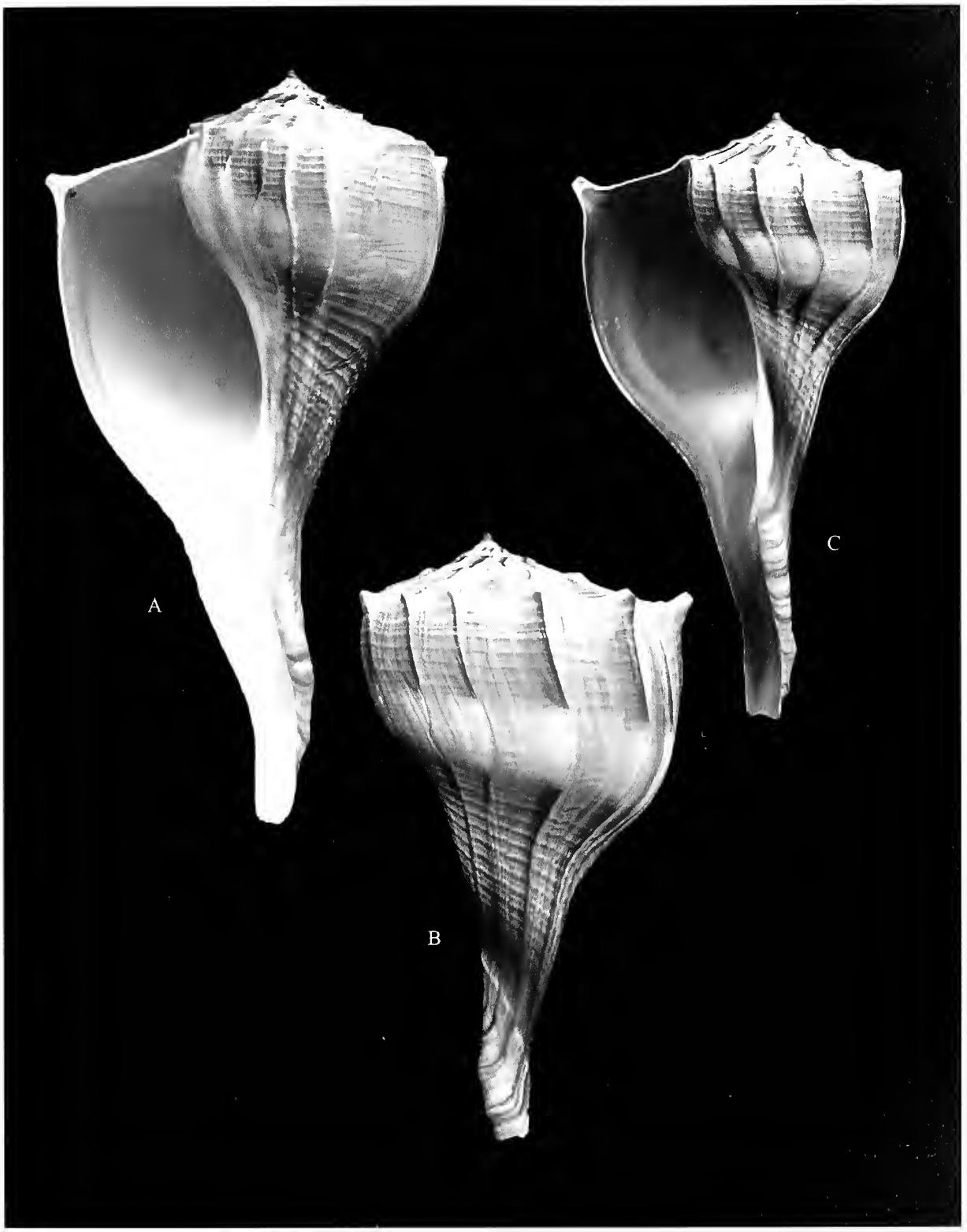


Figure 4.8 *Sinistrofulgur sinistrum* Flat-Spired Variants.
A= *Sinistrofulgur sinistrum* (Hollister, 1958), length 175 mm, found at low tide in a tidal channel, Caxambas Pass, Collier County, Florida. Note the extremely flattened spire whorls.
B, C= *Sinistrofulgur sinistrum* (Hollister, 1958), length 115 mm, found at low tide in a tidal channel, Caxambas Pass, Collier County, Florida. (p. 83)

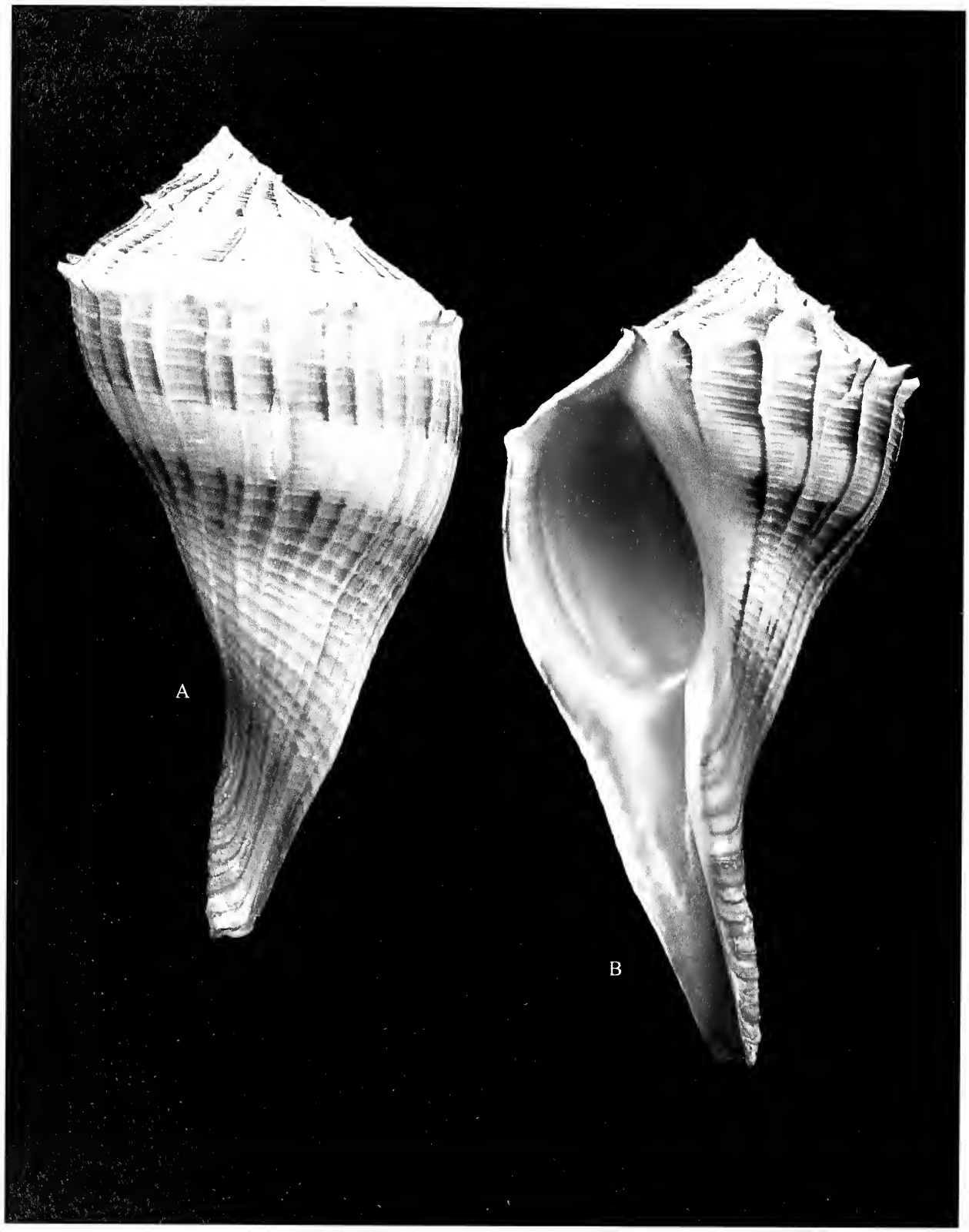


Figure 4.9 *Sinistrofulgur sinistrum* Coral Reef Variant.
A, B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 176 mm, found in a coralline algal bed and *Porites* coral thicket in 2 m depth, off Missouri Key, Middle Florida Keys, Monroe County, Florida. Note the very strong shell sculpture composed of numerous prominent spiral cords. (p. 83)

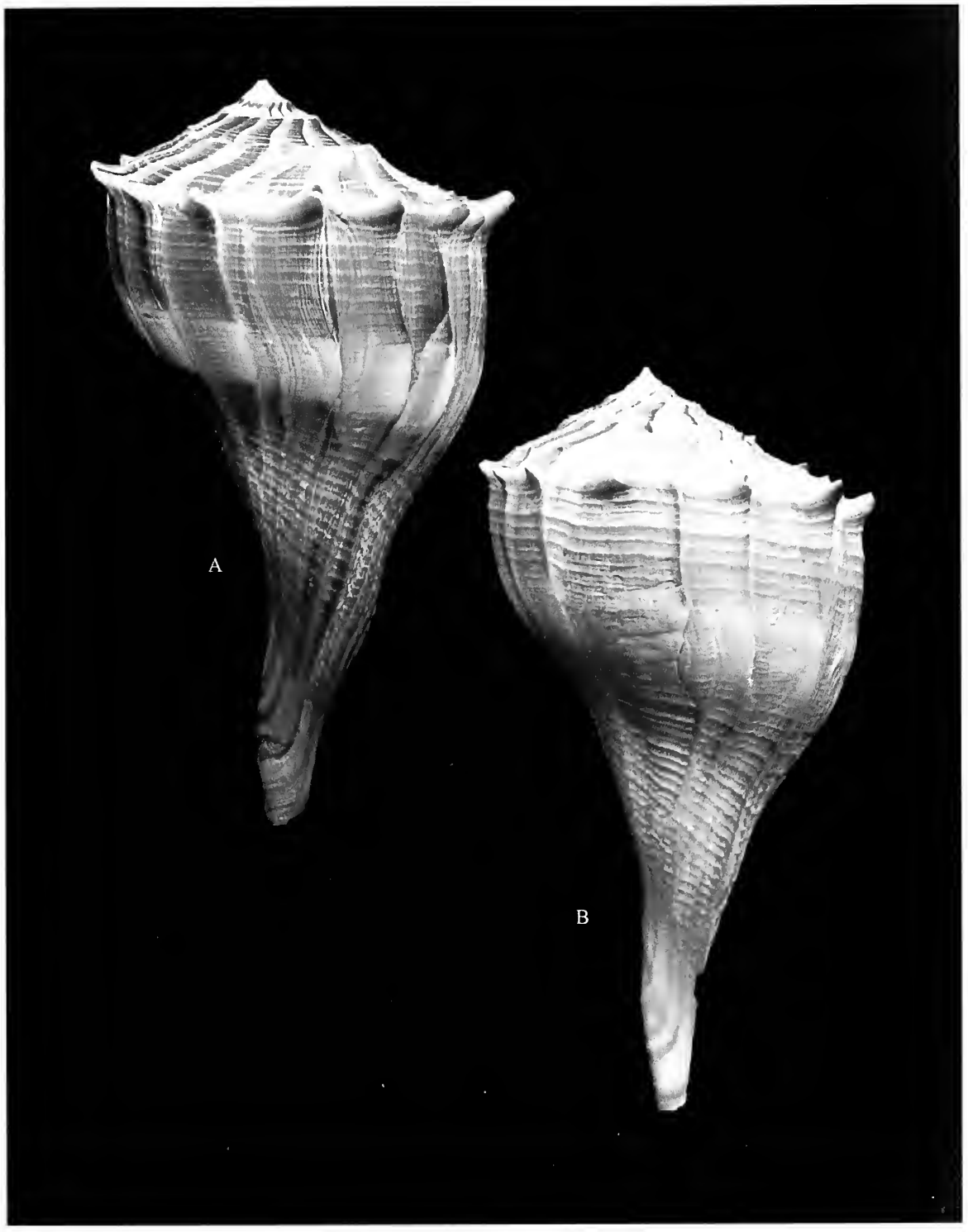


Figure 4.10 *Sinistrofulgur sinistrum* Deep Water Variants.
A= *Sinistrofulgur sinistrum* (Hollister, 1958), length 158 mm, collected in commercial lobster traps placed in 50 m depth, on a pink coralline algal seafloor, north of the Dry Tortugas, Monroe County, Florida. Dark orange and brown color form. Note the heavy shell sculpture composed of numerous strong spiral cords.
B= *Sinistrofulgur sinistrum* (Hollister, 1958), length 156 mm, collected in commercial lobster traps, placed in 50 m depth, on a pink coralline algal seafloor, north of the Dry Tortugas, Monroe County, Florida. Pale orange color form. Note the heavy shell sculpture composed of numerous strong spiral cords. (p. 83)

Figure 4.11 *Sinistrofulgur sinistrum* form *aspinosum*.
A, B= *Sinistrofulgur sinistrum* (Hollister, 1958), form *aspinosum* Hollister, 1958, length 148 mm, found on oyster banks in Pine Island Sound, off Pine Island, Lee County, Florida. This rare variety or form typically has greatly-reduced, or completely absent, shoulder knobs. The smooth-shouldered *aspinosum* form is found primarily in quiet, sheltered lagoons that are subject to fluctuating salinities due to rainfall. (p. 83)

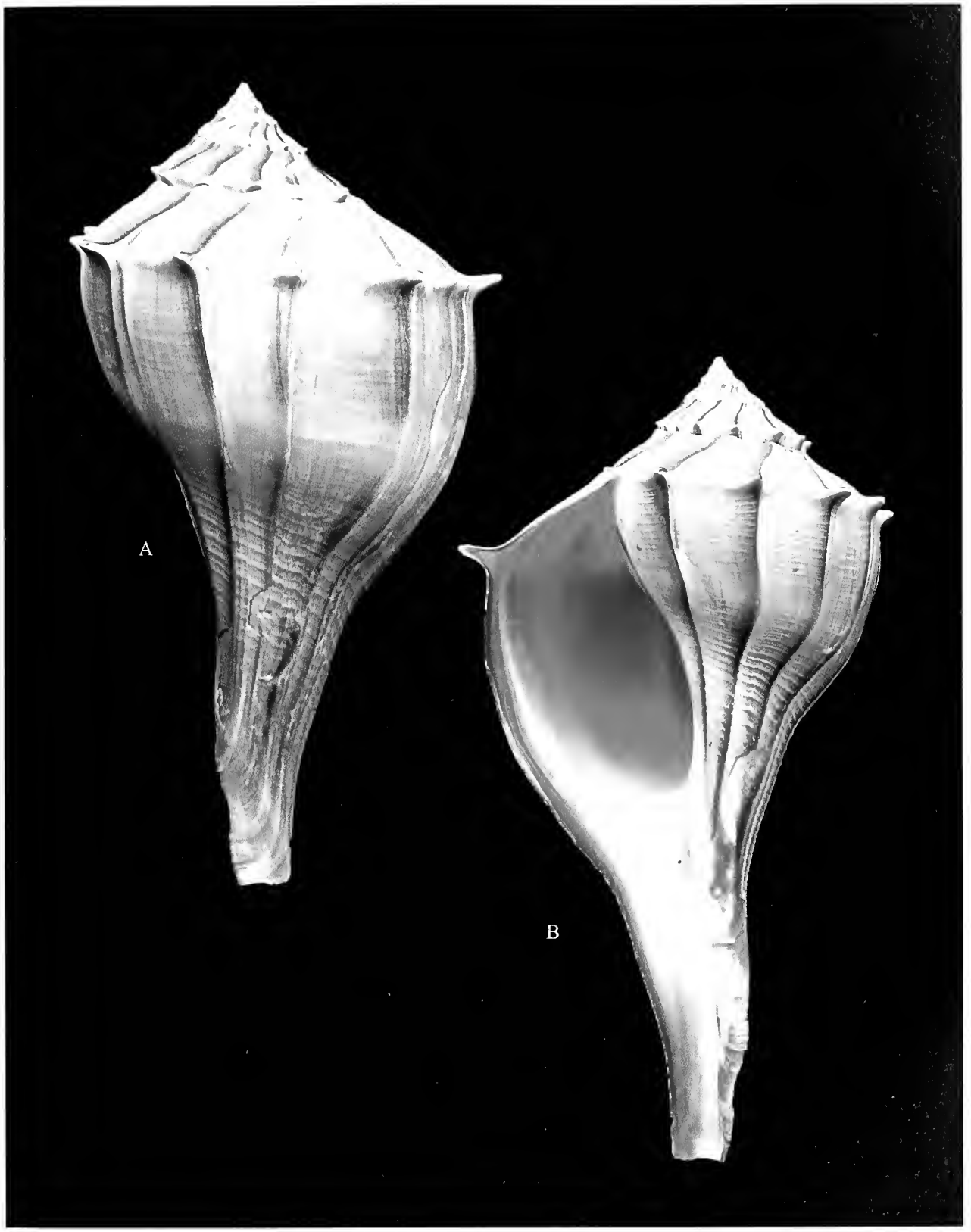


Figure 4.12 *Sinistrofulgur pulleyi*, Typical Specimen.
A, B= *Sinistrofulgur pulleyi* (Hollister, 1958), length 154 mm, found at low tide on a muddy sand flat in West Bay, Galveston Island, Galveston County, Texas. This is the State Shell of Texas. (p. 85)

Figure 4.13 *Sinistrofulgur pulleyi*, Typical Specimens.
A, B= *Sinistrofulgur pulleyi* (Hollister, 1958), length 118 mm, on a sand bar at low tide, Christmas Bay, Brazoria County, Texas.
C, D= *Sinistrofulgur pulleyi* (Hollister, 1958), length 109 mm, on a sand bar at low tide, Christmas Bay, Brazoria County, Texas. (p. 85)

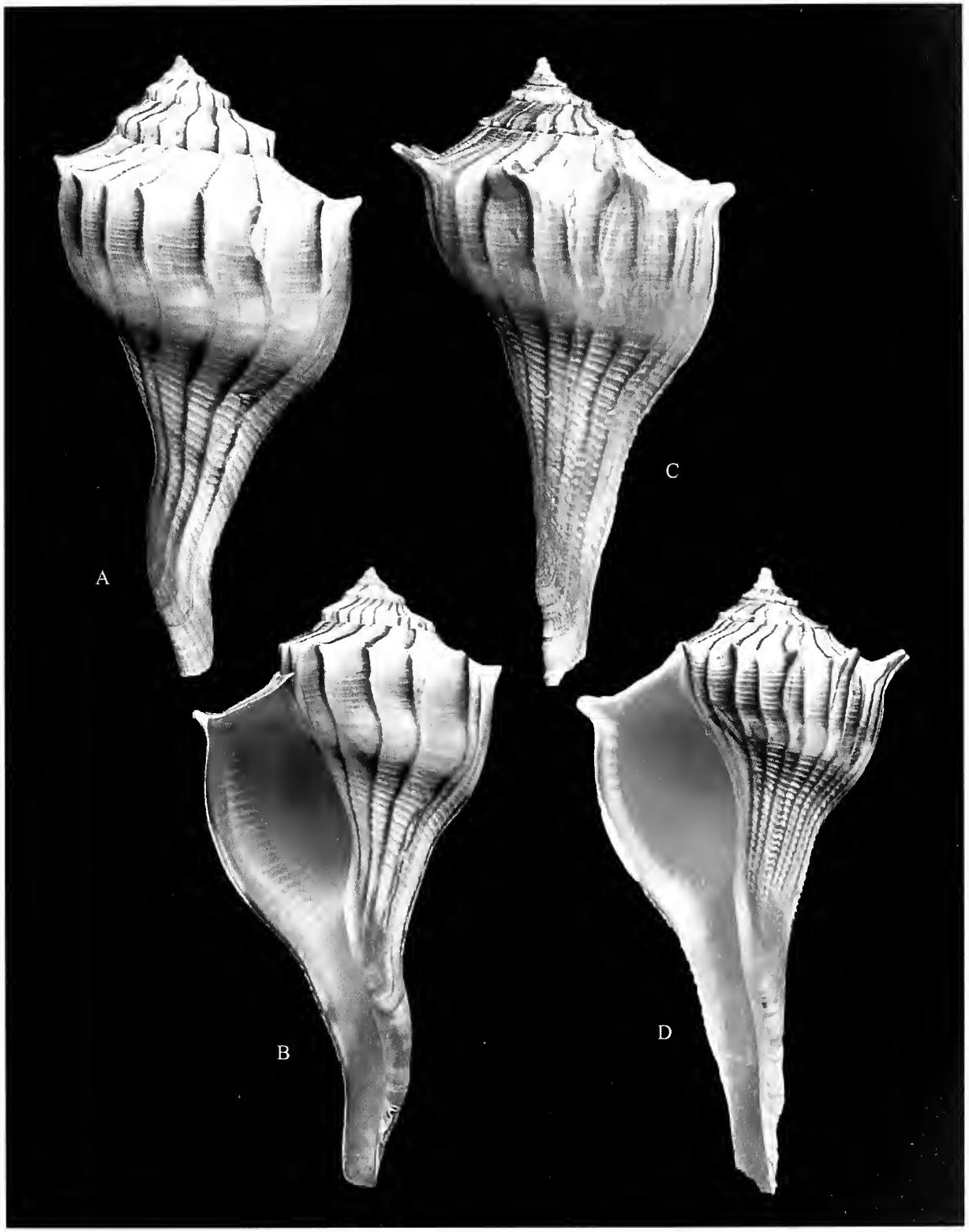


Figure 4.14 *Sinistrofulgur pulleyi* Variants.
A, B= *Sinistrofulgur pulleyi* (Hollister, 1958), length 90 mm, found at low tide along Pass Cavallo, Matagorda Island, Calhoun County, Texas. Variant with a twisted siphonal canal.
C, D= *Sinistrofulgur pulleyi* (Hollister, 1958), length 92 mm, in muddy sand at low tide, Redfish Bay, Port Aransas, Nueces County, Texas. Variant with a low spire and large shoulder spines. (p. 85)

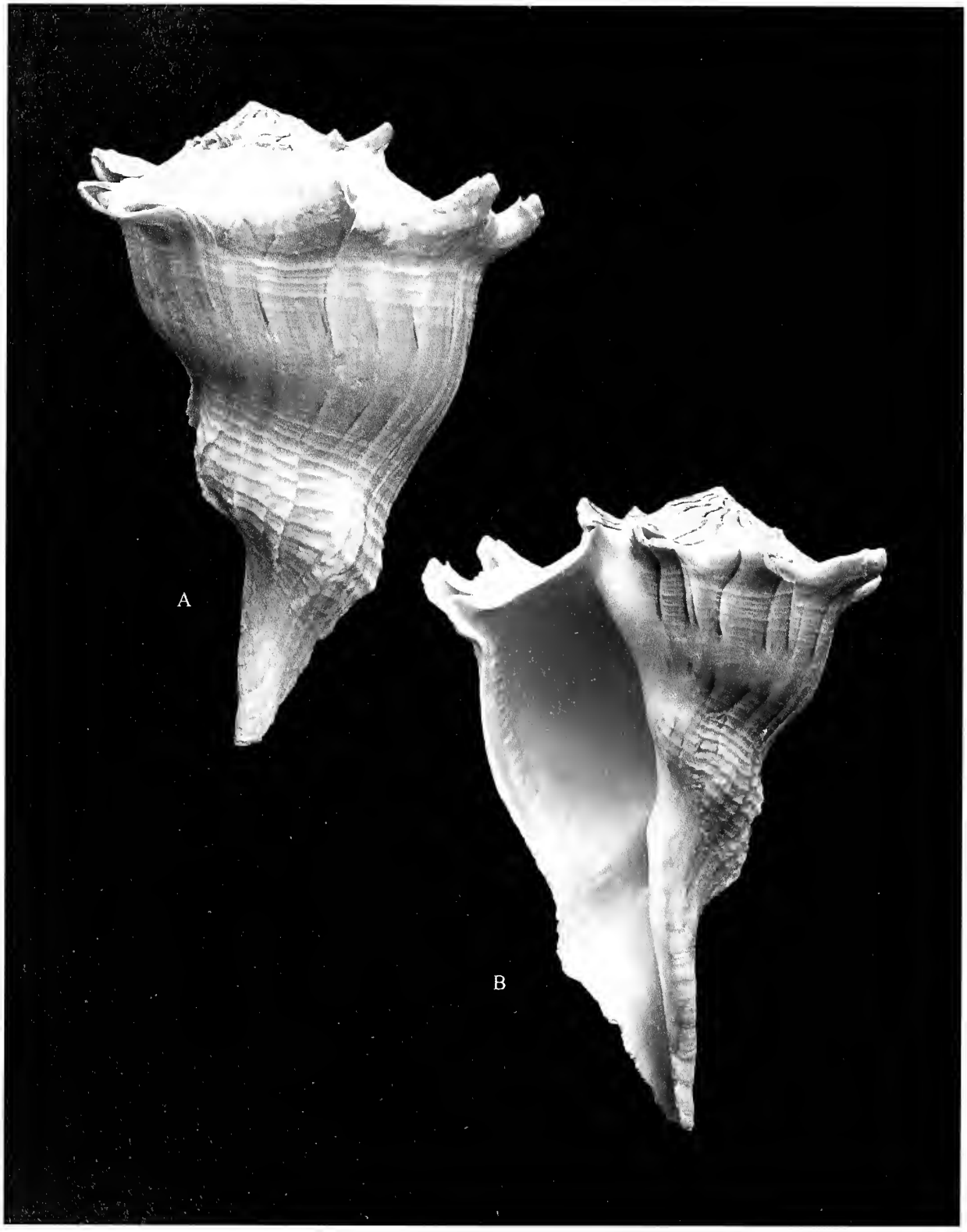


Figure 4.15 *Sinistrofulgur perversum*, Typical Specimen.
A, B= *Sinistrofulgur perversum* (Linnaeus, 1758), length 213 mm, trawled by shrimpers from 25 m depth on the Campeche Bank, off Campeche, Campeche State, Mexico. Note the characteristic wide, fluted, and webbed tumid ridge around the base of the siphonal canal. (p. 87)

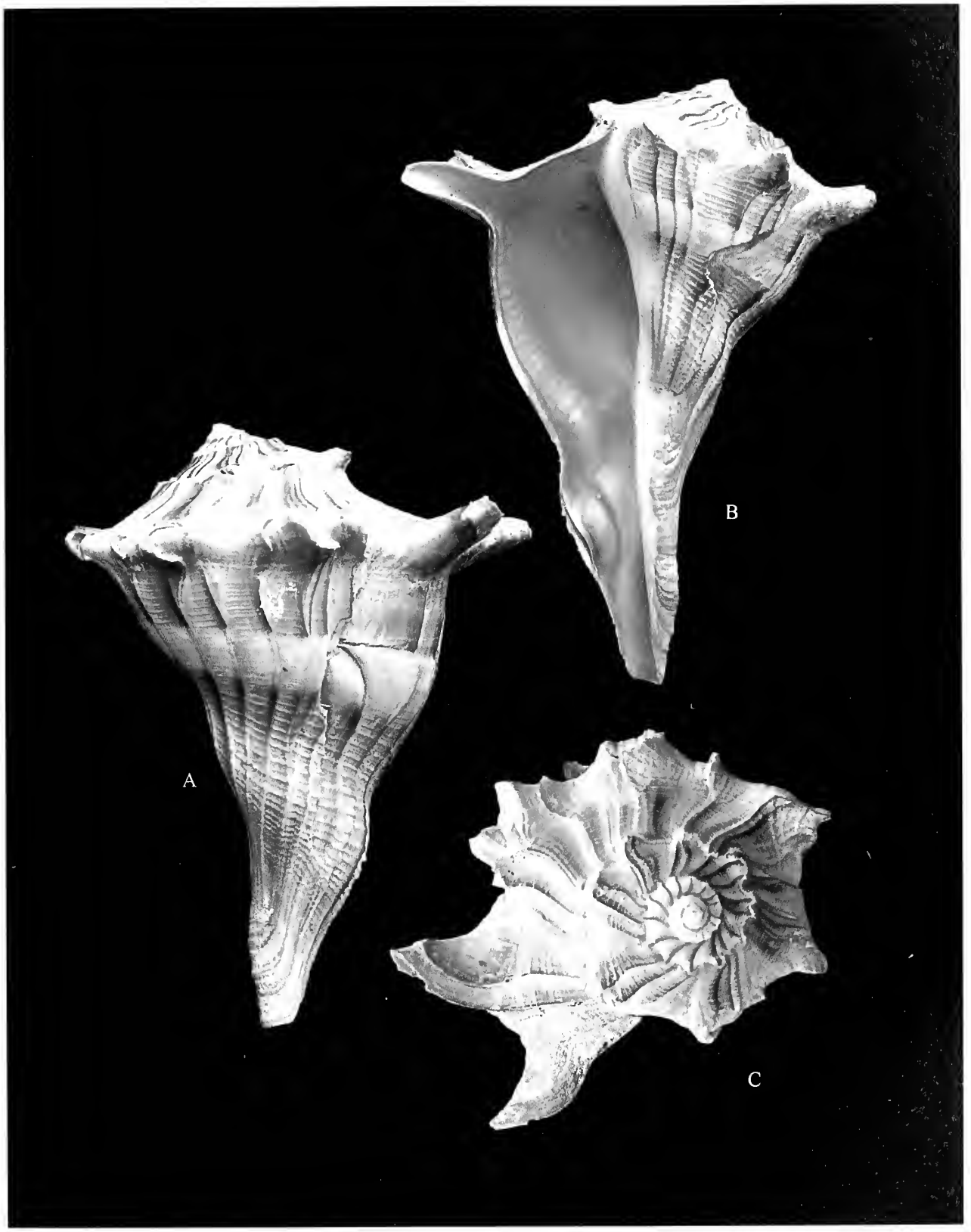


Figure 4.16 *Sinistrofulgur perversum,* Typical Specimen.
A, B, C= *Sinistrofulgur perversum* (Linnaeus, 1758), length 123 mm, 1 m depth on carbonate mud seafloor, Laguna de Terminos, Ciudad del Carmen, Campeche State, Mexico. Small, dark-colored variant. (p. 87)

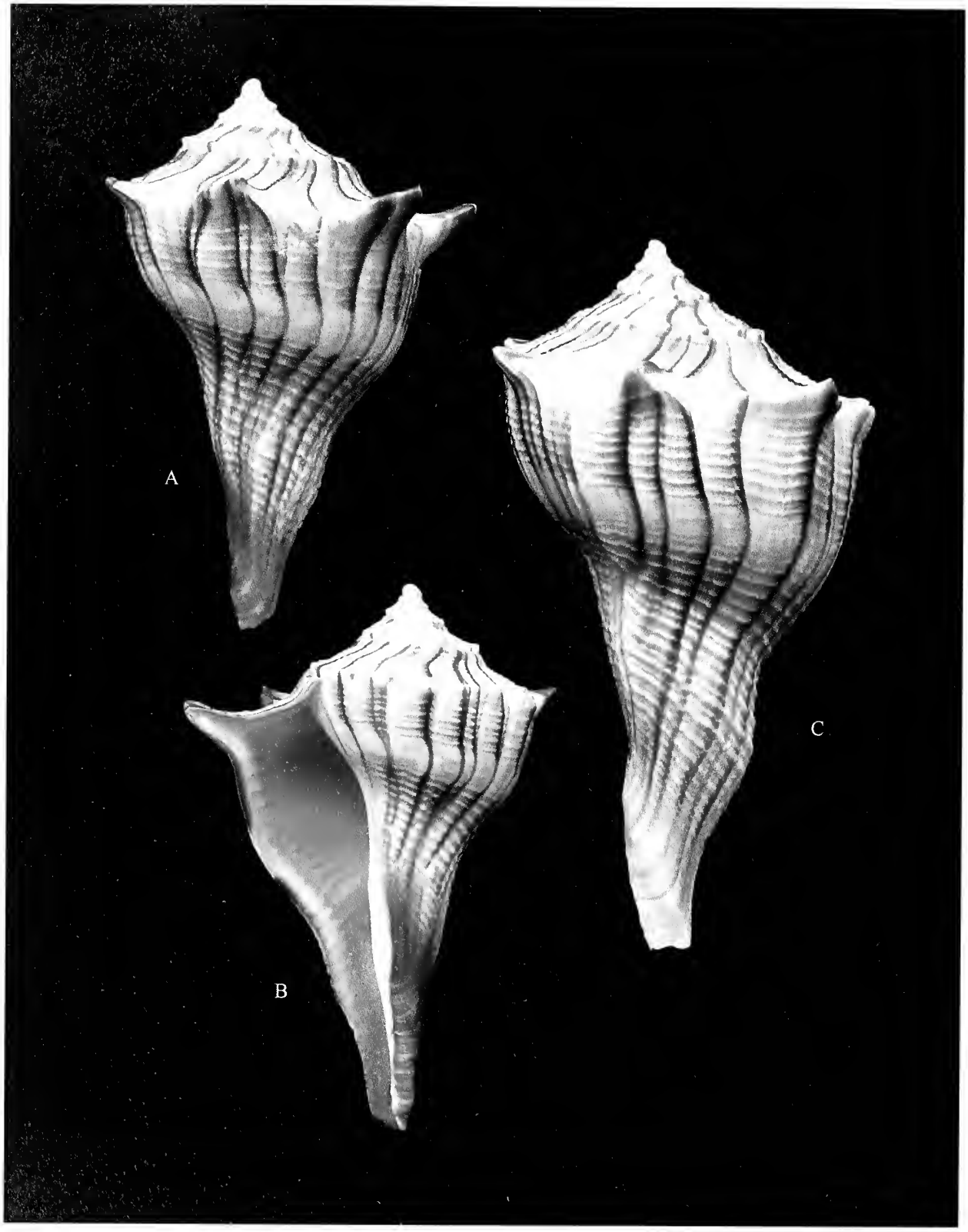


Figure 4.17 *Sinistrofulgur perversum*, Dwarf Variants.
A, B= *Sinistrofulgur perversum* (Linnaeus, 1758), length 53 mm. Dwarf variant with a straight siphonal canal.
C= *Sinistrofulgur perversum* (Linnaeus, 1758), length 68 mm. Dwarf variant.
Both specimens found on carbonate mud and Turtle Grass, off Isla Aguada, Campeche State, Mexico. (p. 87)

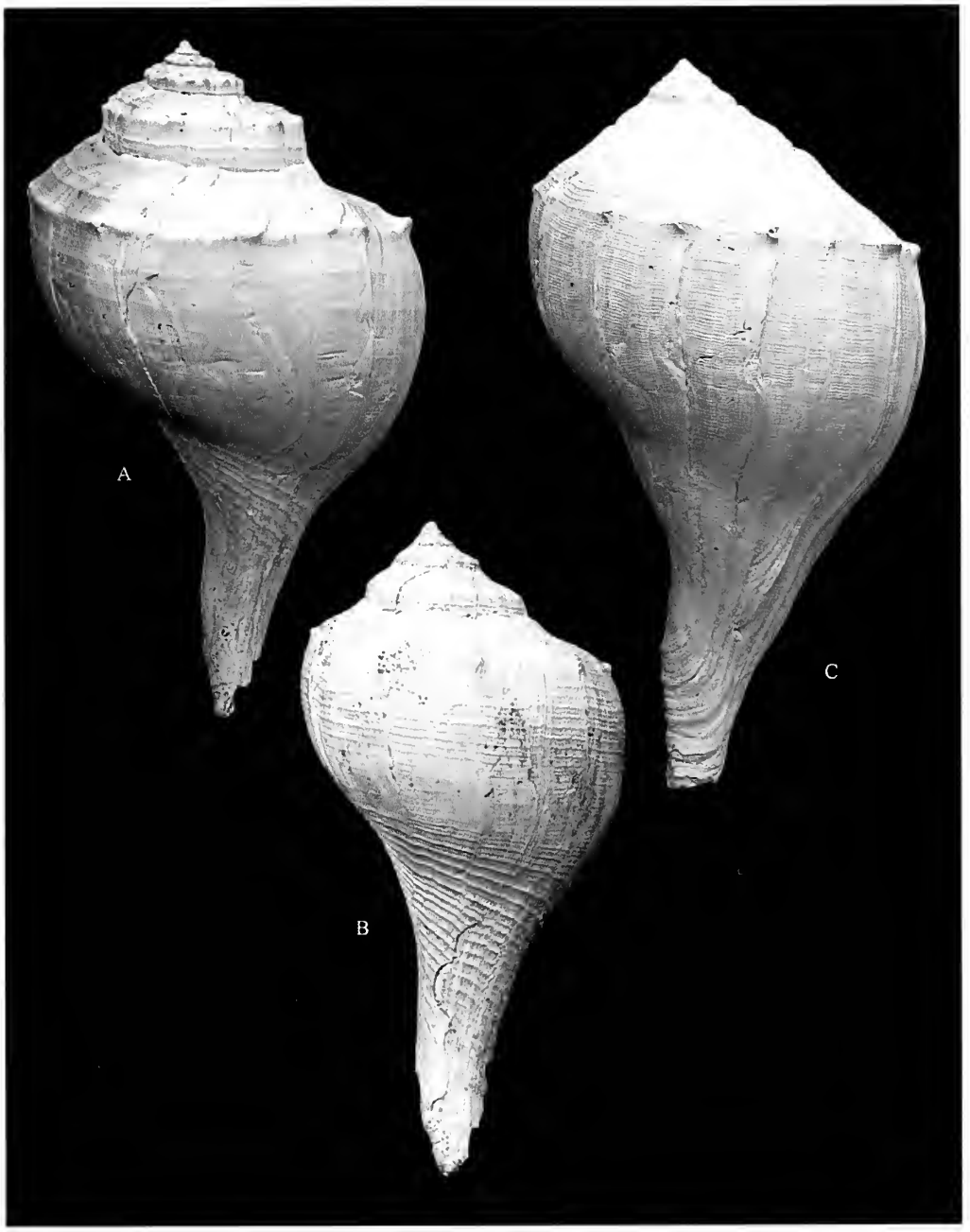


Figure 4.18 Fossil *Sinistrofulgur* Species.
A= *Sinistrofulgur hollisteri* Petuch, 1994, length 141 mm, from Unit 10 in Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida; Buckingham Member of the Tamiami Formation, early Piacenzian (or possibly late Zanclean) Age of the Pliocene. Also found in the lowest beds of the Jackson Bluff Formation, Florida Panhandle. This is the oldest-known *Sinistrofulgur* species. Note the sharply-angled shoulder and high, scalariform spire.
B= *Sinistrofulgur contrarium* (Conrad, 1840), length 72 mm, from Unit 7 in the APAC Pit, Sarasota, Sarasota County, Florida; Pinecrest Member of the Tamiami Formation, Piacenzian Age of the Pliocene. Also found in the contemporaneous Yorktown Formation of Virginia and northern North Carolina and the Duplin Formation of southern North Carolina and northern South Carolina. This specimen closely resembles Conrad's holotype.
C= *Sinistrofulgur adversarium* (Conrad, 1862), length 208 mm, from the middle fossiliferous beds in the Lee Creek Mine, Aurora, Beaufort County, North Carolina; Edenhouse Member of the Chowan River Formation, late Piacenzian Age of the Pliocene. Note the sculpture of fine cords and spiral threads and the characteristic inflated shape. Also found in the upper beds of the Tamiami Formation in southern Florida.

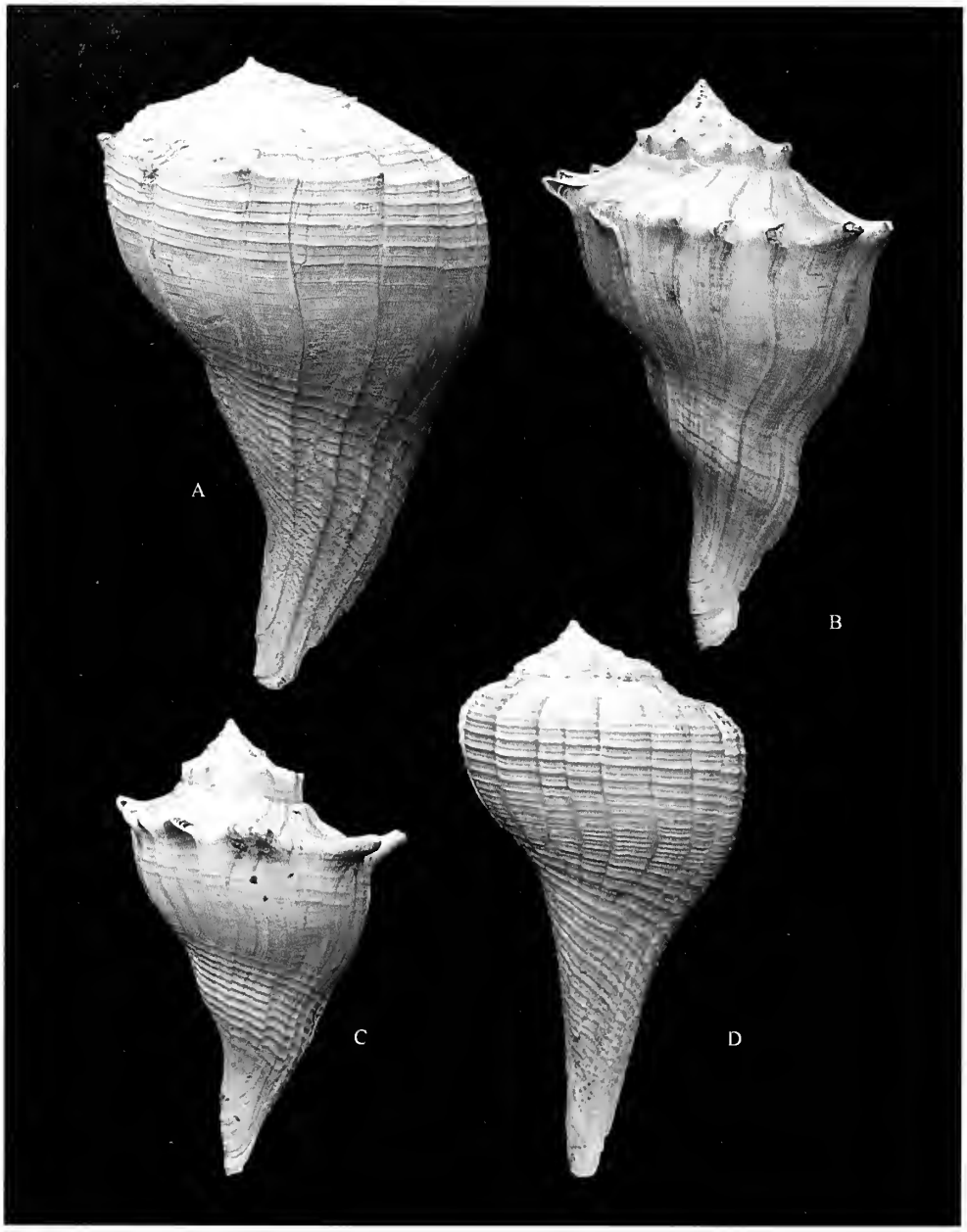


Figure 4.19 Fossil *Sinistrofulgur* Species.
A= *Sinistrofulgur roseae* Petuch, 1991, length 238 mm, North New River Canal excavation south of South Bay, Palm Beach County, Florida; Belle Glade Member of the Bermont Formation, Ionian Age of the Pleistocene. Note the extremely heavy corded sculpture on the body whorl and spire that is so characteristic of this species.
B= *Sinistrofulgur perversum okeechobeensis* Petuch, 1994, length 114 mm, Macasphalt Okeechobee Pit, near Lakeport, Glades County, Florida; Okaloacoochee Member of the Fort Thompson Formation, Tarantian Age of the late Pleistocene. Note the tumid ridge on the siphonal canal that closely resembles that seen on the living *S. perversum*.
C= *Sinistrofulgur perversum okeechobeensis* Petuch, 1994, dwarf form, length 76 mm, from the Ridgdill Pit, west of Moore Haven, Glades County, Florida; Okaloacoochee Member of the Fort Thompson Formation, Tarantian Age of the late Pleistocene.
D= *Sinistrofulgur roseae* Petuch, 1991, young specimen, length 98 mm, from the North New River Canal excavation, south of South Bay, Palm Beach County, Florida; Belle Glade Member of the Bermont Formation, Ionian Age of the Pleistocene. Note the strong corded sculpture.

Figure 4.20 Fossil *Sinistrofulgur* Species.
A= *Sinistrofulgur grabaui* Petuch, 1994, length 205 mm, from Unit 10 in the Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Buckingham Member of the Tamiami Formation, early Piacenzian Age, Pliocene. Note the large weblike flutings on the siphonal canal.
B= *Sinistrofulgur robesonense* (Gardner, 1948), length 225 mm, from the Kissimmee River excavation south of Fort Basinger, Highlands County, Florida. Fruitville Member (Kissimmee facies) of the Tamiami Formation, late Piacenzian Age, Pliocene. Also found in the contemporaneous Duplin and Bear Bluff Formations of the Carolinas. The individual shown here is a full grown adult specimen, which has the same strong spiral cord sculpture that is seen on Gardner's juvenile holotype.
C= *Sinistrofulgur labelleensis* Petuch, 1994, length 243 mm, collected in the Brantley Pit, Arcadia, DeSoto County, Florida. Bee Branch Member of the Caloosahatchee Formation, late Gelasian Age, early Pleistocene. Note the elongated shell shape and high spire.

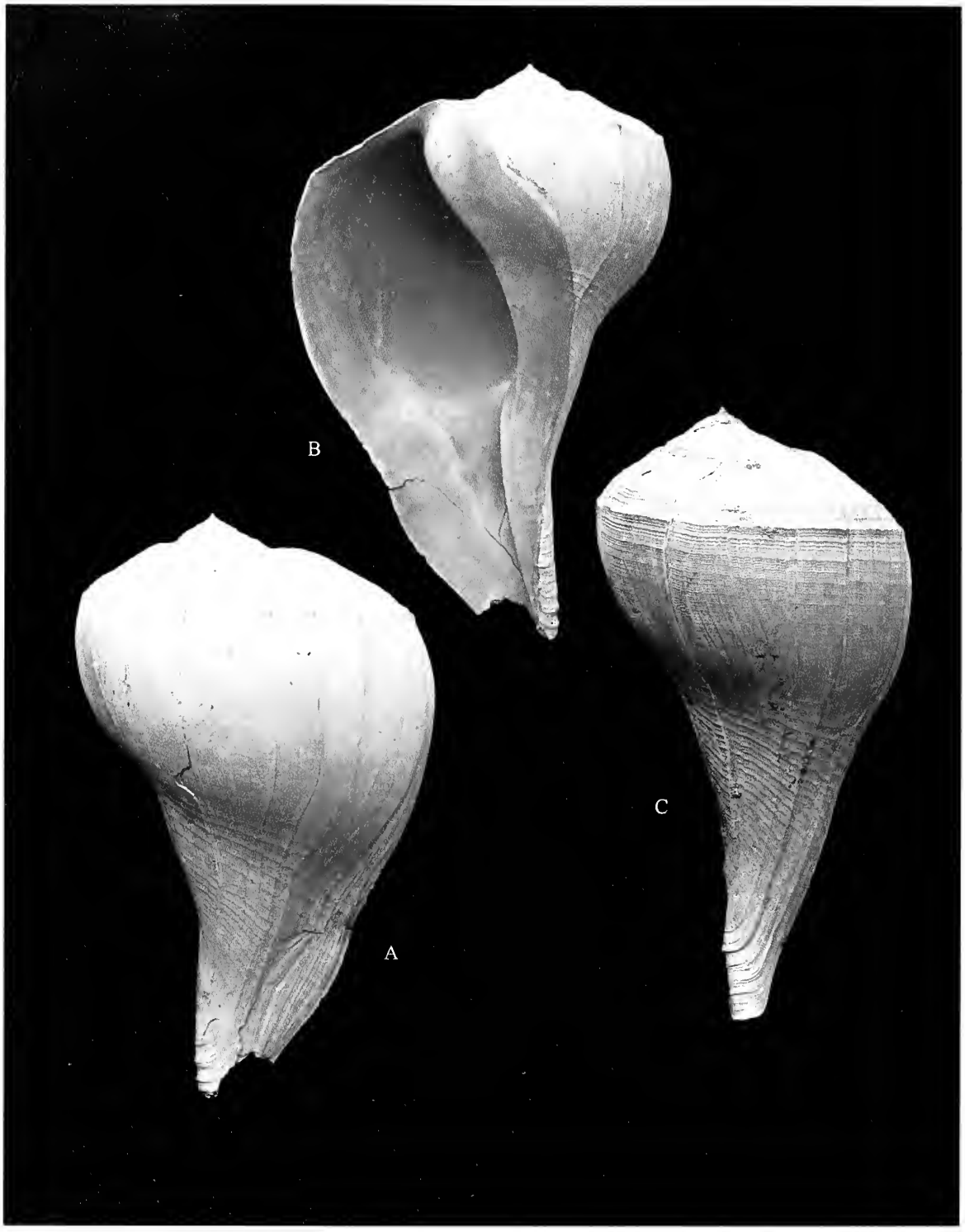


Figure 4.21 Fossil *Sinistrofulgur* Species.
A, B= *Sinistrofulgur palmbeachensis* Petuch, 1994, length 282 mm, from the Miami Canal excavation south of Lake Harbor, Palm Beach County, Florida. Fort Denaud Member of the Caloosahatchee Formation, Gelasian Age of the early Pleistocene. The interior of this species is always a deep red-brown color.
C= *Sinistrofulgur holeylandicum* Petuch, 1994, length 248 mm, from Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida. Holey Land Member of the Bermont Formation, Calabrian Age of the early Pleistocene. Note the fine spiral cords and threads covering the entire shell.

Figure 4.22 Fossil *Sinistrofulgur* Species.
A= *Sinistrofulgur pamlico* Petuch, 1994, length 96 mm, found at the Calabash excavation, Shallotte, Brunswick County, North Carolina. Waccamaw Formation, Gelasian Age of the early Pleistocene. Note the distinctive concave spire whorls, which form a broad, indented channel.
B= *Sinistrofulgur yeehaw* Petuch, 1994, length 152 mm, found in the middle shell beds of the Rucks Pit, Fort Drum, Okeechobee County, Florida. Rucks Pit Member of the Nashua Formation, Gelasian Age of the early Pleistocene.
C= *Sinistrofulgur caloosahatcheensis* Petuch, 1994, length 92 mm, Miami Canal excavation, south of Lake Harbor, Palm Beach County, Florida; Fort Denaud Member of the Caloosahatchee Formation, Gelasian Age of the early Pleistocene.

View of cleaned and stored lobster traps on Conch Key, Florida Keys. Commercial lobster fishermen bait these traps and then drop them in deep water, often in over 100 m depths, where they are left for several months. These are later retrieved and the lobsters that have taken up residence are collected for sale. Hermit crabs, often bearing rare deep water shells, frequently enter these traps and are captured along with the lobsters. Traps dropped into deep water off the Dry Tortugas occasionally capture hermit crab-occupied specimens of the rare busyconid *Lindafulgur lyonsi* (Petuch, 1987). (Photograph by Eddie Matchett)

CHAPTER FIVE

Deep Water Lightning Whelks: Genera *Lindafulgur* and *Busycoarctum*

The genera *Lindafulgur* and *Busycoarctum* are essentially "living fossils", being left-overs of once-thriving groups that were major components of prehistoric marine ecosystems. Both genera were prominent predatory organisms within the shallow water communities that flourished in the Okeechobean Sea during the Pliocene. The fossil record of Florida and eastern Mexico demonstrates that, unlike *Sinistrofulgur*, the relictual genera *Lindafulgur* and *Busycoarctum* have always been confined to the Gulf of Mexico and never ranged into the Atlantic Ocean. This biogeographic pattern is still apparent today, with a single species, each, of *Lindafulgur* and *Busycoarctum* being found along the Yucatan Peninsula of Mexico and a single species of *Lindafulgur* being found only along western Florida. Although they were not very species-rich groups during the Pliocene, both genera were abundant in the fossil beds of Florida, demonstrating that they were successful and important predators at that time. Today, both genera are confined to deeper offshore waters, often in depths of 100-200 m.

The genus *Lindafulgur* is the older of the two groups, having first appeared along the eastern coast of Mexico during the Messinian Miocene (as *L. alancasterae* Perrilliat, 1963). From there, it moved into southern Florida in the early and middle Pliocene, but disappeared from the fossil record by the late Pliocene. It is assumed that the genus found a refugium in the deeper and more climatically-stable waters of the Gulf of Mexico and was extirpated from the shallow water communities during the late Pliocene climatic degenerations. The genus *Busycoarctum* appears later in the fossil record of Florida, during the early Pliocene, and is represented by a still-unnamed species from the basal beds of the Tamiami Formation. These "Turnip Whelks" (named for their distinctive shape) flourished in the Okeechobean Sea and survived well into the Gelasian Age of the early Pleistocene. Although several *Busycoarctum* species, such as *B. tropicalis*, *B. tudiculatum*, and *B. rapum*, are often abundant in Florida fossil beds, the genus as a whole never ranged any farther north than the Florida Peninsula and is completely absent from the rich Plio-Pleistocene fossil beds of the coastal Eastern United States. Like *Lindafulgur*, the genus *Busycoarctum* apparently found a refugium in deeper neritic environments and survived the severe middle and late Pleistocene extinction events.

Although superficially similar to members of the genus *Busycon*, species in the genus *Lindafulgur* differ in being much more elongated and vase-shaped shells, with their siphonal canals grading directly into the body whorl. These deep water whelks also have distinctly flattened spires that often have sharply turreted and stepped whorls, producing an almost pagoda-like appearance. *Lindafulgur* species characteriatically have extremely sharp and angled shoulders, ornamented with very large, flattened, open, paddle-like spines which are often recurved toward the direction of the aperture. These large, flat, recurved spines are very similar to those seen on some *Sinistrofulgur* species, especially *S. perversum* and, overall, *Lindafulgur* species resemble dextral versions of some of the Left-Handed Whelks. The two genera can also be separated by the lengths of their siphonal canals; in *Lindafulgur* species, the siphonal canal is two-thirds to three-quarters the length of the body whorl, while in *Busycon* species, the siphonal canal is only one-half or less the length of the body whorl.

The other deep water genus, *Busycoarctum*, the Turnip Whelks, somewhat resembles *Lindafulgur* but differs in having short, rounded, and inflated body whorls and long, extremely narrow, and straight siphonal canals. The body whorl-siphonal canal juncture is highly constricted and pinched, creating the distinctive "turnip shape" that characterizes this genus. Although the shoulder is somewhat angled, it is much more rounded than the shoulders of the other busyconine genera, both fossil and living. Some of the Pliocene species, such as *Busycoarctum tudiculatum* (Dall, 1890) (Figure 5.7), have smooth and broadly rounded shoulders, while other species, such as the living *B. coarctatum* (Sowerby I, 1825) and the Pliocene *B. superbus* (Petuch, 1994) (Figure 5.7), have shoulders that are ornamented with small spines and knobs. In the Recent, *Busycoarctum* is the most geographically-restricted genus, being found only in the Yucatanean Subprovince of the Carolinian Province, in an area extending from near Veracruz, Mexico, across the Campeche Banks, and to Isla Contoy, Quintana Roo State, Mexico. In the Recent, the single living Turnip Whelk lives far offshore, in relatively deep water, and is only collected by commercial shrimpers and fishermen plying the edge of the continental shelf and deep neritic banks.

The named fossil species of both *Lindafulgur* and *Busycoarctum* are listed on Appendix 1 at the end of this book. The living species, and most of the fossil species, are illustrated in the iconography at the end of this chapter.

Family Busyconidae
Subfamily Busyconinae
Genus *Lindafulgur* Petuch, 2004

Diagnosis (reprinted here from the original; Petuch, 2004: 286): Busyconines of average size for subfamily; with proportionally short, vase-shaped body whorls and extremely long and well-developed siphonal canals; siphonal canals generally 1.5 to 2 times length of body whorl; juncture of siphoanl canal and body whorl gradational; without distinct indentation; spires generally flattened, but with some species having elevated, scalariform spires; shoulders sharply-angled, carinated, ornamented with numerous open, pointed spine-like knobs; body whorls and spire whorls characteristically heavily sculptured with numerous strong, prominent spiral cords, giving shell rough texture; apertures proportionally small, oval, with interiors heavily sculptured with strong cords; protoconchs large, rounded, domelike, composed of 2 whorls.

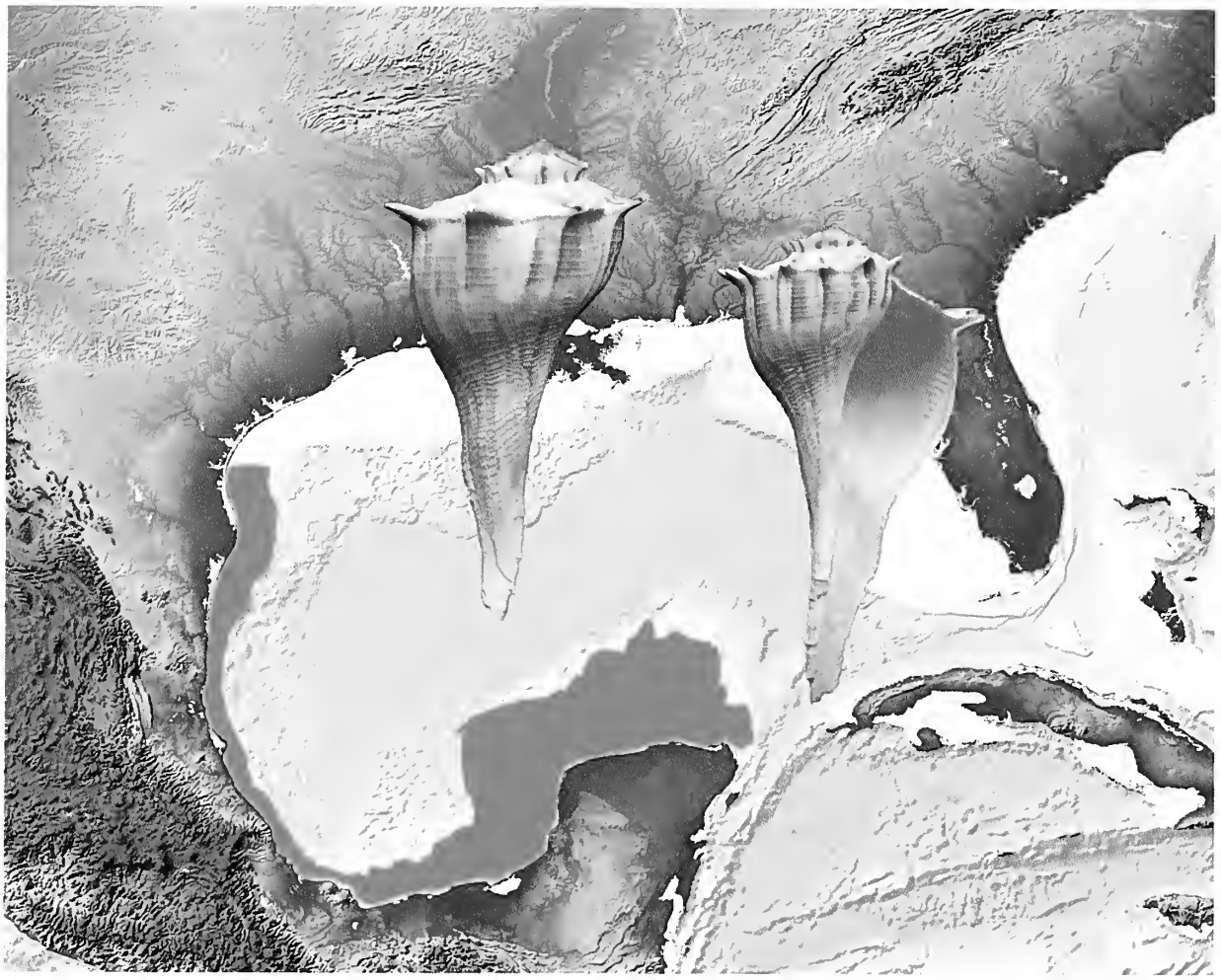
***Lindafulgur candelabrum* (Lamarck, 1816)**
(Figures 5.1)

Synonymy:
Pyrula candelabrum Lamarck, 1816
Fulgur candelabrum (Lamarck) Conrad, 1853
Busycon candelabrum (Lamarck) Abbott, 1974
Lindafulgur candelabrum (Lamarck) Petuch, 2004
Lindafulgur candelabrum (Lamarck) Petuch, 2013

Description: Shell of average size for subfamily, very elongated and protracted, laterally compressed; body whorl vase-shaped, slightly inflated; spire flattened, with distinctly turreted, stepped, and scalariform whorls; shoulder very sharply-angled, carinated, ornamented with 7-12 proportionally very large, paddle-shaped, flattened, open spines; shoulder spines, particularly those that are enlarged and triangular-shaped, are often strongly recurved in the direction of the aperture; body whorl, siphonal canal, and spire whorls heavily ornamented with numerous strong spiral cords, with the cords on the siphonal canal being stronger, better-developed, and more closely-packed; wide smooth band present around the mid-section of the body whorl, corresponding to a blade-like extension on the outer edge of the lip; siphonal canal proportionally very long, often 1.5 to 2 times the length of the body whorl, straight, grading directly into the body whorl with only a faint constriction at the siphonal canal-body whorl juncture; shell colored white, pale cream-yellow, or pale yellow-tan, overlaid with evenly-spaced thin orange-tan longitudinal stripes and flammules; aperture proportionally wide and open, with numerous large and prominent cords on the inside of the lip, pale yellow-cream or cream-white on the interior; periostracum dark brown, thin, and tightly adherent.

Discussion: With its graceful, elongated shape and large, flattened shoulder spines, this uncommon and distinctive shell is one of the most beautiful and desirable species in the family Busyconidae. In overall shell shape and form, *Lindafulgur candelabrum* could only be confused with the close-related *L. lyonsi* (Petuch, 1987) from deep water off western Florida (Figures 5.2 and 5.3), which differs, however, in being a smaller, much thinner and more fragile shell, in having much smaller and more numerous shoulder spines, and a bright orange or salmon-orange shell color instead of cream-white or pale yellow.

Biogeographical Range: This distinctive dextral busyconid is essentially restricted to the Yucatanean Subprovince of the Carolinian Province, but does range northward into the Texan Subprovince as far as Corpus Christi, Texas (Map 7). From Veracruz, Mexico, northward to southern Texas, *Lindafulgur candelabrum* lives in deeper water offshore areas. Very large specimens are commonly collected off Cabo Catoche, Quintana Roo State, Mexico.



Map 7. The biogeographical range of *Lindafulgur candelabrum* extends from near Freeport, Brazoria County, Texas, southward across the Yucatan Peninsula and Campeche Bank, to Isla Contoy, Quintana Roo, Mexico. *Lindafulgur candelabrum* is generally a deeper water, offshore species, preferring depths of 10 to 100 m.

Lindafulgur lyonsi (Petuch, 1987)
(Figures 5.2 and 5.3)

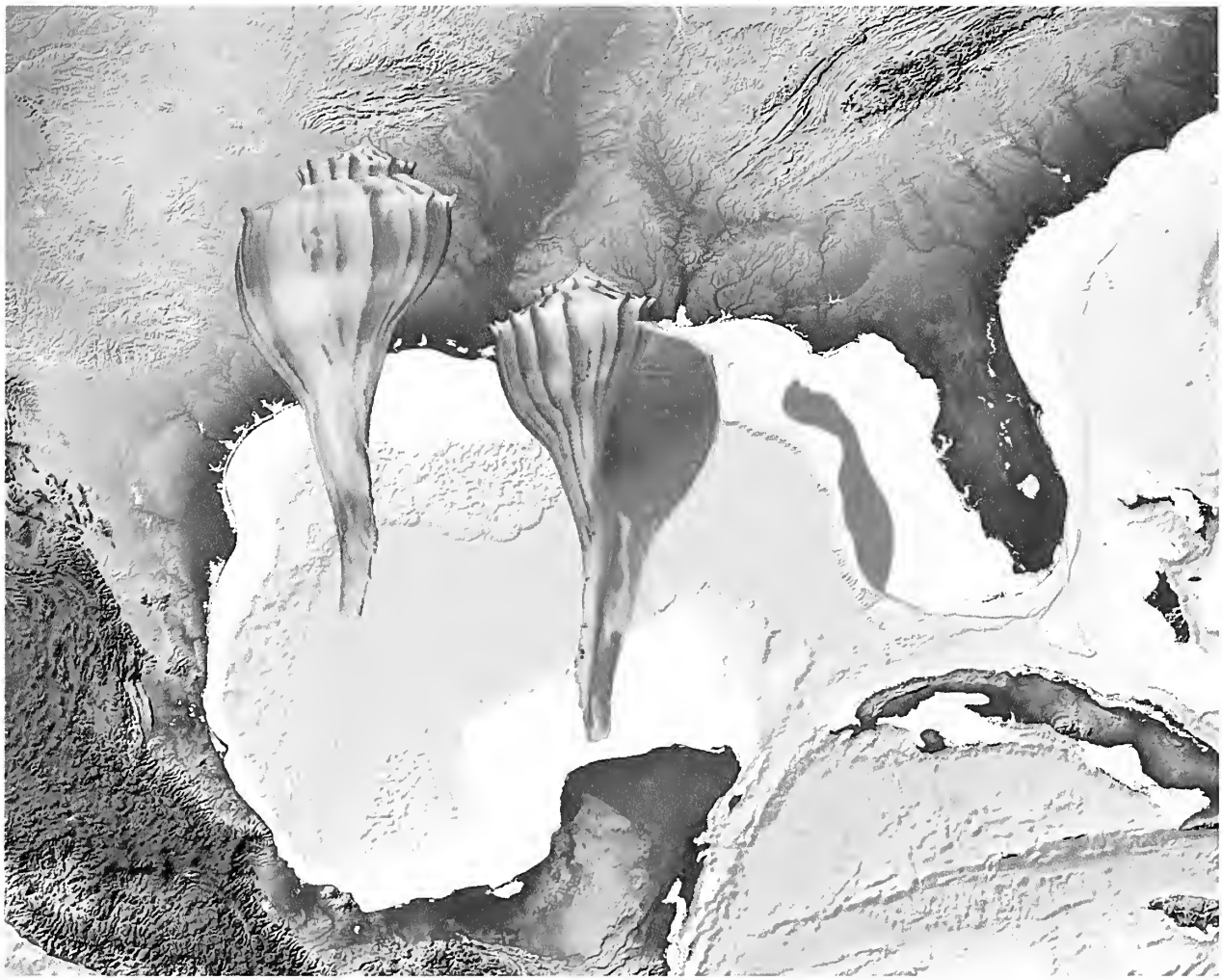
Synonymy:
Busycon (Busycoarctum) lyonsi Petuch, 1987
Lindafulgur lyonsi (Petuch) Petuch, 2004
Lindafulgur lyonsi (Petuch) Petuch, 2013

Description (reprinted here from the original; Petuch, 1987: 15-16): Shell small for genus, thin and fragile, with body whorl inflated; siphonal canal long, very narrow in proportion to body whorl; shoulder carinated, with 15-18 sharp, spikelike knobs on last whorl; aperture wide, flaring; columella with one large, slanting fold; interior of lip with numerous ribs that extend back into interior of aperture; protoconch very large in proportion to shell size, composed of 2 whorls, orange in color; shell color bright pinkish-orange overlaid with 3 wide bands of darker orange, one below shoulder, one below mid-body, and one around anterior end of siphonal canal; shell

marked with numerous prominent dark orange-brown, thin, longitudinal flammules running entire length of shell; spire whorls with regularly-spaced dark orange-brown radiating flammules; interior of aperture bright orange; periostracum thin, adherent.

Discussion: The western Floridian *Lindafulgur lyonsi* is similar in appearance to the Texas and Yucatan *L. candelabrum*, but differs in being a smaller, much more fragile shell, in having a proportionally lower spire, a narrower and longer siphonal canal, and a bright pinkish-orange shell color with a bright orange aperture. *Lindafulgur lyonsi* also has more numerous, smaller, and more sharply-pointed shoulder spines than does *L. candelabrum*. The shoulder spines of the western Florida shell never develop into the wide, flat paddle-like knobs that are frequently seen on the Yucatan species. The western Floridian *Lindafulgur* also occurs in deeper water than does its Yucatan and southern Texas congener, often being dredged from depths of around 200 m (Petuch, 1987; 2013). Here, it is a major predatory component of the coralline algal rubble sea floor ecosystems off the Dry Tortugas and Tampa, and occurs together with a rich endemic molluscan assemblage that contains such rare and seldom-seen gastropods as the ovulids *Cyphoma lindae* Petuch, 1987, muricids *Chicoreus rachelcarsonae* Petuch, 1987, *Vokesimurex lindajoyceae* (Petuch, 1987), and *Favartia lindae* Petuch, 1987, the terebrid *Myurellina lindae* Petuch, 1987, the volutid *Scaphella (Caricellopsis) matchetti* Petuch and Sargent, 2011, the cancellariid *Cancellaria richardpetiti* Petuch, 1987, and the conid *Dauciconus aureonimbosus* (Petuch, 1987), and the pectinid bivalve *Lindapecten lindae* Petuch, 1995.

Biogeographical Range: As shown on Map 8, *Lindafulgur lyonsi* is restricted to deep water areas of the Suwannean Subprovince of the Carolinian Province, being found in 100 to 200 m depths along the outer edge of the western Florida continental shelf, from north of the Dry Tortugas northward to south of Apalachicola. Here, it occurs on a sea floor made up of dense accumulations of coralline algal rhodoliths and is one of the major predators on thin-shelled deep water bivalves such as the arcid *Anadara baughmani* (Hertlein, 1951), the glycymerid *Tucetona subtilis* Nicol, 1956, the lucinids *Cavilinga blanda* (Dall, 1901) and *Myrtea sagrinata* (Dall, 1886), and the cardiid *Americardia lightbourni* Lee and Huber, 2012.



Map 8. The biogeographical range of *Lindafulgur lyonsi* extends all along the western continental shelf of Florida (Florida Platform), from south of Apalachicola southward to the Dry Tortugas. *Lindafulgur lyonsi* is a deep water species, preferring depths of 100 to 200 m.

Family Busyconidae
Subfamily Busyconinae
Genus *Busycoarctum* Hollister, 1958

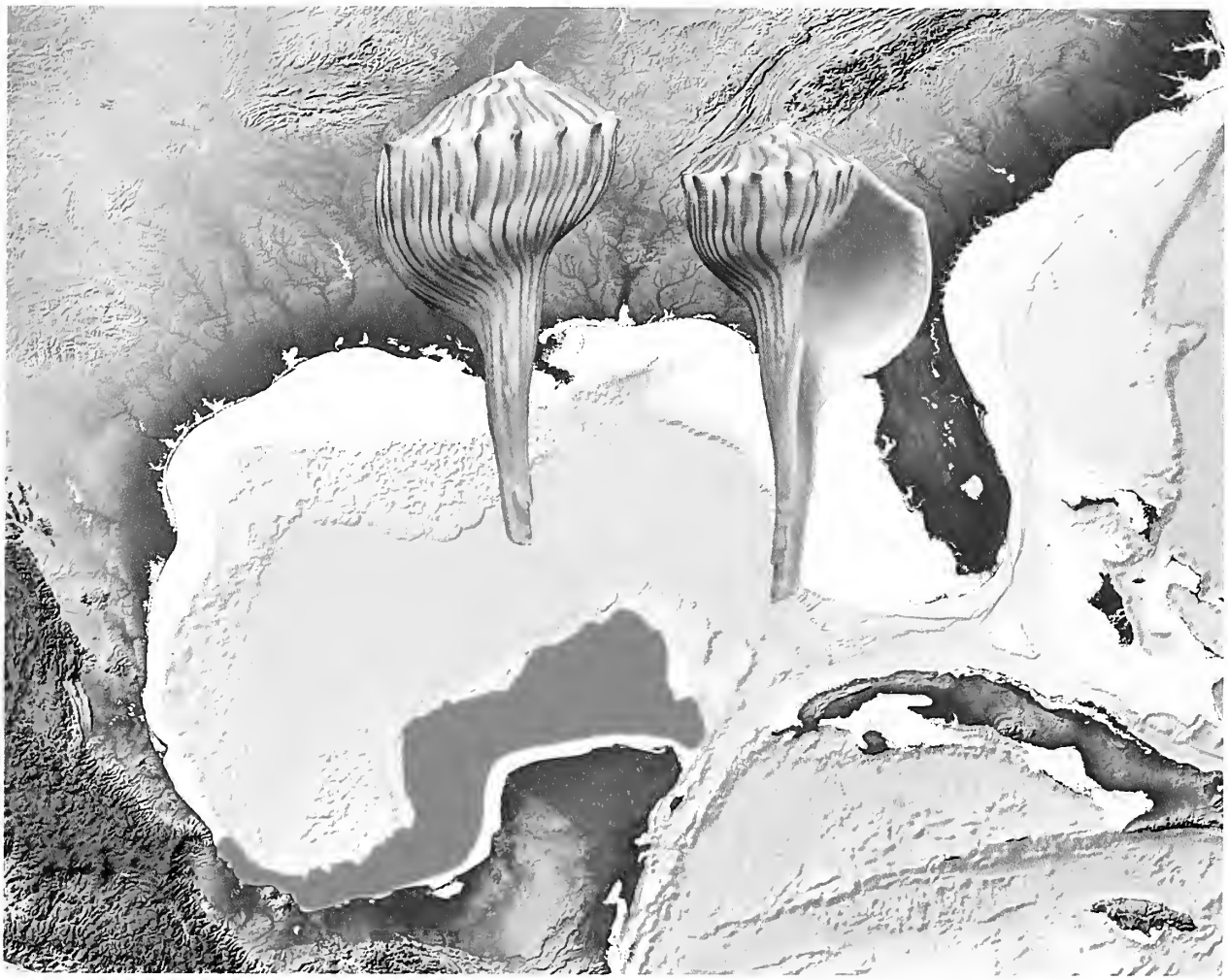
***Busycoarctum coarctatum* (Sowerby I, 1825)**
(Figures 5.5 and 5.6)

Description: Shell small for subfamily, extremely turnip-shaped, with a rounded, globose body whorl and low, flattened spire; shoulder angled but broadly rounded, ornamented with 15-18 small, low, evenly-spaced spike-like knobs; body whorl, spire whorls, and siphonal canal covered with fine spiral cords and threads, with the cords becoming stronger and more prominent on the siphonal canal; globose body whorl separated from the extremely long, straight, and

narrow siphonal canal by an abrupt constriction at the body whorl-siphonal canal juncture, producing the characteristic turnip shape; siphonal canal 1.5 to 2 times the length of the body whorl; base shell color pale pinkish-orange or yellow-orange overlaid with 3 wide bands of a darker orange color, one around the shoulder area, one around the base of the body whorl, and one around the siphonal canal; entire shell covered with numerous, closely-packed dark orange-tan or light brown thin longitudinal lines and flammules; shoulder spines darker brown in color; spire whorls covered with numerous, closely-packed, thin reddish-brown radiating lines and flammules; aperture wide and rounded, with numerous large and well-developed cords on the interior of the lip; interior of aperture a dark yellow or yellow-orange color; protoconch large, rounded, domelike, composed of 2 whorls, pale yellow-orange in color; periostracum thin, dark brown, lightly adherent.

Discussion: With its bright orange shell color and odd shell shape, the Turnip Whelk, *Busycoarctum coarctatum*, is one of the most iconic of the Yucatan Peninsula gastropods. Although seldom seen in shell collections and considered to be a rare species (Abbott, 1974: 222), the Turnip Whelk is actually relatively common in deep water communities along the edge of the Campeche Banks. Living in depths of 50-200 m, *Busycoarctum coarctatum* is rarely seen washed up on beaches and is only collected by deep water shrimpers ("Royal Red Shrimp") and offshore fishing boats.

Biogeographical Range: As shown on Map 9, *Busycoarctum coarctatum* is restricted to the Yucatanean Subprovince of the Carolinian Province, where it ranges from near Veracruz, Veracruz State, Mexico eastward to the Campeche Banks and offshore cays, and along the coast of the Yucatan Peninsula as far as Isla Contoy, Quintana Roo State, Mexico.



Map 9. The biogeographical range of *Busycoarctum coarctatum* is confined to the Mexican coast, from off Veracruz, Veracruz State, along the Yucatan Peninsula and Campeche Bank, to Isla Contoy, Quintana Roo State. Within this range, *Busycoarctum coarctatum* prefers deeper offshore areas, mostly in depths of 50 to 200 m.

Iconography of Living and Fossil *Lindafulgur* and *Busycoarctum* Species

The following sets of figures illustrate both typical specimens and variations of the living species of the genera *Lindafulgur* and *Busycoarctum*. Besides the living species, most of the named fossil *Lindafulgur* taxa, and all of the named fossil *Busycoarctum* species, are also illustrated here.

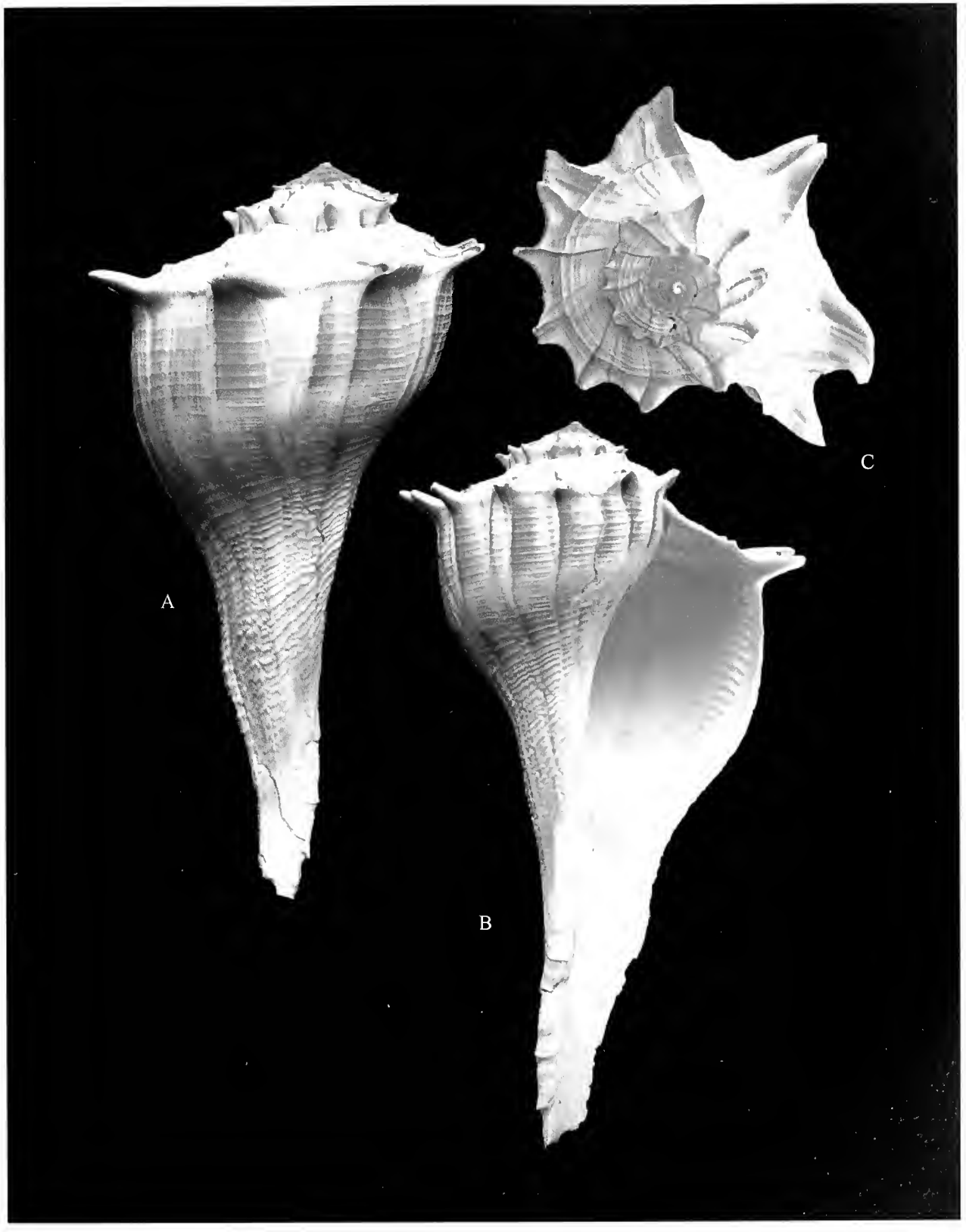


Figure 5.1 *Lindafulgur candelabrum*, Typical Specimen.
A, B, C= *Lindafulgur candelabrum* (Lamarck, 1816), length 177 mm, trawled by commercial shrimpers from 50 m depth on the Campeche Bank, off Progreso, Campeche State, Mexico. (p. 114)

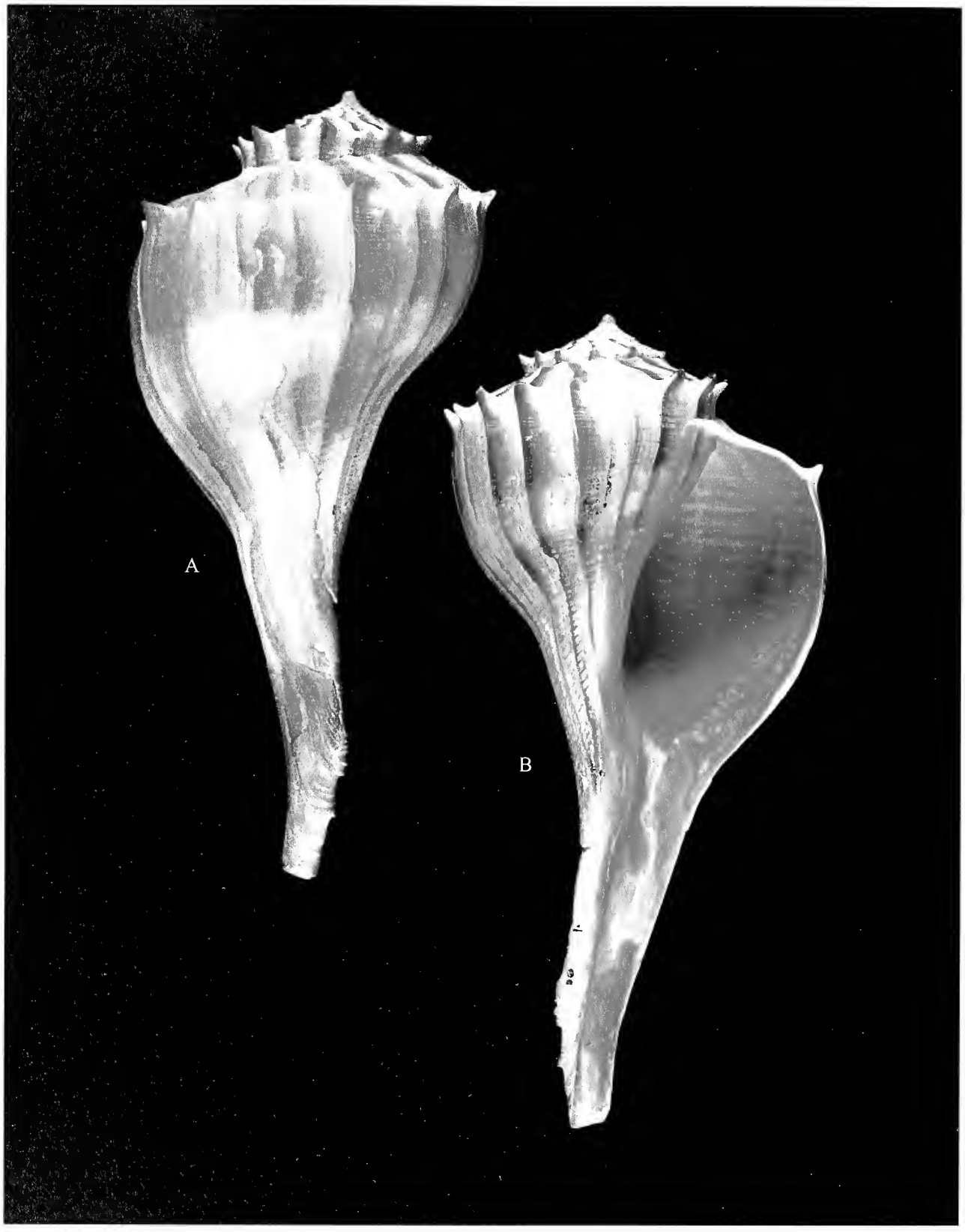


Figure 5.2 *Lindafulgur lyonsi*, Holotype Specimen.
A, B= *Lindafulgur lyonsi* (Petuch, 1987), length 132 mm, dredged from 128 m depth on the western Florida Platform, 90 km west of Clearwater, Pinellas County, Florida. USNM 859803 (Smithsonian Institution). (p. 116)

Figure 5.3 *Lindafulgur lyonsi*, Typical Specimen.
A, B= *Lindafulgur lyonsi* (Petuch, 1987), length 110 mm, dredged from 160 m depth, 150 km due west of Tampa, Hillsborough County, Florida. Specimen obtained from Louie Rundo. Note the bright yellow-orange aperture color that distinguishes this species from the larger *Lindafulgur candelabrum* from the Yucatan Peninsula. (p. 116)

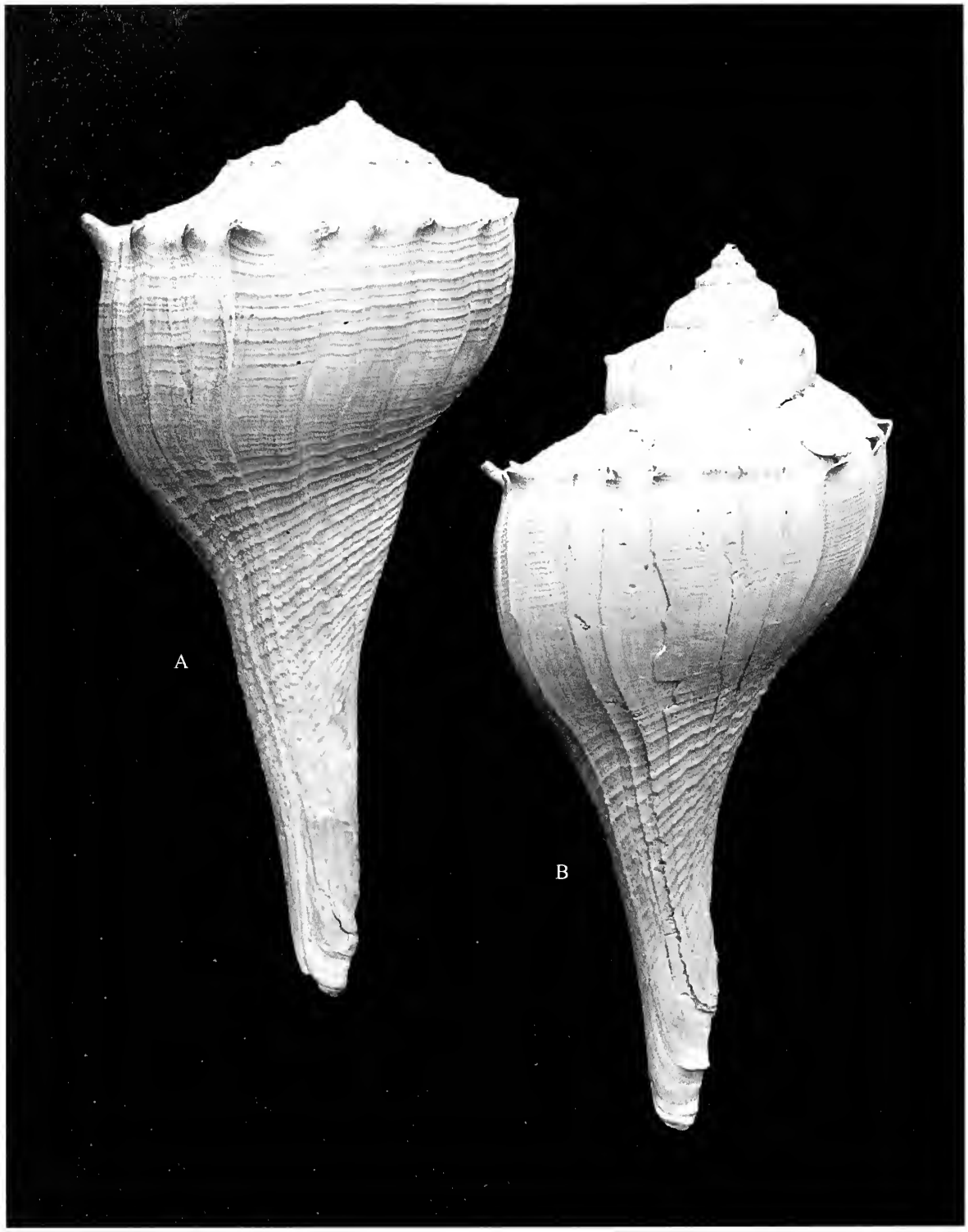


Figure 5.4 Fossil *Lindafulgur* Species.
A= *Lindafulgur lindajoyceae* (Petuch, 1991), length 114 mm, from Unit 10 in Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida; Buckingham Member of the Tamiami Formation, early Piacenzian (or possibly late Zanclean) Age of the Pliocene. Type species of the genus *Lindafulgur* Petuch, 1991.
B= *Lindafulgur miamiensis* (Petuch, 1991), length 160 mm, from the Bird Road (Lakes of the Meadows) excavation, Miami, Dade County, Florida; lower beds of the Golden Gate Member of the Tamiami Formation, Piacenzian Age of the Pliocene.

Figure 5.5 *Busycoarctum coarctatum*, Typical Specimens.
A, B= *Busycoarctum coarctatum* (Sowerby I, 1825), length 115 mm, trawled by commercial shrimpers from 100 m depth on the Campeche Bank, west of Alacran Reef, Campeche State, Mexico. Note the dark reddish-brown color of the shoulder spines.
C, D= *Busycoarctum coarctatum* (Sowerby I, 1825), dwarf variant, length 54 mm, trawled from 50 m depth off the Arcas Cays, Campeche Banks, Campeche State, Mexico. (p. 118)

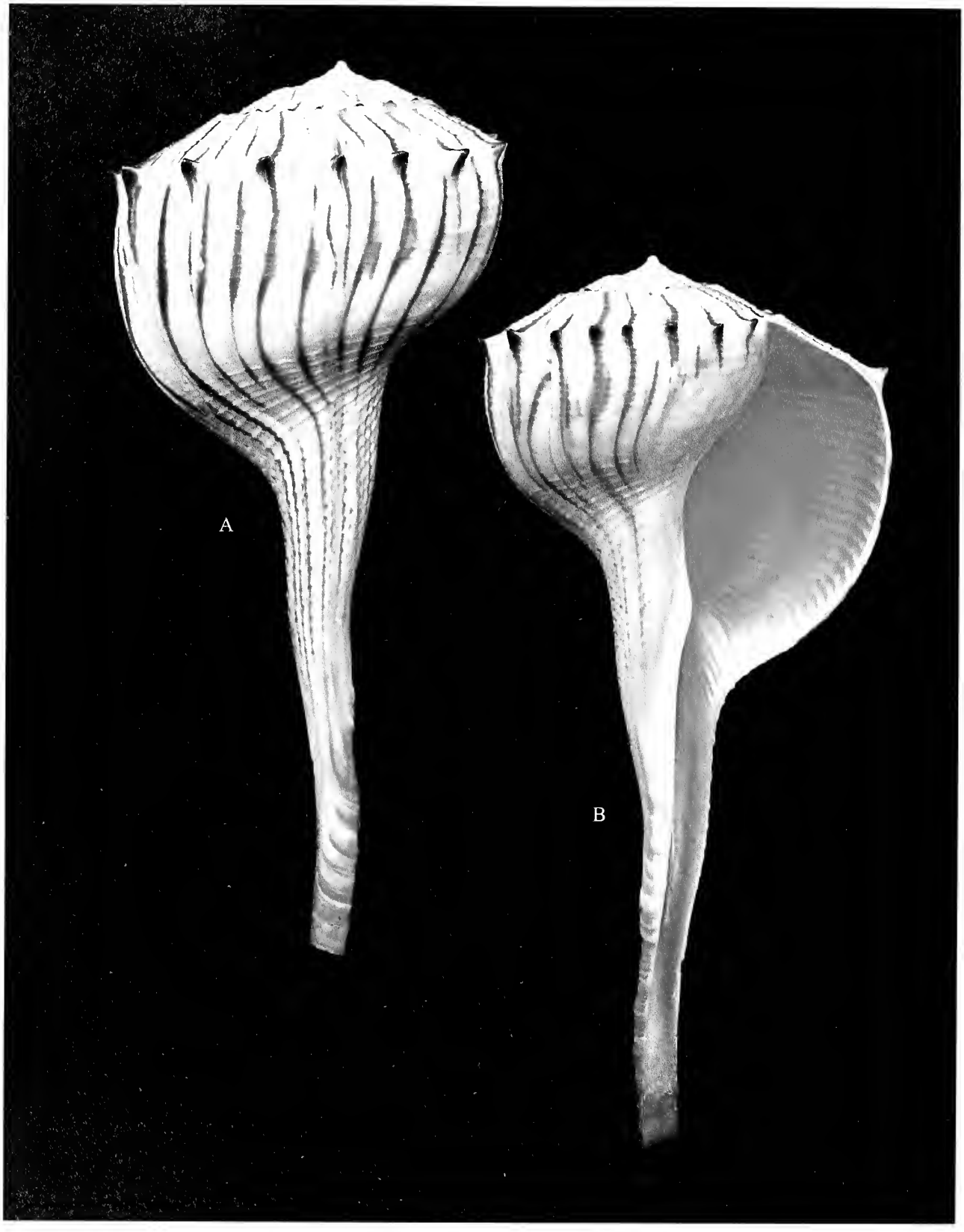


Figure 5.6 *Busycoarctum coarctatum*, Pale Color Variant.
A, B= *Busycoarctum coarctatum* (Sowerby I, 1825), length 138 mm, trawled by commercial shrimpers from 100 m depth off Contoy Light, Isla Contoy, Quintana Roo State, Mexico. (p. 118)

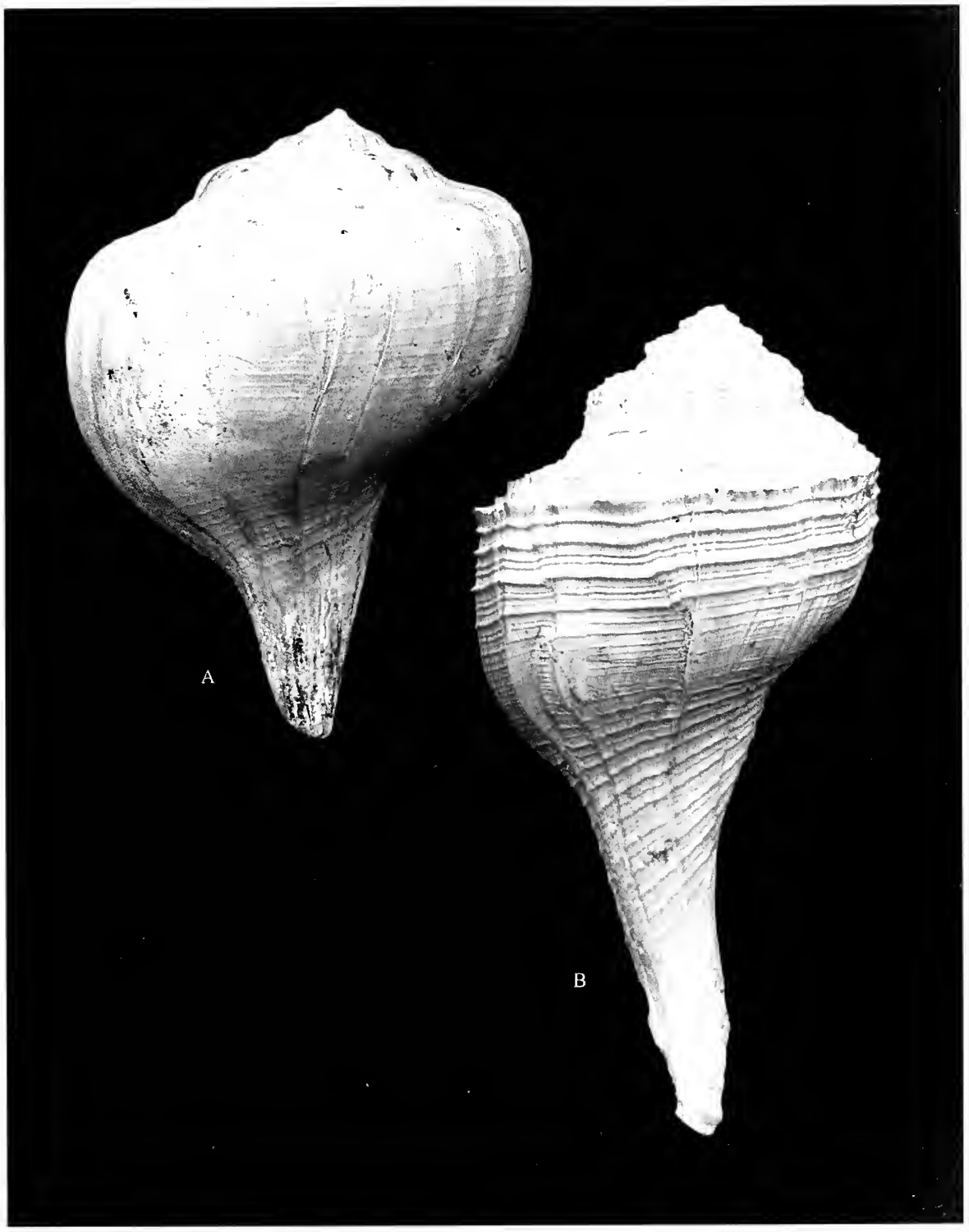


Figure 5.7 Fossil *Busycoarctum* Species.
A= *Busycoarctum tudiculatum* (Dall, 1890), length 72 mm, from the upper shell bed at Alum Bluff, Liberty County, Florida, along the Apalachicola River; Jackson Bluff Formation, early Piacenzian Age of the Pliocene. Also found in the contemporaneous Buckingham Member of the Tamiami Formation in southern Florida.
B= *Busycoarctum superbus* (Petuch, 1994), length 116 mm, from the fossil coral reef excavations in the Florida Rock Industries Naples Mine (old Mule Pen Quarry), East Naples, Collier County, Florida; Golden Gate Member of the Tamiami Formation, Piacenzian Age of the Pliocene. Note the extremely heavy spiral cord sculpture.

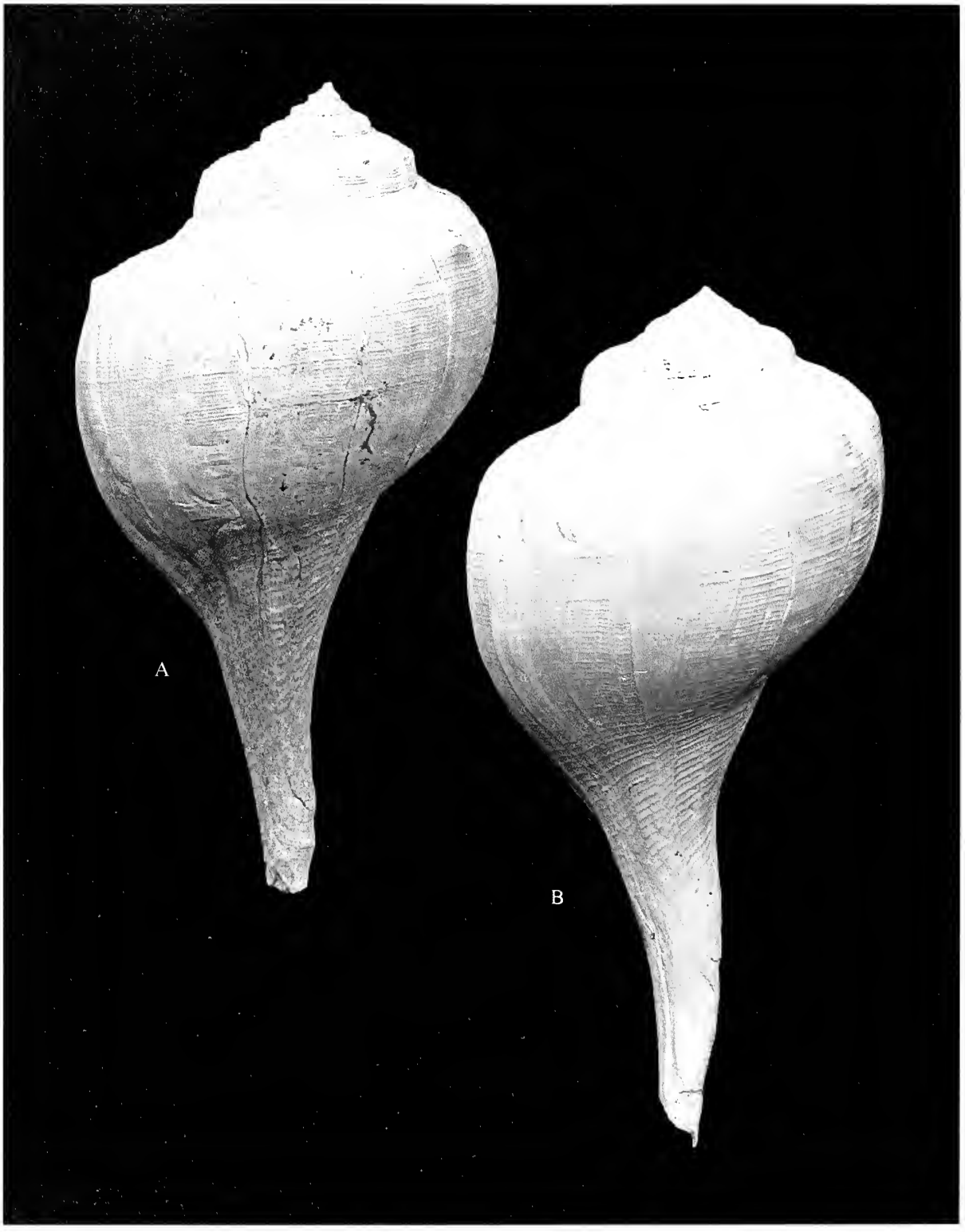


Figure 5.8 Fossil *Busycoarctum* Species.
A= *Busycoarctum tropicalis* (Petuch, 1994), length 174 mm, from Unit 7 in the APAC Pit, Sarasota, Sarasota County, Florida; Pinecrest Member of the Tamiami Formation, Piacenzian Age of the Pliocene.
B= *Busycoarctum rapum* (Heilprin, 1886), length 177 mm, from the Miami Canal excavation south of Lake Harbor, Palm Beach County, Florida. Fort Denaud Member of the Caloosahatchee Formation. Gelasian Age of the early Pleistocene.

CHAPTER SIX

The Channeled Whelks: Genus *Busycotypus*

The large Channeled Whelk, *Busycotypus canaliculatus*, is the archetype for the busyconid subfamily Busycotypinae and is one of the classic shells found along the eastern coastline of the United States. Descended from a distinctive lineage of large Pliocene and Pleistocene species, the Channeled Whelk of the Recent Virginian and Carolinian Provinces is the only surviving member of this important group of busyconids. Six species of fossil *Busycotypus* have been described to date and all of these are shown here in the iconography at the end of this chapter. The single living representative of this once more-diverse genus is relatively invariant throughout its entire range, showing only slight variations in shell color or shell sculpture. Even specimens from the population that was introduced into San Francisco Bay in the 1930's show very little morphological variation and are identical to their East Coast progenitors. Although the genus is now absent from southern and western Florida, it was much more wide-ranging during the early Pliocene, being found in the Florida Panhandle (*Busycotypus libertiense*) and along the coastline near Sarasota (*Busycotypus bicoronatum*).

Like all members of the subfamily Busycotypinae, *Busycotypus canaliculatus* has a thick, very hairy and bristly, double-layered periostracum. The hairy periostracum of *Busycotypus*, however, differs greatly from the fine velvet-like hairs seen on the periostracum of the other living member of the subfamily Busycotypinae, the genus *Fulguropsis* (see Chapter 7). The development of the periostracal hairs can be used to distinguish the genera *Busycotypus* and *Fulguropsis* and demonstrates that the two genera, although distantly related, are distinct from one another.

Family Busyconidae
Subfamily Busycotypinae
Genus *Busycotypus* Wenz, 1943

***Busycotypus canaliculatus* (Linnaeus, 1758)**
(Figures 6.1, 6.2, and 6.3)

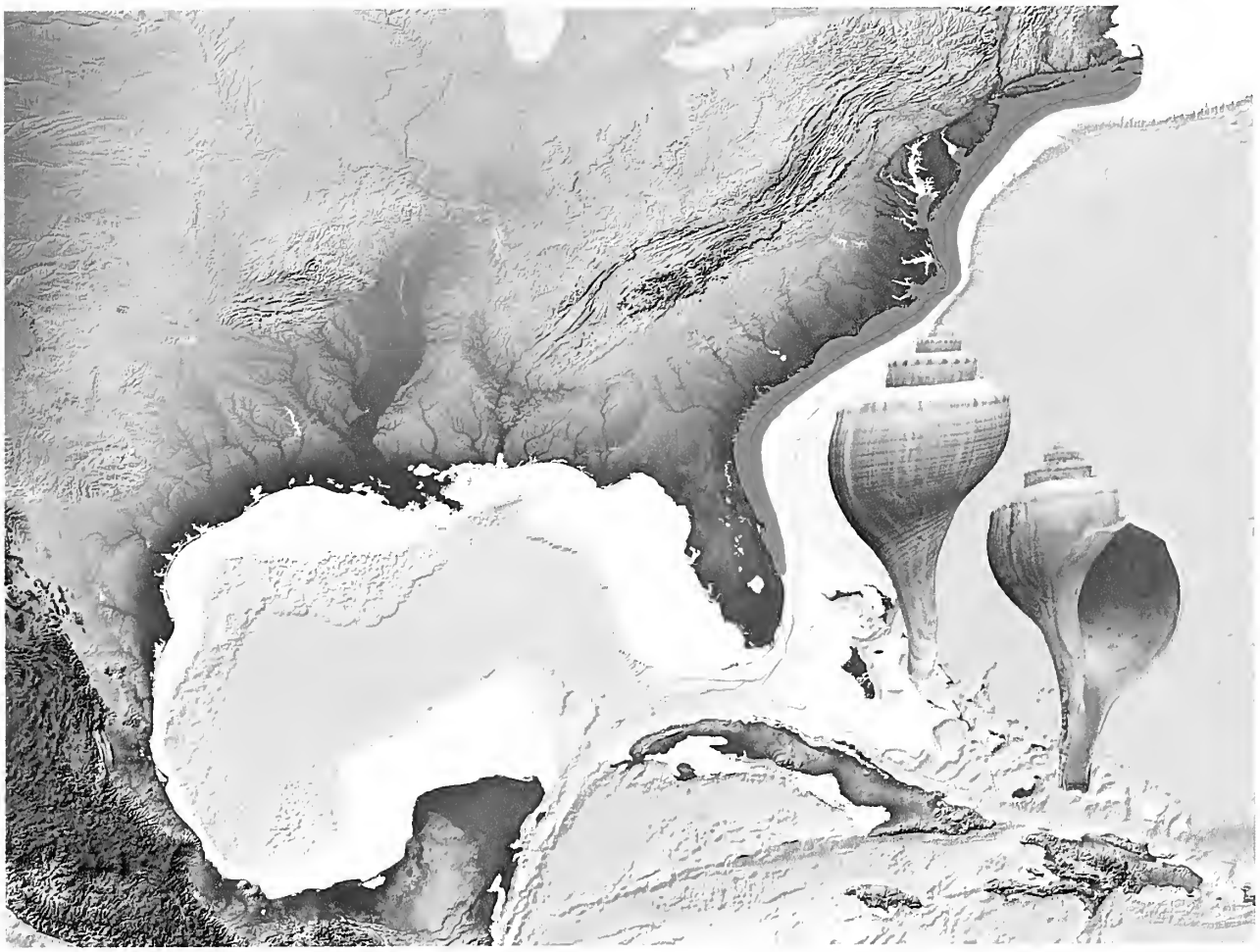
Synonymy:
Murex canaliculatus Linnaeus, 1758
Busycon canaliculatum ("Gmelin") Röding, 1798
Pyrula canaliculata (Linnaeus) Lamarck, 1816
Fulgur canaliculatus (Linnaeus) Conrad, 1853
Busycotypus (Busycotypus) canaliculatus (Linnaeus) Hollister, 1958
Busycotypus canaliculatus (Linnaeus) Petuch, 2013

Description: The shell is of average size for the family, highly inflated and globose, with rounded sides; shoulder broadly rounded, ornamented with a large and prominent thick carina; the shoulder carina bears numerous small, closely-packed, rounded beads that are stronger on the early whorls and are absent on the later whorls; spire high, protracted, and scalariform, with distinctly stepped whorls; subsutural areas of the spire whorls sloping; the suture of the spire

whorls is bounded by a very large, wide, and deep channel that is roughly 'U"-shaped in cross-section; body whorl smooth and silky, sculptured with extremely numerous small spiral cords and threads; spiral cords stronger and more pronounced on the spire whorls and on the siphonal canal; the siphonal canal is straight, narrow, and relatively short, being equal to, or shorter than, the length of the body whorl; a distinct constriction is present at the siphonal canal-body whorl juncture, causing the inflated body whorl to transform abruptly into the narrow siphonal canal; shell color varying from a uniform pale lavender-tan, to a grayish-tan, to a darker tan with two wide light brown bands, to a solid tan-orange; aperture proportionally very wide and open, rounded in shape, with the interior color varying with the shell color (being lavender, grayish-tan, light tan, or orange); protoconch rounded, domelike, composed of two whorls; periostracum very thick, light brown, hairy and bristly, composed of two parallel layers.

Discussion: Although relatively invariant in shell color, shape, and size, some populations of *Busycotypus canaliculatus* from the southern end of its range have produced some interesting local forms and varieties. Florida specimens, in particular, show the greatest amount of variability, with some individuals being encircled with prominent thin brown lines and cords (Figure 6.3A) and with others having white spire whorls and wide bands of dark tan on the body whorl (Figure 6.3B).

Biogeographical Range: As shown on Map 10, *Busycotypus canaliculatus* ranges from Cape Cod, Massachusetts southward to Cape Canaveral, Florida. The species is found in the Montaukian and Delawarean Subprovinces of the Virginian Province and in the Georgian Subprovince of the Carolinian Province.



Map 10. The biogeographical range of *Busycotypus canaliculatus* extends from Cape Cod, Massachusetts to near Fort Pierce, Florida. In the northern part of its range, *Busycotypus canaliculatus* occurs in shallow water, often intertidal, areas. In the southern part of its range, the Channeled Whelk is found offshore in deeper water.

Iconography of Living and Fossil *Busycotypus* Species

The following sets of figures illustrate both typical specimens and variations of *Busycotypus canaliculatus*. All of the named fossil *Busycotypus* taxa are also shown here.

Figure 6.1 *Busycotypus canaliculatus*, Typical Specimen.
A, B= *Busycotypus canaliculatus* (Linnaeus, 1758), length 168 mm, found in sand at low tide, off Shackleford Island, Carteret County, North Carolina. This is the type species of the genus *Busycotypus* Wenz, 1943. (p. 129)

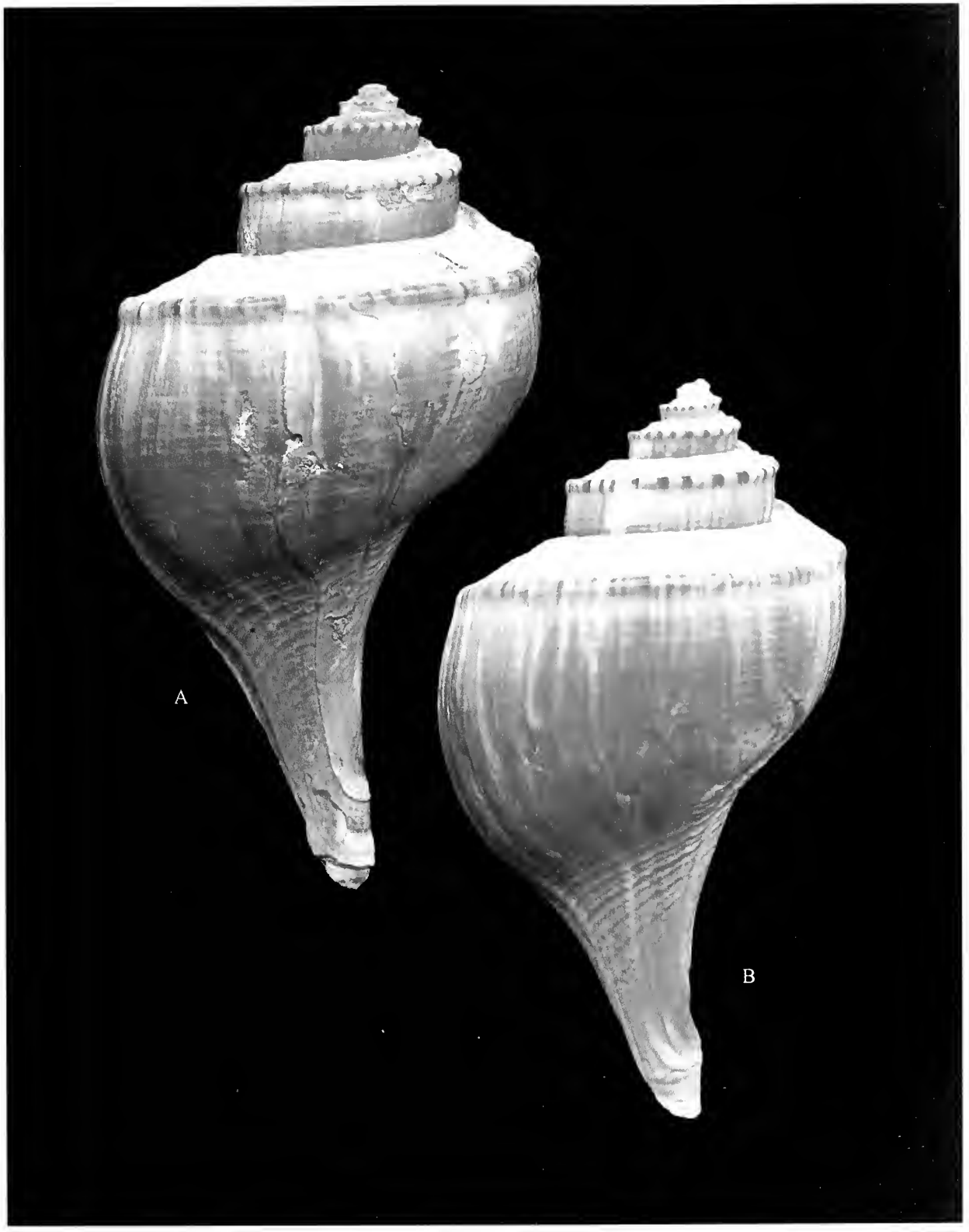


Figure 6.2 *Busycotypus canaliculatus*, Typical Small Specimens.
A= *Busycotypus canaliculatus* (Linnaeus, 1758), length 127 mm, found on the beach after a heavy storm, Cape May, Cape May County, New Jersey.
B= *Busycotypus canaliculatus* (Linnaeus, 1758), length 115 mm, found on the beach after a heavy storm, Cape May, Cape May County, New Jersey. (p. 129)

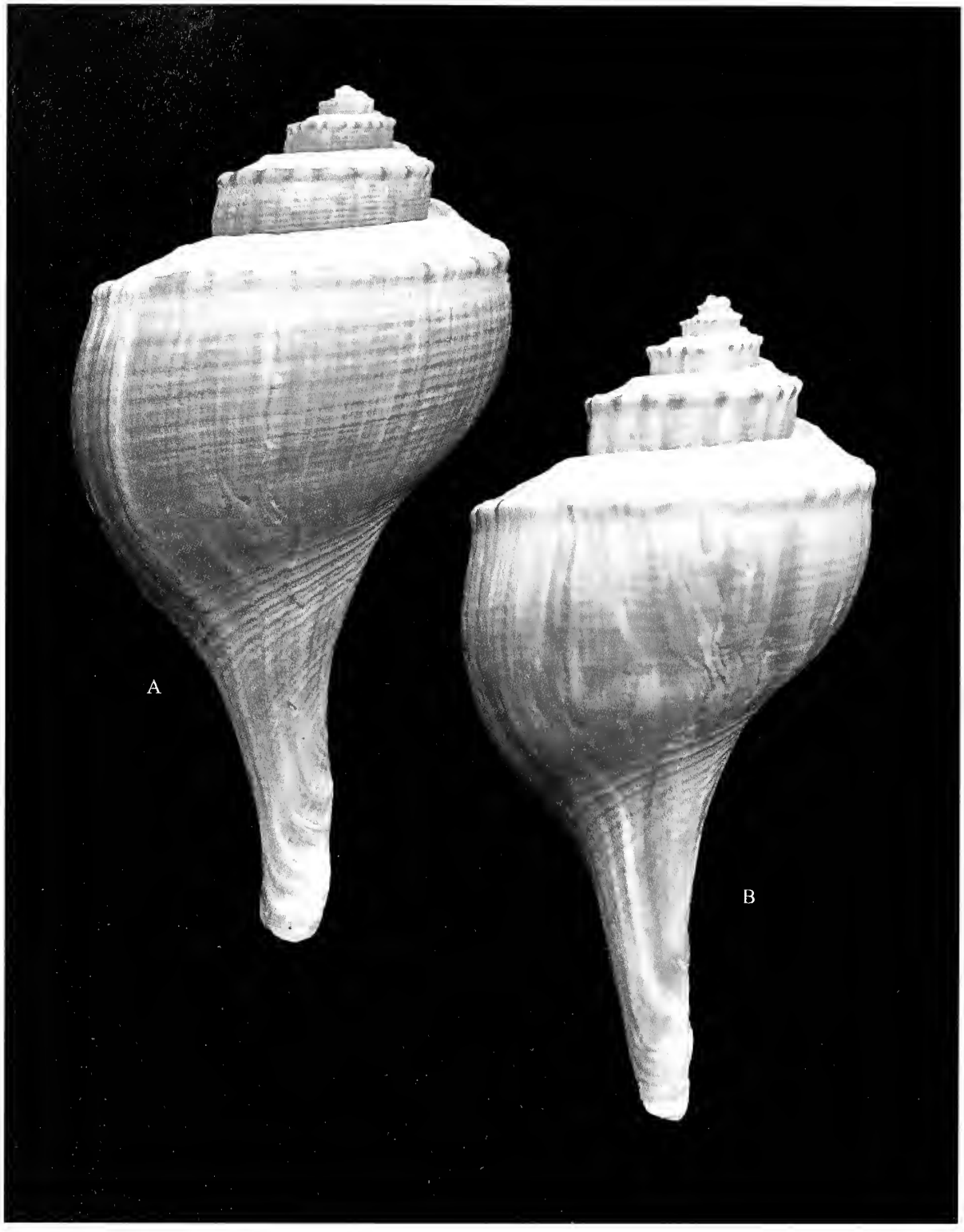


Figure 6.3 *Busycotypus canaliculatus* Variants.
A= *Busycotypus canaliculatus* (Linnaeus, 1758), length 132 mm, trawled by commercial scallop boat from 20 m depth off Cape Canaveral, Brevard County, Florida. Ornate variant with a shell sculpture composed of strong spiral cords and with a color pattern composed of thin brown spiral bands.
B= *Busycotypus canaliculatus* (Linnaeus, 1758), length 113 mm, trawled by commercial scallop boat from 25 m depth off Cape Canaveral, Brevard County, Florida. Pale color form with white spire whorls. (p. 129)

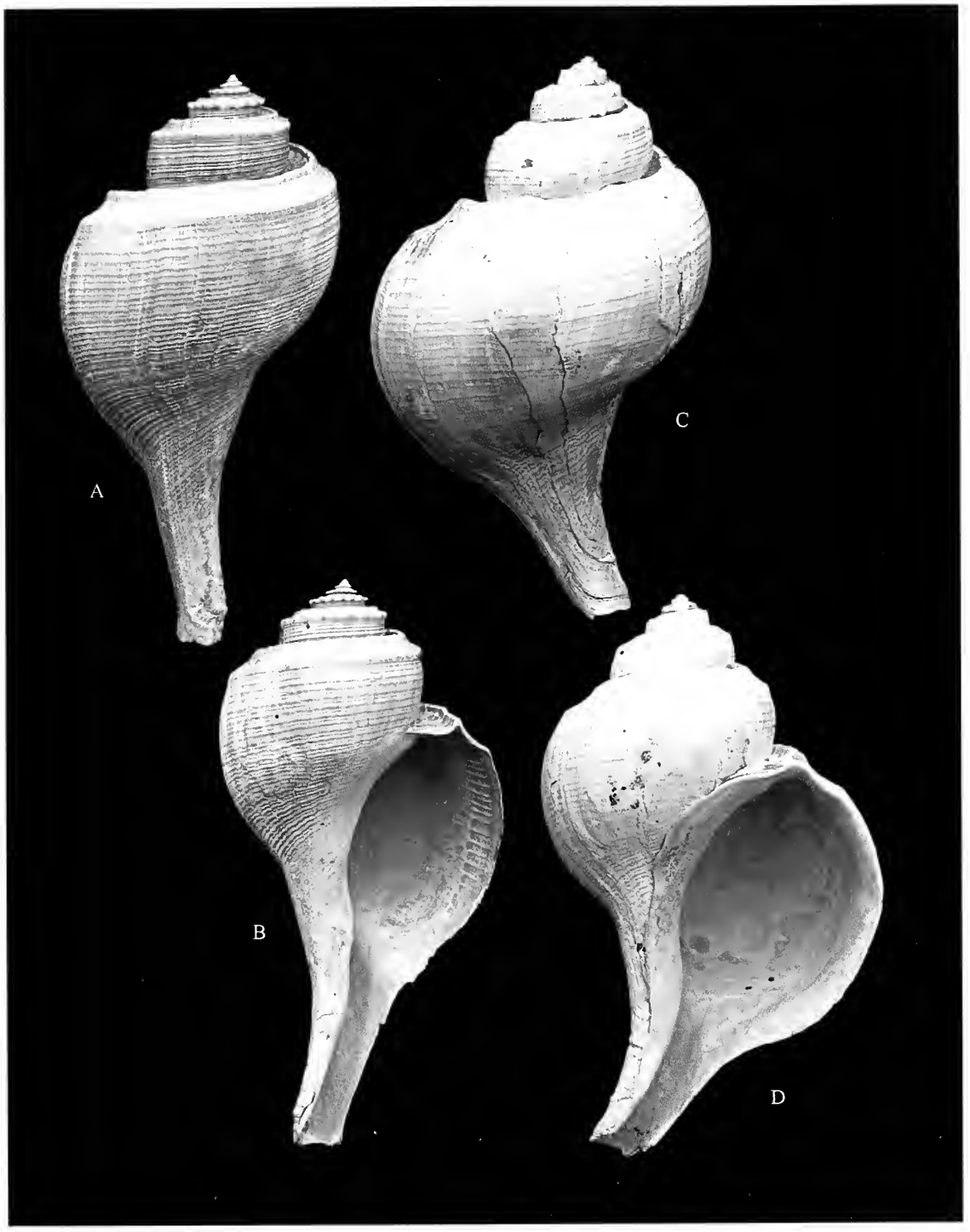


Figure 6.4 Fossil *Busycotypus* Species.
A, B= *Busycotypus libertiense* (Mansfield, 1930), length 164 mm, from Unit 10 in Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida; Buckingham Member of the Tamiami Formation, early Piacenzian (or late Zanclean) Age of the Pliocene. Also found in the contemporaneous Jackson Bluff Formation at Alum Bluff, Liberty County, Florida, along the Apalachicola River. This is the oldest-known true *Busycotypus* species.
C, D= *Busycotypus incile* (Conrad, 1833), length 168 mm, found in the Lone Star Cement Company Pit (now Lone Star Lakes), Chuckatuck, Isle of Wight County, Virginia. Rushmere Member (lower Zone 2) of the Yorktown Formation, Piacenzian Age of the Pliocene.

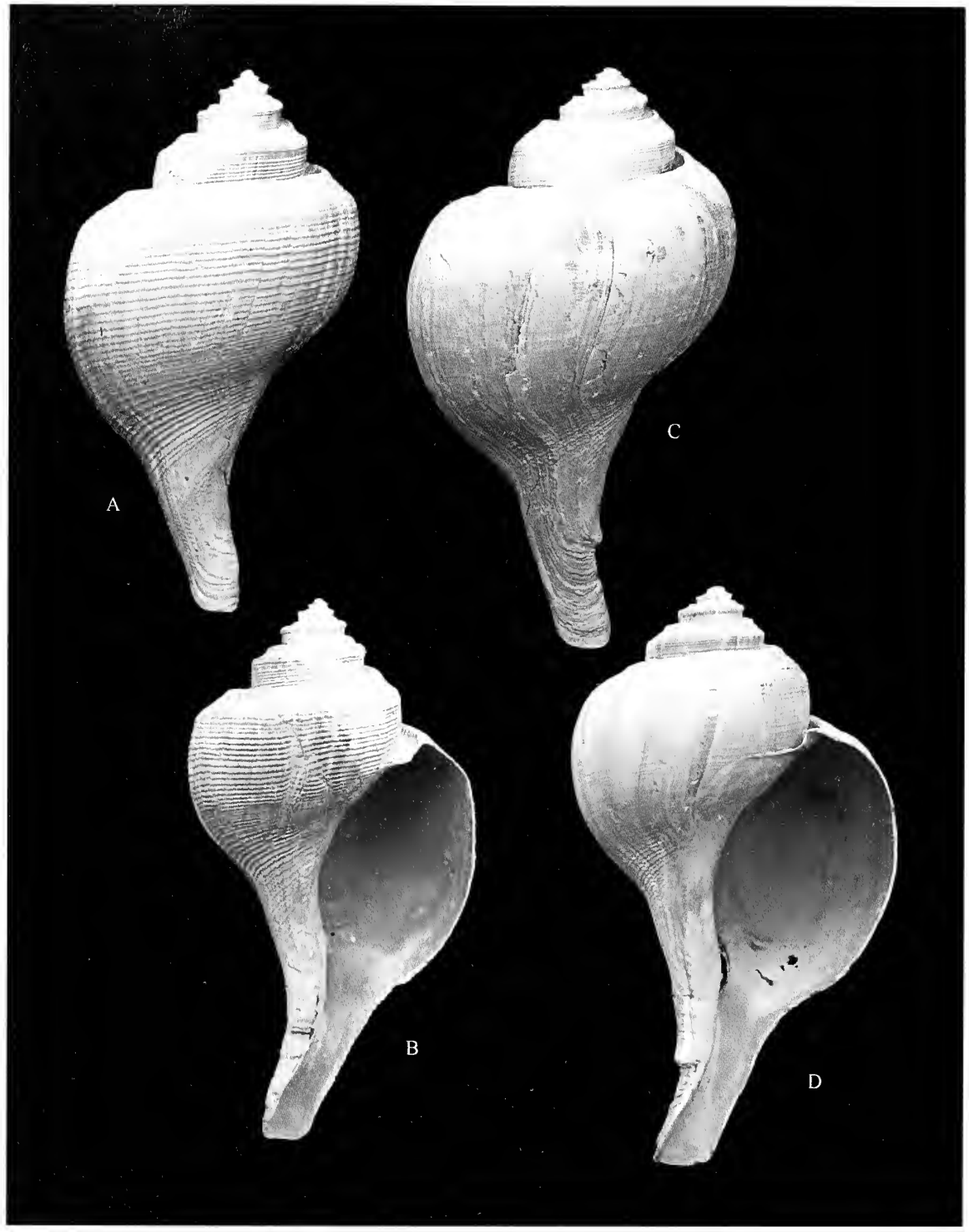


Figure 6.5 Fossil *Busycotypus* Species.
A, B= *Busycotypus concinnum* (Conrad, 1875), length 112 mm, found in the middle fossiliferous bed of the Lee Creek Mine, Aurora, Beaufort County, North Carolina. Edenhouse Member of the Chowan River Formation, late Piacenzian Age of the Pliocene. Also found in the contemporaneous Fruitville Member (Unit 2 Kissimmee River beds) of the Tamiami Formation, southern Florida.
C, D= *Busycotypus scotti* Petuch, 1994, length 169 mm, found in the Dickerson Aggregates Indrio Pit, Indrio Road, Fort Pierce, Indian River County, Florida. Rucks Pit Member of the Nashua Formation, Gelasian Age of the early Pleistocene.

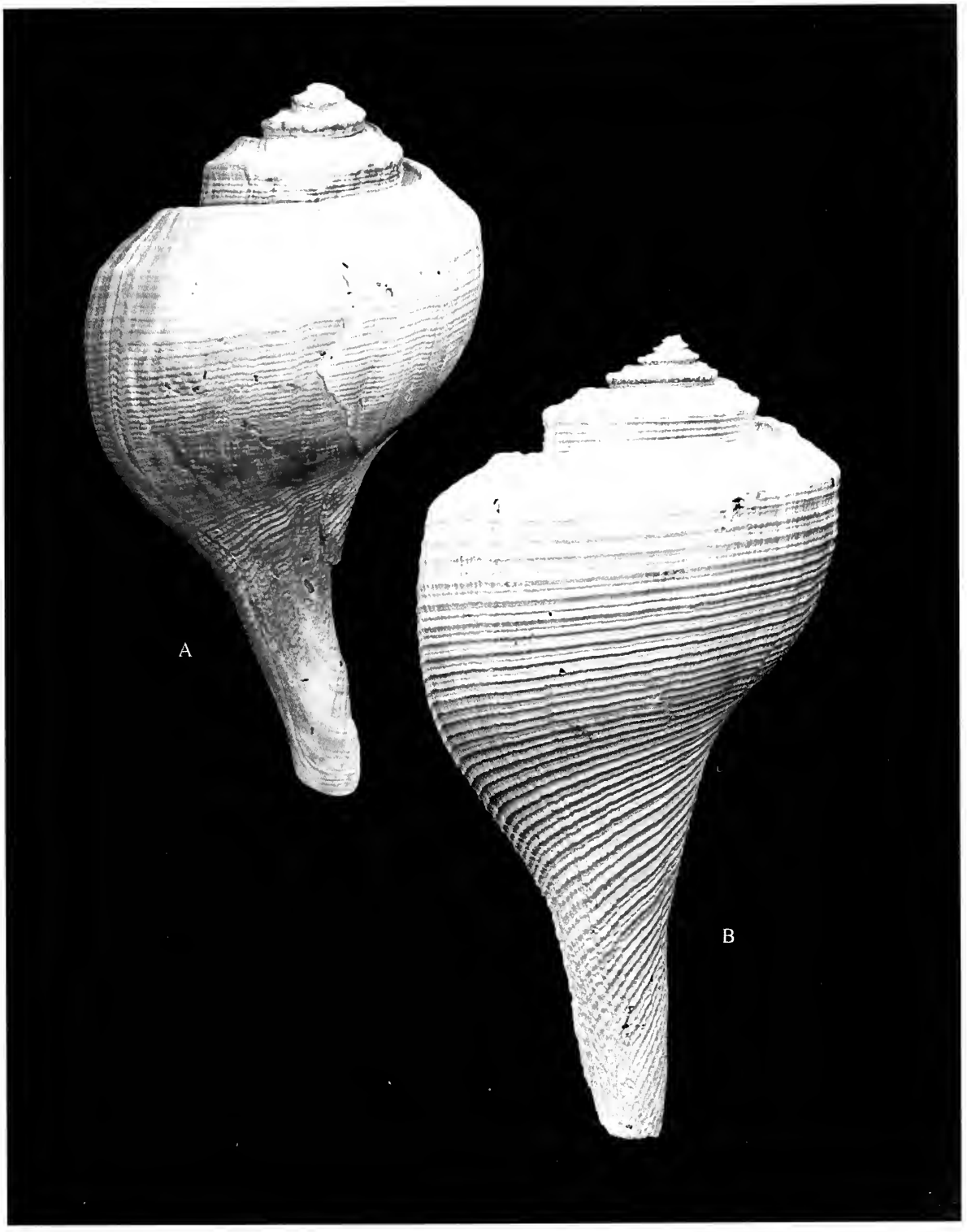


Figure 6.6 Fossil *Busycotypus* Species.
A= *Busycotypus mansfieldi* Petuch, 1994, length 111 mm, found in Unit 10, Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida, Buckingham Member of the Tamiami Formation. Early Piacenzian Age, Pliocene. Also found in the contemporaneous Jackson Bluff Formation of the Florida Panhandle.
B= *Busycotypus bicoronatum* (Tripp, 1988), length 88 mm, found in Unit 7 of the APAC Pit, Sarasota, Sarasota County, Florida, Pinecrest Member of the Tamiami Formation. Piacenzian Age of the Pliocene.

Egg cases of the Left-Handed Whelk *Sinistrofulgur sinistrum* washed ashore among other shells at low tide on Sanibel Island.

CHAPTER SEVEN

The Pear Whelks: *Fulguropsis spiratus* Species Complex

The *Fulguropsis spiratus* species complex is completely confined to the Carolinian Province (both Atlantic and Gulf of Mexico regions) and encompasses four distinct species, each of which is confined to a different subprovince. These include (from north to south) *Fulguropsis rachelcarsonae* Petuch and Myers, new species (confined to the Georgian Subprovince), *Fulguropsis keysensis* Petuch, 2013 (confined to the Floridian Subprovince), *Fulguropsis pyruloides* (Say, 1822) (confined to the Suwannean Subprovince), and *Fulguropsis spiratus* (Lamarck, 1816) (found in both the Texan and Yucatanean Subprovinces). Many previous workers, especially Abbott (1974), have considered all four of these taxa to belong to a single variable species, *Fulguropsis spiratus*. Closer studies of their shell morphology and biogeographic patterns, however, have shown that the four members of the complex are actually distinct and separate species. Examples of each species and its variations are illustrated in the iconography at the end of this chapter.

The generic placement of this group of small pear-shaped whelks has also been in a state of flux for many decades, with different workers placing them in several different higher taxa. Some of these have included *Busycotypus (Pyrofulgur)* (Hollister, 1958), *Busycon (Fulguropsis)* (Abbott, 1974), *Busycotypus* (Tunnell *et al.*, 2010), and *Fulguropsis* (Petuch, 2004; 2013). Hollister (1958) erected the subgenus *Pyrofulgur* for this group of channeled Pear Whelks, differentiating them from the larger and more deeply-channeled genus *Busycotypus*. In his redecription of the genus *Busycotypus*, however, Hollister (1958: 93-94) incorrectly invalidated the older Pear Whelk genus *Fulguropsis* Marks, 1950, based on the idea that Marks included both Wenz's *Busycotypus* and typical Pear Whelks, such as the fossil species *excavatum* and *pyriformis*, in his genus. In our interpretation of the busyconid higher taxa, *Busycotypus* should be removed from Marks' *Fulguropsis* as a full, valid genus and that the remaining typical Pear Whelk species should be retained in the genus *Fulguropsis*. Hollister's *Pyrofulgur*, then, represents an unnecessary renaming of Marks' *Fulguropsis* and that genus should be considered, by the Law of Priority, to be the proper generic name for the Pear Whelks. Hollister's taxon (*Pyrofulgur*) is here considered to be a synonym of Marks' taxon (*Fulguropsis*). As is typical of the subfamily Busycotypinae, members of *Fulguropsis* all have fuzzy or bristly periostraca.

Although actually encompassing six different species and one subspecies, the genus *Fulguropsis* Marks, 1950 (=*Pyrofulgur* Hollister, 1958) breaks into two distinct and separate species complexes; one with relatively rounded shoulders and a pyriform shell shape (the *Fulguropsis spiratus* Species Complex) and one with a more vase-shaped shell and a prominent sharp keel (carina) around the shoulder (the *Fulguropsis plagosus* Species Complex). Both species groups have separate fossil records and also have separate biogeographical distributions; with the *Fulguropsis spiratus* complex ranging throughout all five subprovinces of the Carolinian Province, and with the *Fulguropsis plagosus* complex being confined to the Gulf of Mexico (Suwannean, Texan, and Yucatanean Subprovinces). In this book, we separate the two species complexes and deal with them in two separate sections (Chapters 7 and 8). The first of these groups, the *Fulguropsis spiratus* complex, is discussed in this chapter and specimens of all the living and described fossil species are illustrated in the iconography at the end of the chapter.

Family Busyconidae
Subfamily Busycotypinae
Genus *Fulguropsis* Marks, 1950

***Fulguropsis spiratus* (Lamarck, 1816)**
(Figure 7.1)

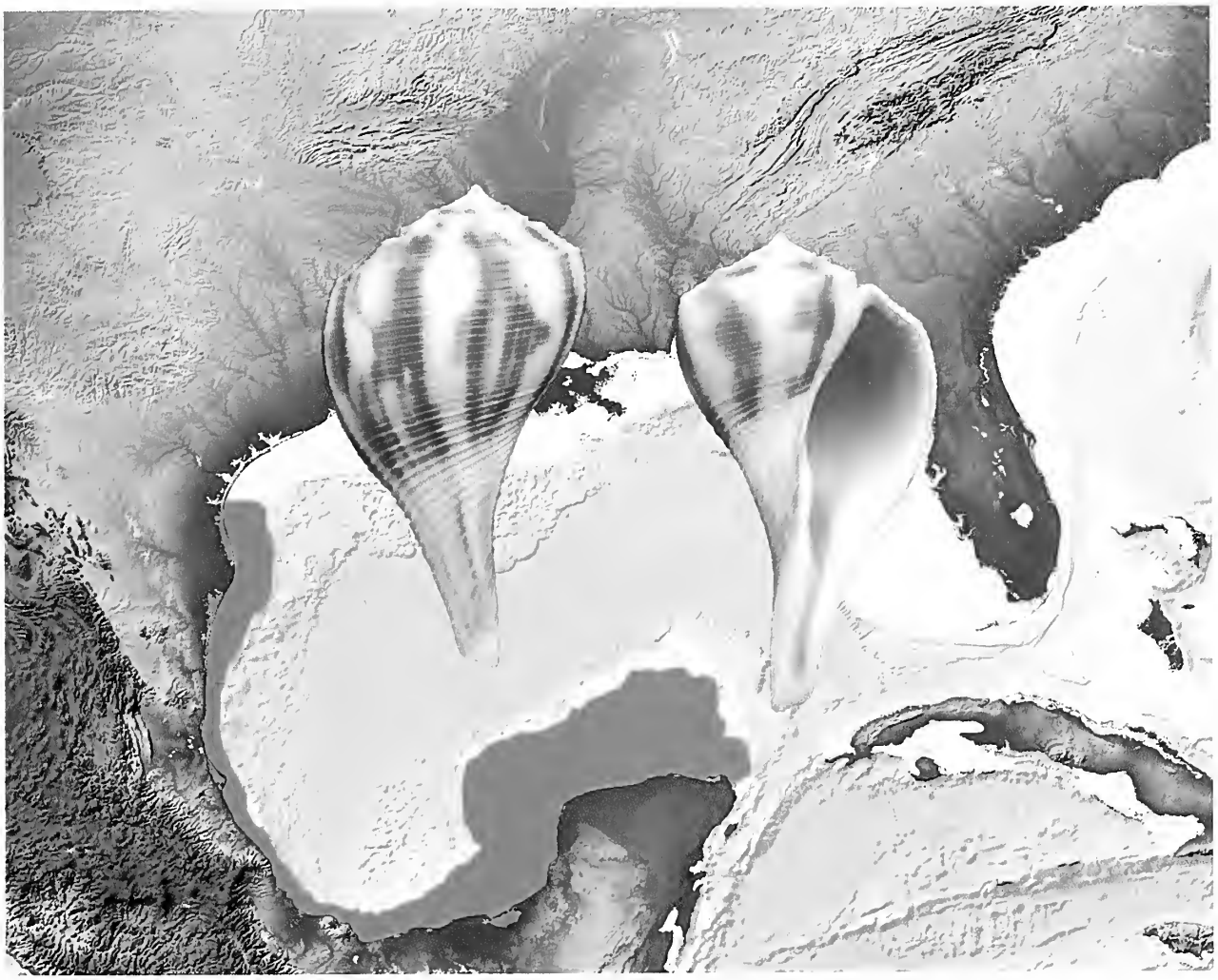
Synonymy:
Pyrula spirata Lamarck, 1816
Bulla pyrum Dillwyn, 1817
Busycotypus (Pyrofulgur) spiratus (Lamarck) Hollister, 1958
Busycon (Fulguropsis) spiratum spiratum (Lamarck) Abbott, 1974
Busycotypus spiratus (Lamarck) Tunnell, *et al.*, 2010
Fulguropsis spiratus (Lamarck) Petuch, 2013

Description: The shell is of average size for the genus and is typically pyriform in shape, with an inflated and globose body whorl and rounded sides; the spire varies from low to moderately elevated, with a deep and wide "U"-shaped channel bordering the suture; shoulder broadly rounded, with a small shoulder carina being present on some specimens; the body whorl, spire whorls, and siphonal canal are highly sculptured with numerous closely-packed strong spiral cords and ribs, with the cords on the siphonal canal being the strongest and best developed; siphonal canal straight, grading directly into the body whorl without a strong constriction, approximately equal in length to the body whorl; shell color white, overlaid with large dark brown or orange-brown amorphous longitudinal flammules; spire whorls with widely-spaced brown flammules arranged in a radiating pattern; end of siphonal canal light orange-brown or tan; aperture wide, flaring, oval in shape, with numerous strong and prominent cords; interior of aperture white in color with a tan patch on the inside of the siphonal canal; protoconch proportionally large, rounded, domelike, composed of two whorls, white in color; peristracum thick and adherent, covered with short hairs and bristles, producing a velvety appearance.

Discussion: Although resembling the Suwannean Subprovince *Fulguropsis pyruloides* in shape, color, and size, the Texan and Yucatanean Subprovince *F. spiratus* differs in having a much heavier and thicker shell that is more heavily-sculptured with strong spiral cords, and in having very strong and prominent ribs within the aperture. *Fulguropsis pyrum* (Dillwyn, 1817) is an absolute synonym of Lamarck's *F. spiratum*, as both Dillwyn and Lamarck used the same specimen as the holotype for their species (Hollister, 1958: 100-101). Since Lamarck's taxon was named one year before Dillwyn's, priority insures that Lamarck's *spiratus* is the proper name for the Texan and Yucatanean shell. The name *pyrum* was often applied to the Georgian Subprovince species, but since that taxon is a synonym of *spiratus*, it was unavailable and the new name *rachelcarsonae* was given to the East Coast species (see the following description).

Biogeographical Range: As shown on Map 11, *Fulguropsis spiratus* ranges from southern Texas, near Corpus Christi, across the northern Yucatan Penisula and the offshore Campeche Banks, to Isla Contoy, Quintana Roo State, Mexico. This is the only member of the species group that ranges into two separate biogeographical regions, the Texan and Yucatanean

Subprovinces of the Carolinian Province. Specimens of *Fulguropsis spiratus* from southern Texas are more globose and inflated and may represent an undescribed subspecies.



Map 11. The biogeographical distribution of *Fulguropsis spiratus* is confined to the western Gulf of Mexico, where it ranges from southern Texas, across the Yucatan Peninsula and Campeche Bank, to Isla Contoy, Quintana Roo State, Mexico.

Fulguropsis rachelcarsonae Petuch, Myers, and Berschauer, new species (Figures 7.2, 7.3, and 7.4)

Synonymy:
Busycotypus (Pyrofulgur) spiratus pyruloides (Say) Hollister, 1958 (in part)
Busycon (Fulguropsis) spiratum pyruloides (Say) Abbott, 1974 (in part)
Fulguropsis spiratum pyruloides (Say) Petuch, 2013 (in part)

Description: Shell of average size for genus, very inflated and globose, distinctly pyriform, with rounded sides; spire relatively low, subpyramidal; the suture of the spire whorls is bordered by a narrow, but deeply-incised, "U"-shaped channel; the spire whorls are distinctly sloping; shoulder

is broadly rounded, slightly angled, often marked with a faint carina; the body whorl, spire whorls, and siphonal canal are heavily sculptured with numerous coarse spiral threads and small cords, giving the shell a rough, corrugated texture; the spiral cords on the siphonal canal are stronger and larger than those on the body whorl; siphonal canal straight, narrow, grading directly into the body whorl, without a distinct constriction; siphonal canal proportionally short, less than one-half the total length of the body whorl; base shell color pale tan-white or bluish-white, overlaid by 2 broad bands of closely-packed dark brown patches, one above the shell mid-body and one below the shell mid-body; numerous dark brown longitudinal lines and flammules intersect the 2 broad bands, often producing a checkered appearance; the siphonal canal typically is stained a brown or bluish-brown color, with the anteriormost tip being white or yellow-white; the aperture is wide and flaring, oval in shape, with numerous fine, weak cords; in some specimens, the apertural cords are absent or only faintly developed; interior of aperture colored a dark brown or purple-brown, with the edge of the outer lip being white; protoconch pale tan in color, rounded, domelike, composed of 2 whorls; periostracum thick, light brown in color, with fine hairs and a velvet-like texture.

Type Material: HOLOTYPE: length 76 mm, width 37 mm, trawled by a commercial scallop boat from 20 m depth off Cape Canaveral, Brevard County, Florida, LACM 3418 (deposited in the molluscan collections of the Los Angeles County Museum of Natural History, Los Angeles, California); PARATYPES: lengths 96 and 98 mm, in Shoal Grass beds at low tide, off Pine Point, Singer Island, Lake Worth Lagoon, Palm Beach County, Florida, in the research collection of the senior author.

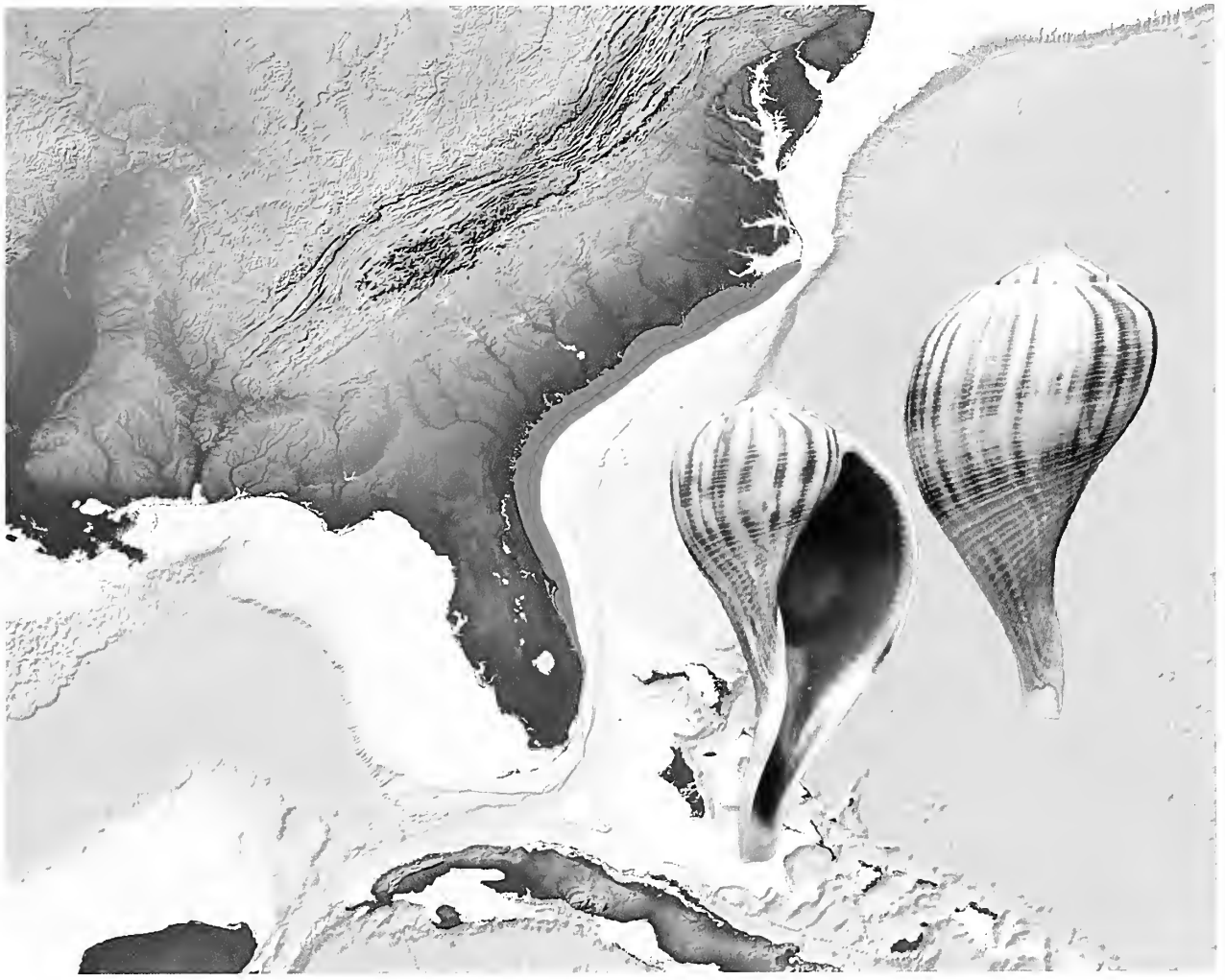
Type Locality: 20 m depth, on a shell hash and sand bottom, off Cape Canaveral, Brevard County, Florida.

Biogeographical Range: As shown on Map 12, *Fulguropsis rachelcarsonae* ranges from Cape Hatteras, North Carolina southward to southern Palm Beach County, Florida, and is completely confined to the Georgian Subprovince of the Carolinian Province and the Palm Beach Provinciatone transition zone.

Etymology: Named in honor of Rachel L. Carson, renowned author and marine biologist, who, with the publication of her book *Silent Spring*, became the founder of the American environmentalist movement.

Discussion: This common East Coast whelk has been incorrectly referred to as "*Busycotypus spiratus pyruloides*" by almost all previous authors, including the senior author. Based on superficial similarities between Pear Whelks found on the eastern and western coasts of Florida, Hollister (1958) and Abbott (1974) assumed that a single species ranged from North Carolina, around Florida, and northward in the Gulf of Mexico to the Mississippi River Delta. Subsequent studies showed, however, that the eastern Florida Pear Whelk did not range into the Florida Keys, but was replaced by a very different-looking endemic species that occurred throughout the entire Floridian Subprovince (*Fulguropsis keysensis*, discussed later in this chapter). The western Florida Pear Whelks, then, were found to be cut-off from the eastern populations, separated by the ecological barrier of the Florida Keys tropical carbonate environments (see Petuch, 2013). During the late Pleistocene (Tarantian Age) sea level high stands, a single species, *Fulguropsis*

pyruloides pahayokee Petuch, 1994 (Figure 7.13), was distributed all across the flooded Florida Peninsula. When sea levels dropped at the end of the Pleistocene, this ancestral Pear Whelk was genetically isolated into three separate populations, and these later gave rise to the east and west coast and Keys whelk species.



Map 12. The biogeographical range of *Fulguropsis rachelcarsonae* extends from Cape Hatteras, North Carolina southward to Dania Beach, Broward County, Florida.

A close comparison of the western Florida *Fulguropsis* species with that of eastern Florida shows that, although similar in shape and color pattern, the two have major morphological differences. The eastern species consistently is heavily sculptured, with strong spiral cords and ribs on the body whorl and spire, and has a rough, coarsely-textured shell. The western species is much smoother, with a sculpture made up only of fine spiral threads, and has a distinct silky texture to the body whorl and spire. The intervening Florida Keys *Fulguropsis keysensis*, on the other hand, is very heavily sculptured with strong spiral ribs and cords and differs greatly from both the eastern and western *Fulguropsis* species. In trying to find the proper name for the Florida Pear Whelk, Hollister discovered that the only possible available name, "*Fulgur pyruloides* Say, 1822" was essentially a *nomen dubium*, as the holotype was lost and there was no designated type locality. In order to preserve Say's taxon, Hollister (1958: 100-101)

designated a neotype specimen (deposited in the collection of the Paleontological Research Institution, Ithaca, New York; PRI 24943) and a new type locality, "Siesta Key, Sarasota, Manatee County" (in error, as Siesta Key is actually in Sarasota County). By establishing a new type locality and neotype specimen, Hollister fixed the taxon to the smooth western Florida species, leaving the allopatric eastern Florida and American East Coast species without a name. For this reason, we here name the heavily-sculptured eastern species *Fulguropsis rachelcarsonae*.

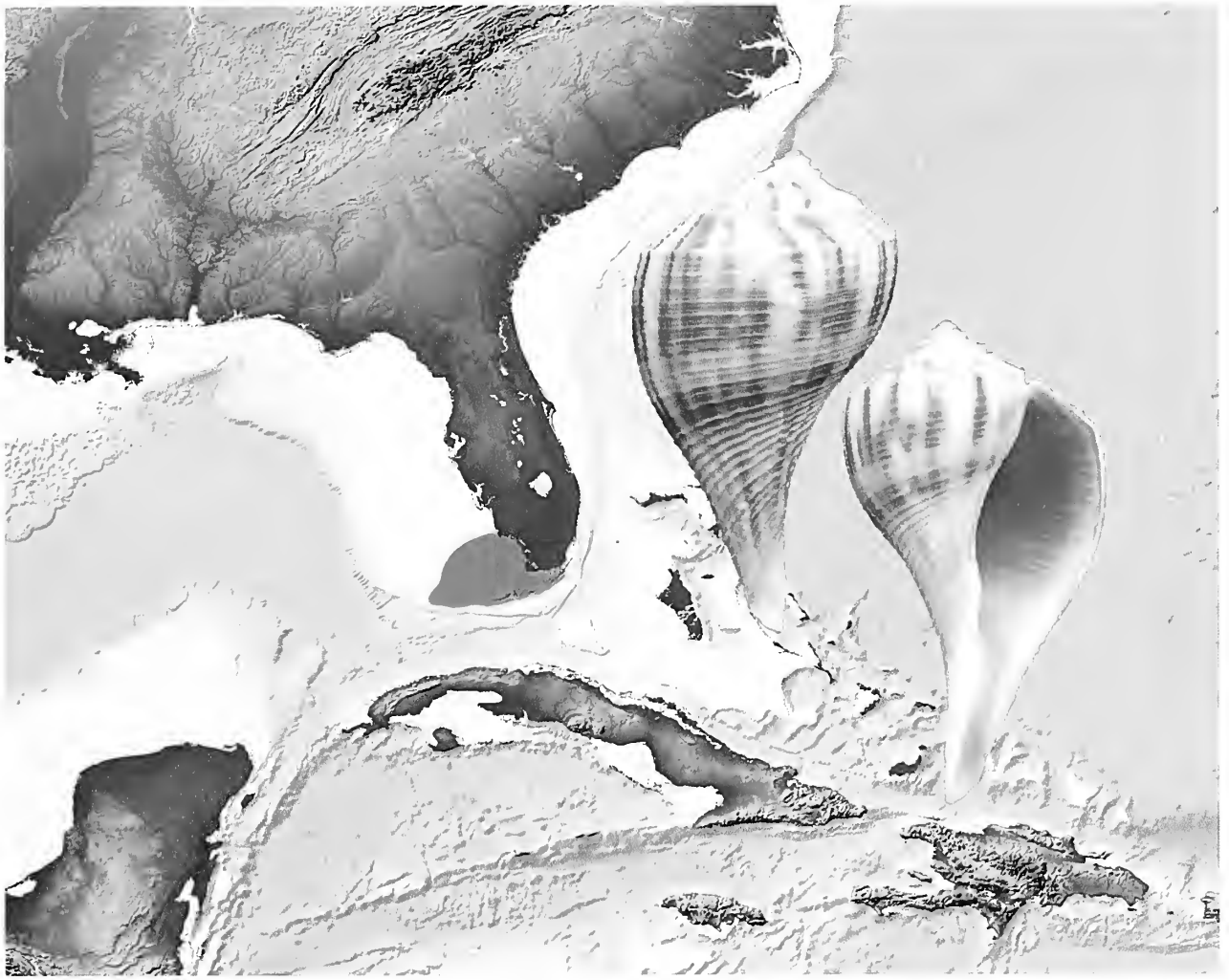
Fulguropsis keysensis Petuch, 2013
(Figures 7.5, 7.6, and 7.7)

Synonymy:
Fulguropsis spiratum subspecies Petuch and Sargent, 2011
Fulguropsis spiratum keysensis Petuch, 2013
Fulguropsis keysensis (Petuch) Petuch and Myers, 2014

Description (modified from the original; Petuch, 2013: 205): Shell of average size for genus, heavy and thickened, distinctly pyriform; the shoulder is sharply angled, bordered by a strong raised carina; the subsutural area is sloping on the body whorl, becoming flatter and slightly depressed or canaliculate on the spire whorls; the spire varies from high, stepped, and scalariform (as on the holotype) to low and subpyramidal; the suture of the spire whorls is bordered by a deep, narrow "U"-shaped channel; body whorl, spire whorls, and siphonal canal heavily ornamented with numerous strong spiral cords and ribs, which are better-developed on the siphonal canal; base shell color white, pale bluish-gray, or cream-yellow overlaid with 2 wide bands of dark reddish-brown patches, one above the shell mid-body and one below the shell mid-body; these wide band are, in turn, overlaid with numerous, closely-packed thin, dark reddish-brown longitudinal flammules and stripes, which extend onto the spire whorls; siphonal canal straight, relatively short, less than one-half the length of the body whorl; siphonal canal colored pale reddish-tan with a distinctive white tip; aperture wide and flaring, oval in shape, with the interior being heavily ornamented with numerous strong lirae and ribs, colored deep brown within; inner edge of lip and siphonal canal white with scattered small brown patches; protoconch pale tan, proportionally large, rounded, domelike, composed of one and one-half whorls; periostracum thick, light brown in color, with a velvet-like texture.

Discussion: Although most similar in overall shape, color, and size to the eastern Florida and southeastern United States *Fulguropsis rachelcarsonae*, *F. keysensis* differs in having much stronger spiral cord shell sculpture and in having a much more sharply-angled shoulder that is bounded by a distinct carina. Of the seven known *Fulguropsis* taxa, *F. keysensis* is the most highly ornate species, with a unique sculpture pattern made up of a pair of large, thick spiral cords with an intercollated smaller threadlike cord. This three-cord pattern repeats over and over again across the entire shell surface, creating a texture that is reminiscent of that seen on members of the family Ficidae.

Biogeographical Range: As shown on Map 13, *Fulguropsis keysensis* is confined to the Florida Keys and the Floridian Subprovince of the Carolinian Province, where it ranges from the Dry Tortugas to the southern Ten Thousand Islands and Cape Sable, to Key Largo and Elliott Key, and northward to near Dania Beach, Broward County, Florida.



Map 13. The biogeographical distribution of *Fulguropsis keysensis* is confined to the carbonate environments of southernmost Florida and the Florida Keys. There it ranges from Key Largo and Florida Bay, westward along the entire Florida Keys island chain to the Dry Tortugas, and northward along the Ten Thousand Islands.

Fulguropsis pyruloides (Say, 1822)
(Figures 7.8 - 7.11)

Synonymy:
Fulgur pyruloides Say, 1822
Busycotypus (Pyrofulgur) spiratus pyruloides (Say) Hollister, 1958
Busycon (Fulguropsis) spiratus pyruloides (Say) Abbott, 1974
Fulguropsis spiratus pyruloides (Say) Petuch, 2013
Fulguropsis pyruloides (Say) Petuch and Myers, 2014

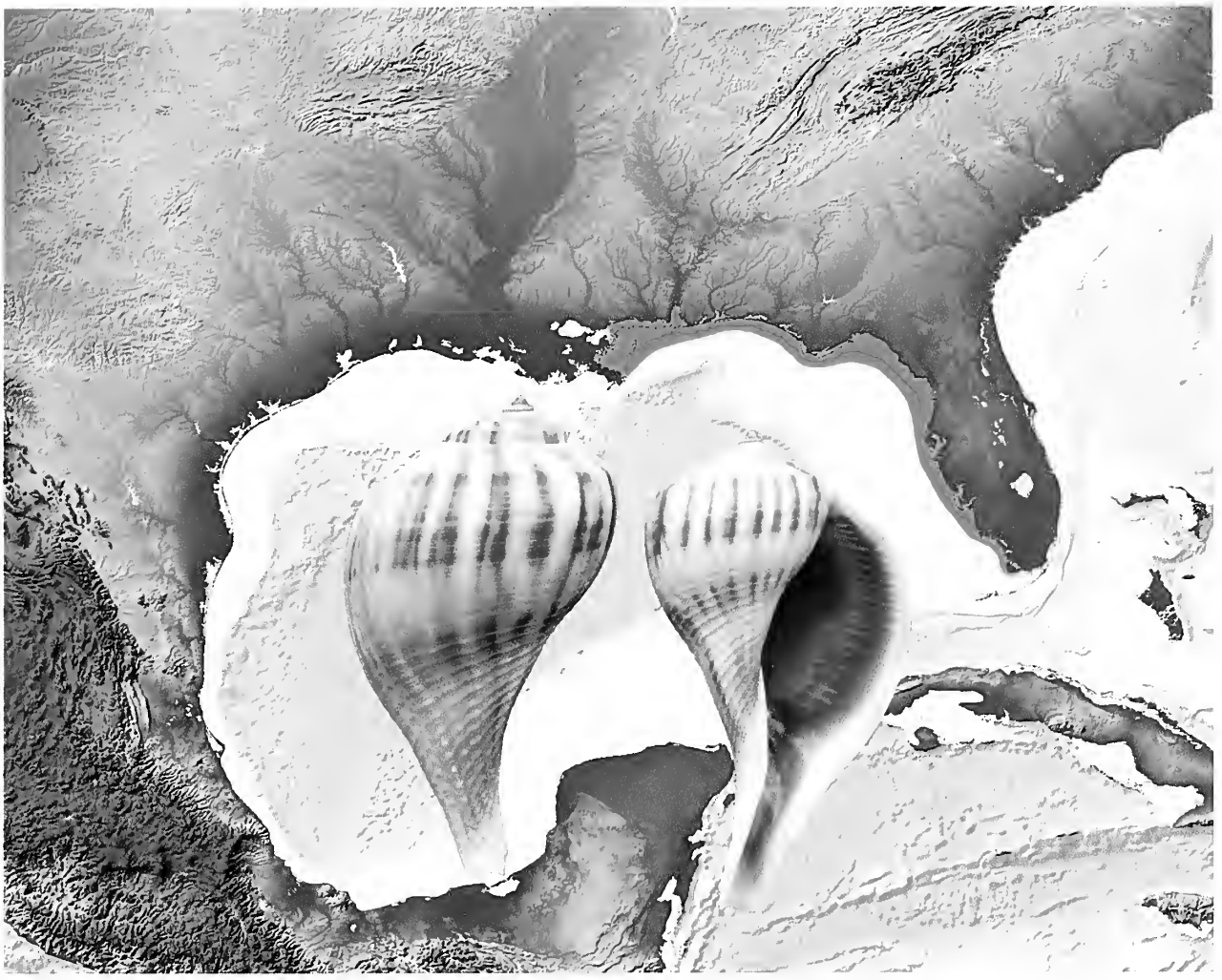
Description: Shell of average size for the genus, globose and inflated, distinctly pyriform, with rounded sides; spire proportionally low, subpyramidal; shoulder broadly rounded, with a faint angle and a wide, rounded carina on some individuals; spire whorls slightly sloping, bordered with a deep and narrow "U"-shaped channel along the suture; body whorl and spire whorls ornamented with very numerous, extremely fine, closely-packed spiral threads, giving the shell a

distinctive silky texture; siphonal canal proportionally short, straight, less than one-half the total length of the body whorl, ornamented with strong and prominent spiral cords; shell base color variable, ranging from pale bluish-gray to cream-white, to pale orange overlaid with 2 wide bands of reddish-brown patches and amorphous flammules, one above the shell mid-body and one below the shell mid-body; many specimens have a clear mid-body band that is devoid of any brown flammules or patches; siphonal canal light brown or bluish-purple, with a distinct white anterior tip; aperture wide and flaring, oval in shape, dark reddish-brown within the interior, and with numerous faint, poorly-developed lirae and cords; many individuals completely lack cords and; lirae within the aperture, having a smooth interior; protoconch pale tan or pale purple-gray, proportionally large and domelike, composed of one and one-half whorls; periostracum thick, light brown in color, with a velvet-like texture.

Discussion: As mentioned previously in this chapter, *Fulguropsis pyruloides* most closely resembles *F. rachelcarsonae*, and the two sibling species evolved from their common ancestor, *F. pyruloides pahayokee*, during the late Pleistocene. Gene flow between the two siblings was stopped during the Tarantian Age and their shell morphology has begun to diverge. Although similar in shell shape, size, and color pattern, the two allopatric species diverged primarily in relation to shell sculpture; with the Georgian Subprovince *F. rachelcarsonae* becoming much more heavily ornamented with strong spiral cords and with the Suwannean *F. pyruloides* retaining the smooth and silky shell texture of the ancestral *F. pyruloides pahayokee*.

Biogeographical Range: As shown on Map 14, *Fulguropsis pyruloides* is restricted to the Suwannean Subprovince of the Carolinian Province, ranging from the Ten Thousand Islands, Collier County, southwestern Florida, northward to the Florida Panhandle and the coasts of Alabama and Mississippi.

Fulguropsis keysensis and *Fulguropsis pyruloides* are sympatric species only in the southern portion of the Ten Thousand Islands where they can occasionally be found together on some of the outer islands.



Map 14. The biogeographical range of *Fulguropsis pyruloides* extends from the Ten Thousand Islands of Collier County, extreme southwestern Florida, northward along the entire western coast of Florida and the Florida Panhandle, to the coasts of Alabama and Mississippi. The species does not range westward of the Mississippi River Delta, which acts as a biogeographical and ecological barrier.

Iconography of Living and Fossil Pyriform *Fulguropsis* Species (*Fulguropsis spiratus* Species Complex)

The following sets of figures illustrate both typical specimens and variations of four *Fulguropsis* species; *F. spiratus*, *F. rachelcarsonae*, *F. keysensis*, and *F. pyruloides*. Besides the living *Fulguropsis* species, all of the named fossil taxa are also illustrated in the following iconography.

Figure 7.1 *Fulguropsis spiratus*, Typical Specimen.
A, B= *Fulguropsis spiratus* (Lamarck, 1816), length 64 mm, dredged by commercial shrimpers from 20 m depth on the Campeche Banks, off Progreso, Campeche State, Mexico. This is the type species of the genus *Fulguropsis*. (p.140)

Figure 7.2 *Fulguropsis rachelcarsonae* Holotype.
A, B= *Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species, **Holotype (LACM 3418)**, length 76 mm, trawled by a commercial scallop boat from 20 m depth, off Cape Canaveral, Brevard County, Florida. Note the prominent shell sculpture composed of strong spiral cords; this differs greatly from the smooth and silky-textured *Fulguropsis pyruloides* of western Florida. (p. 141)

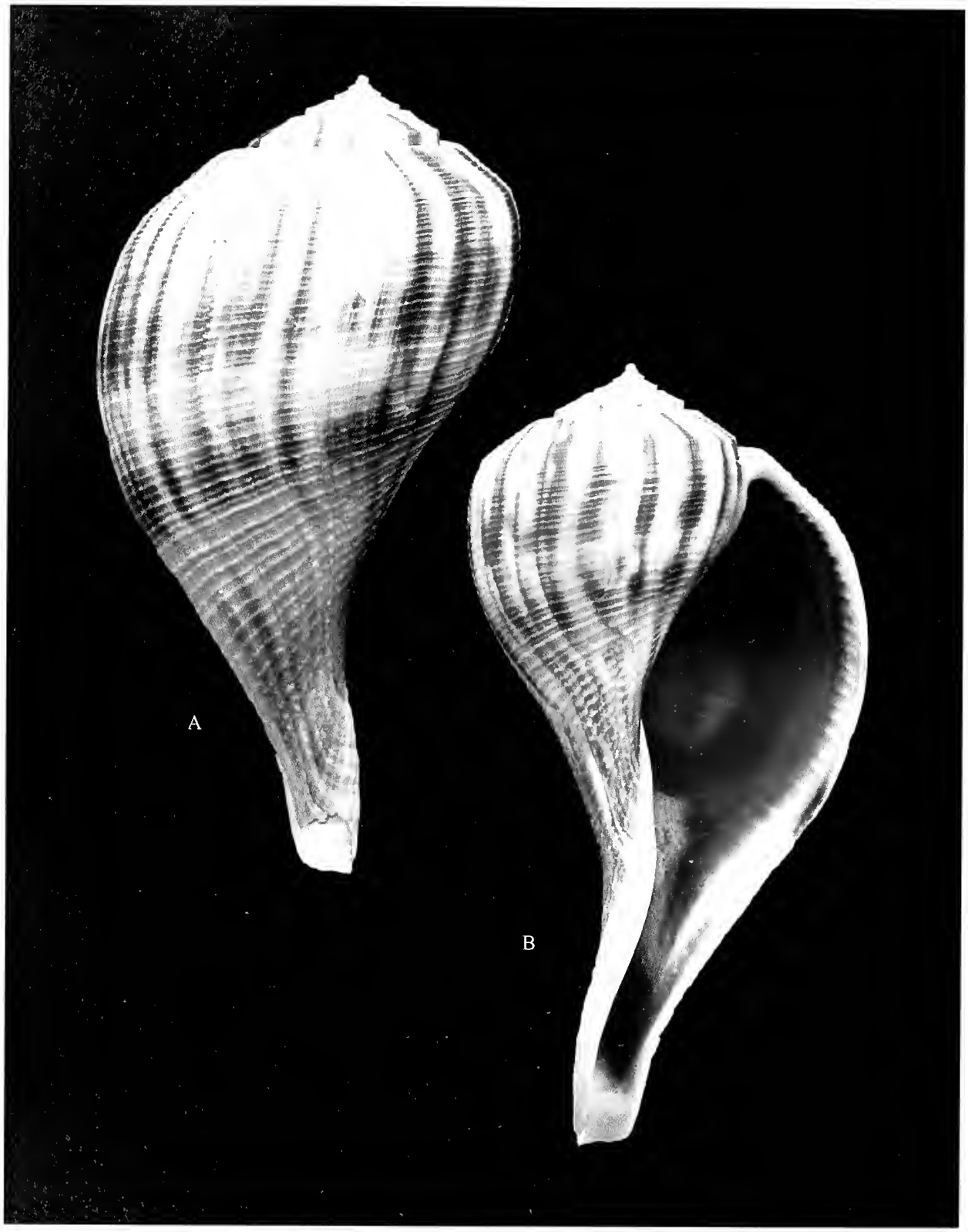


Figure 7.3 *Fulguropsis rachelcarsonae* new species.
A, B= *Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species, length 96 mm. Found in a Shoal Grass (*Halodule wrightii*) bed at low tide, off Pine Point, Singer Island, Lake Worth Lagoon, Palm Beach County, Florida. (p. 141)

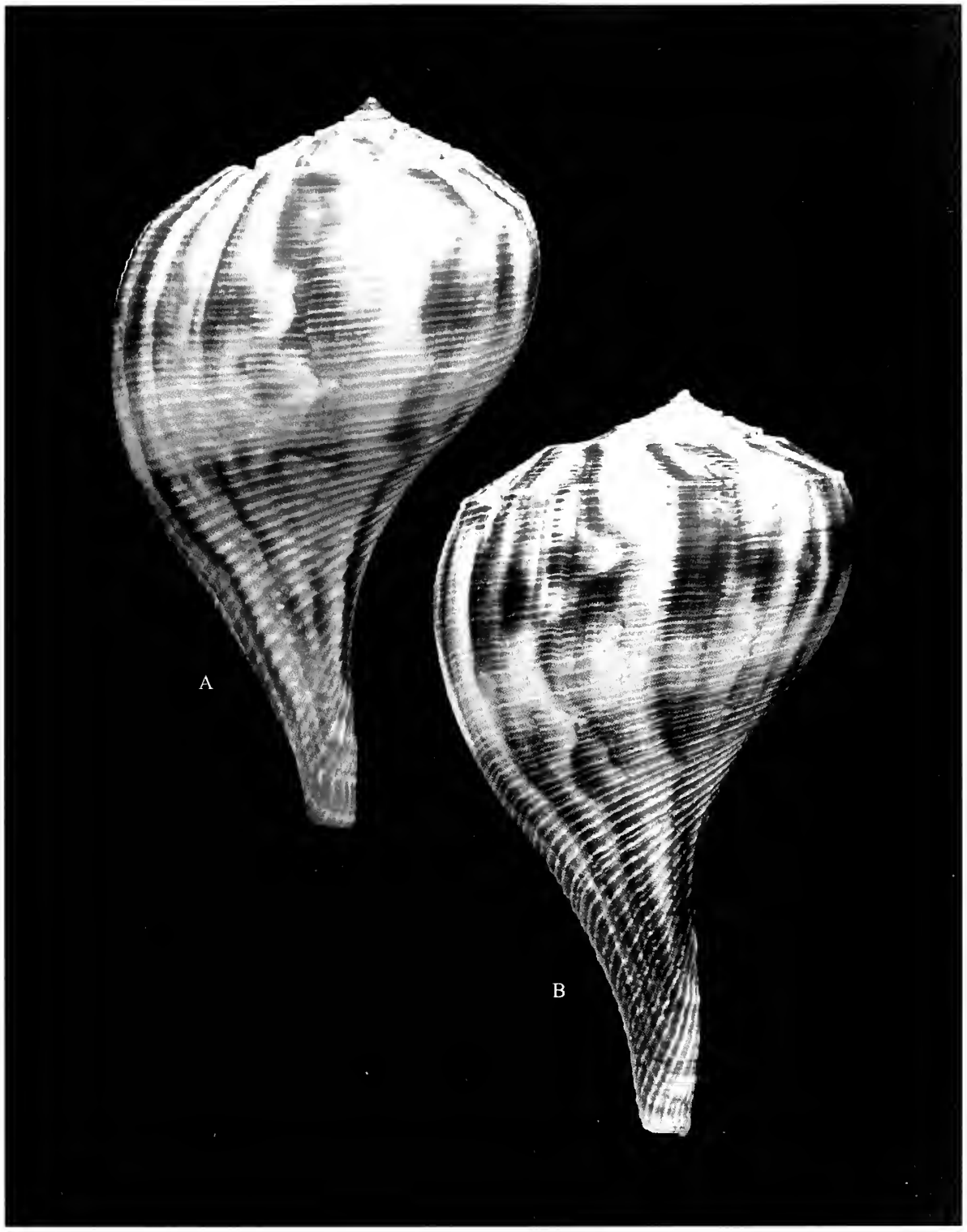


Figure 7.4 *Fulguropsis rachelcarsonae* Variants.
A= *Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species, length 75 mm. Globose and inflated variant.
B= *Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species, length 88 mm. Specimen with flattened spire and sharply-angled shoulder. Collected by Isabella Spiritoso.
Both of the specimens shown here were collected at low tide, in a Shoal Grass (*Halodule wrightii*) bed, off Pine Point, Singer Island, Lake Worth Lagoon, Palm Beach County, Florida. (p. 141)

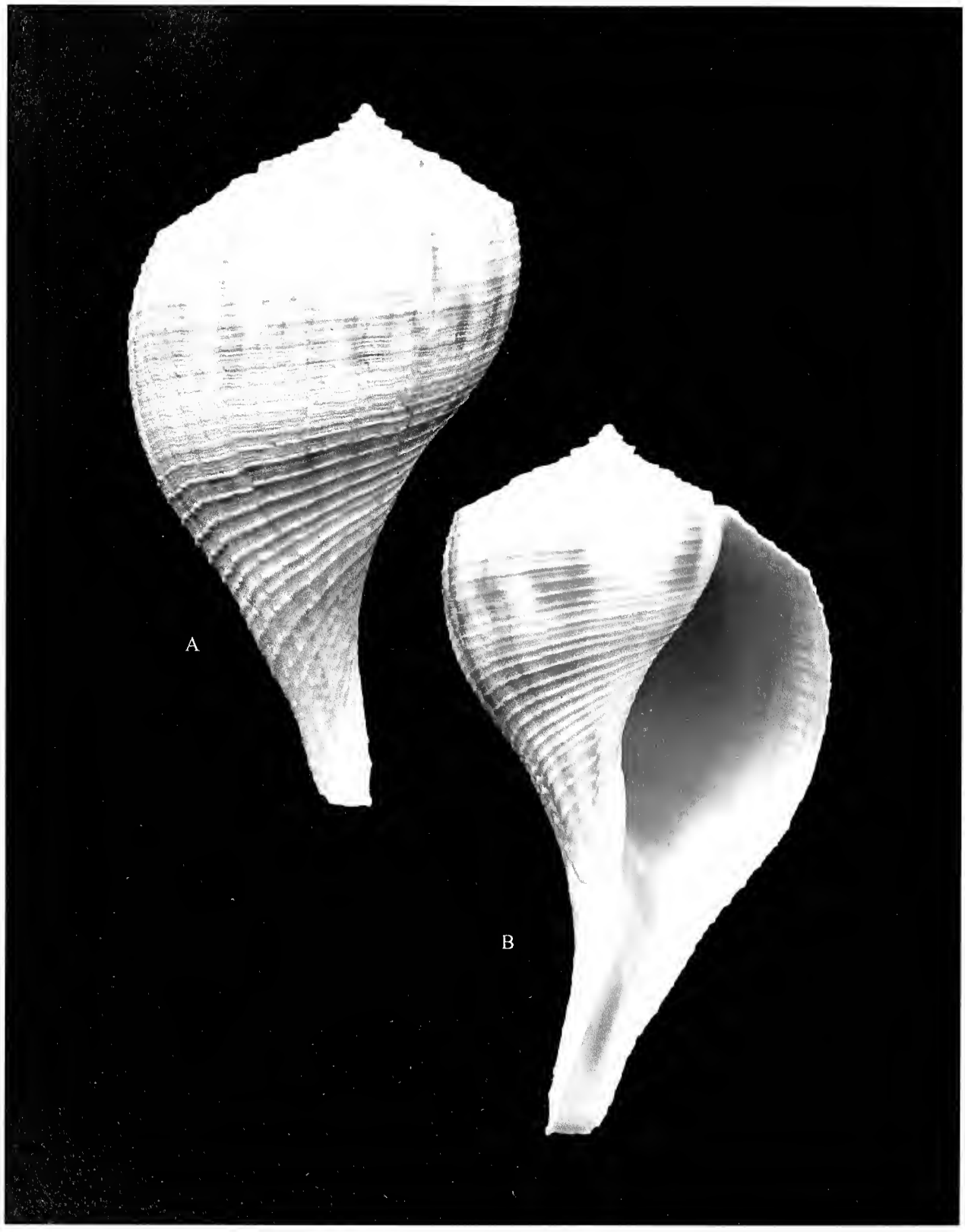


Figure 7.5 *Fulguropsis keysensis*, Typical Specimen.
A, B= *Fulguropsis keysensis* Petuch, 2013, length 87 mm; found in coarse carbonate sand near large sponge bioherms, 2 m depth, off Howe Key, Lower Florida Keys, Monroe County, Florida. Note the sharply-angled shoulder and prominent shell sculpture composed of strong, heavy spiral cords. (p. 144)

Figure 7.6 *Fulguropsis keysensis*, Typical Specimens.
A, B= *Fulguropsis keysensis* Petuch, 2013, length 68 mm; found in coarse carbonate sand near sponge bioherms, 2 m depth, off Middle Torch Key, Lower Florida Keys, Monroe County, Florida.
C, D= *Fulguropsis keysensis* Petuch, 2013, length 65 mm; found in a patch of coarse carbonate sand between large sponge bioherms, 2 m depth off No Name Key, Lower Florida Keys, Monroe County, Florida. (p. 144)

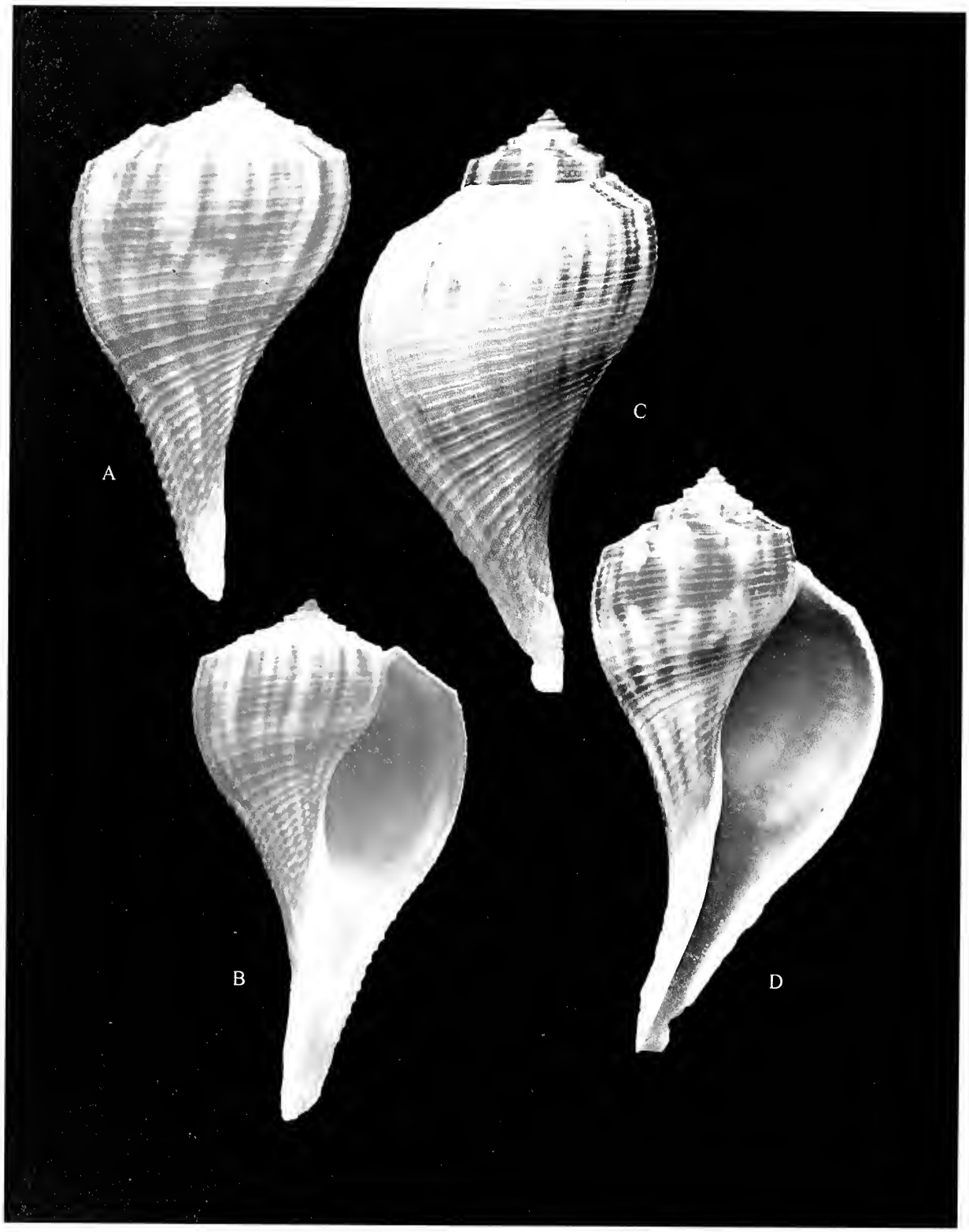


Figure 7.7 *Fulguropsis keysensis* Variants.
A, B= *Fulguropsis keysensis* Petuch, 2013, length 57 mm. Orange color variant found in coarse carbonate sand and Turtle Grass, 2 m depth, off Missouri Key, Middle Florida Keys, Monroe County, Florida.
C, D= *Fulguropsis keysensis* Petuch, 2013, length 82 mm. Elongated variant found in a sponge bioherm at low tide, on the vermetid worm shell reef complex off Demijohn Key, Ten Thousand Islands, Collier County, Florida. This is the farthest north that the species has been collected. (p. 144)

Figure 7.8 *Fulguropsis pyruloides*, Typical Specimen.
A, B= *Fulguropsis pyruloides* (Say, 1822), length 77 mm, found in a Shoal Grass bed at low tide, off Rabbit Key, Ten Thousand Islands, Collier County, Florida. Note the fine silky texture of the shell sculpture. (p. 145)

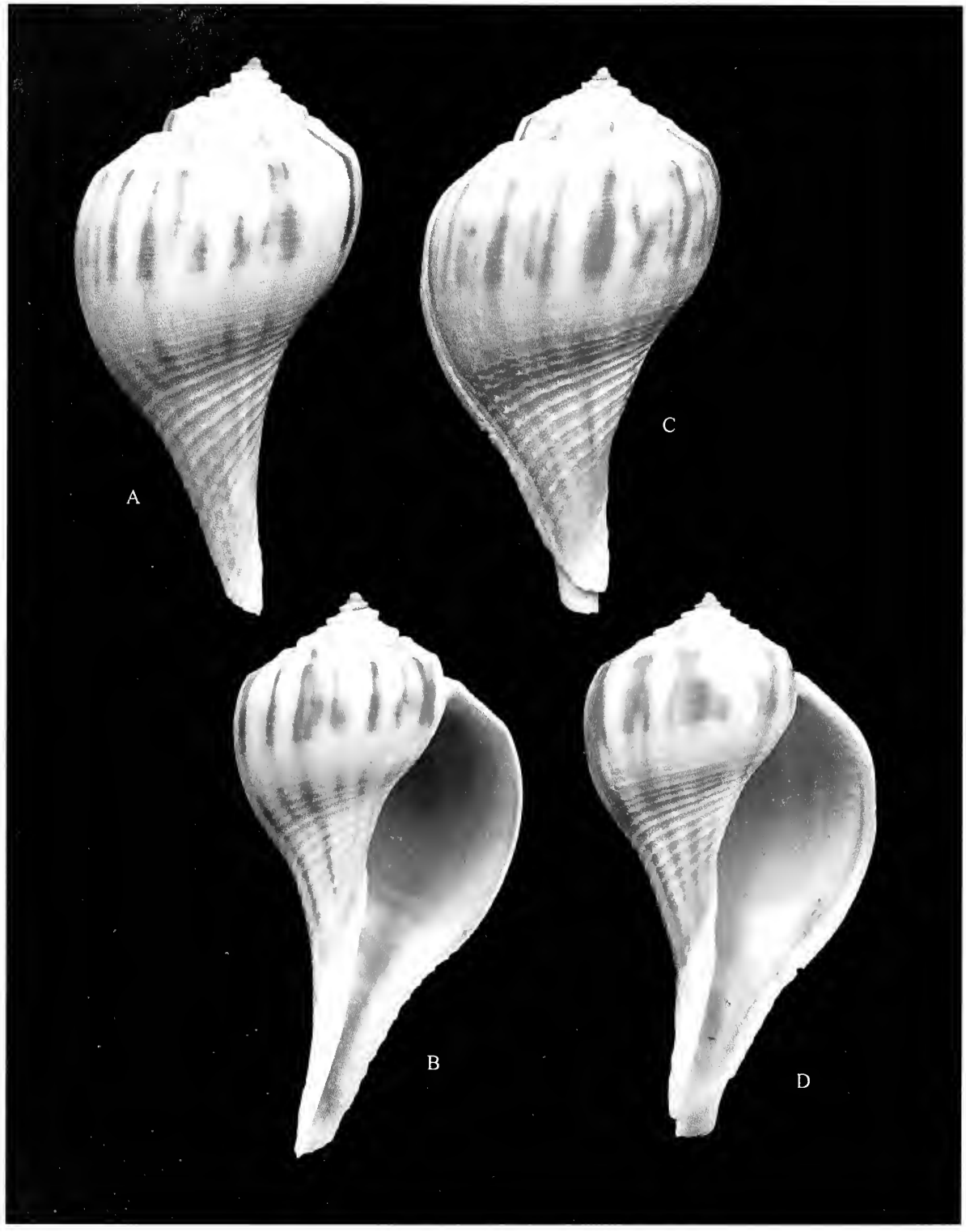


Figure 7.9 *Fulguropsis pyruloides* Pale Color Variants.
A, B= *Fulguropsis pyruloides* (Say, 1822), length 62 mm, found in clean quartz sand at low tide, St. Petersburg Beach, Pinellas County, Florida. Pale color variant, with a white base color and small, pale orange patches.
C, D= *Fulguropsis pyruloides* (Say, 1822), length 68 mm, found on clean quartz sand at low tide, Lumber Key, Ten Thousand Islands, Collier County, Florida. Pale color variant, with a white base color and small, pale orange patches. (p. 145)

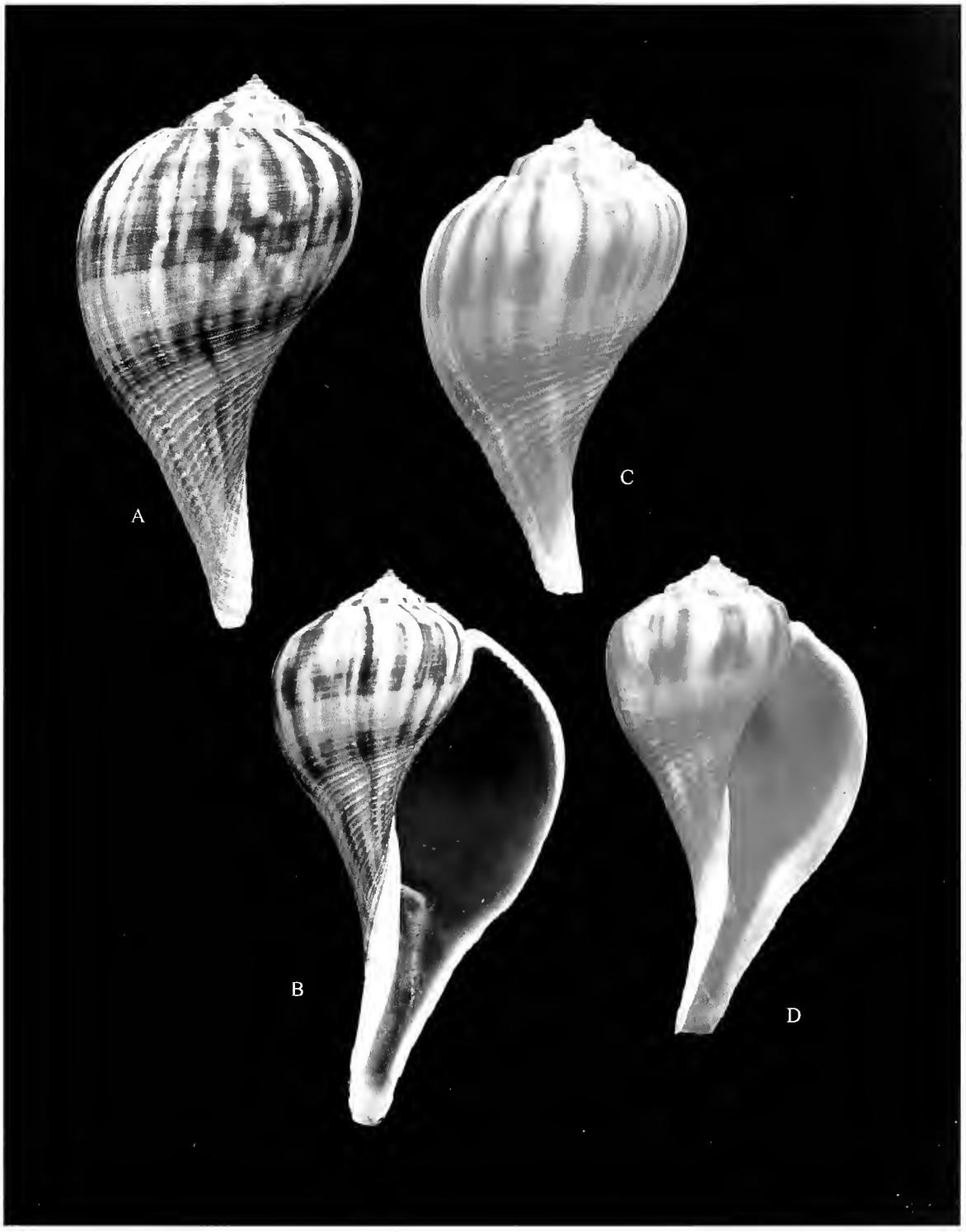


Figure 7.10 *Fulguropsis pyruloides* Color Variants.
A, B= *Fulguropsis pyruloides* (Say, 1822), length 113 mm, found at low tide on the vermetid worm shell reef off Rabbit Key, Ten Thousand Islands, Collier County, Florida. Large, dark-colored variant with a deep blue base color and numerous brown patches. (p. 145)
C, D= *Fulguropsis pyruloides* (Say, 1822), length 62 mm, found at low tide in clean quartz sand and worm shell fragments, at the edge of the lagoon along the southern side of Lumber Key, Ten Thousand Islands, Collier County, Florida (see Figure 2.5, Chapter 2). Rare orange-colored variant; note the intense orange color within the aperture.

Figure 7.11 *Fulguropsis pyruloides* Variants.
A, B= *Fulguropsis pyruloides* (Say, 1822), length 71 mm, found on a sand bar at low tide, off Pine Island, Pine Island Sound, Lee County, Florida. High-spired variant.
C= *Fulguropsis pyruloides* (Say, 1822), length 47 mm, found in a tide pool at low tide, on the vermetid worm shell reef complex off Rabbit Key, Ten Thousand Islands, Collier County, Florida. Flat-spired variant with an angled shoulder. (p. 145)

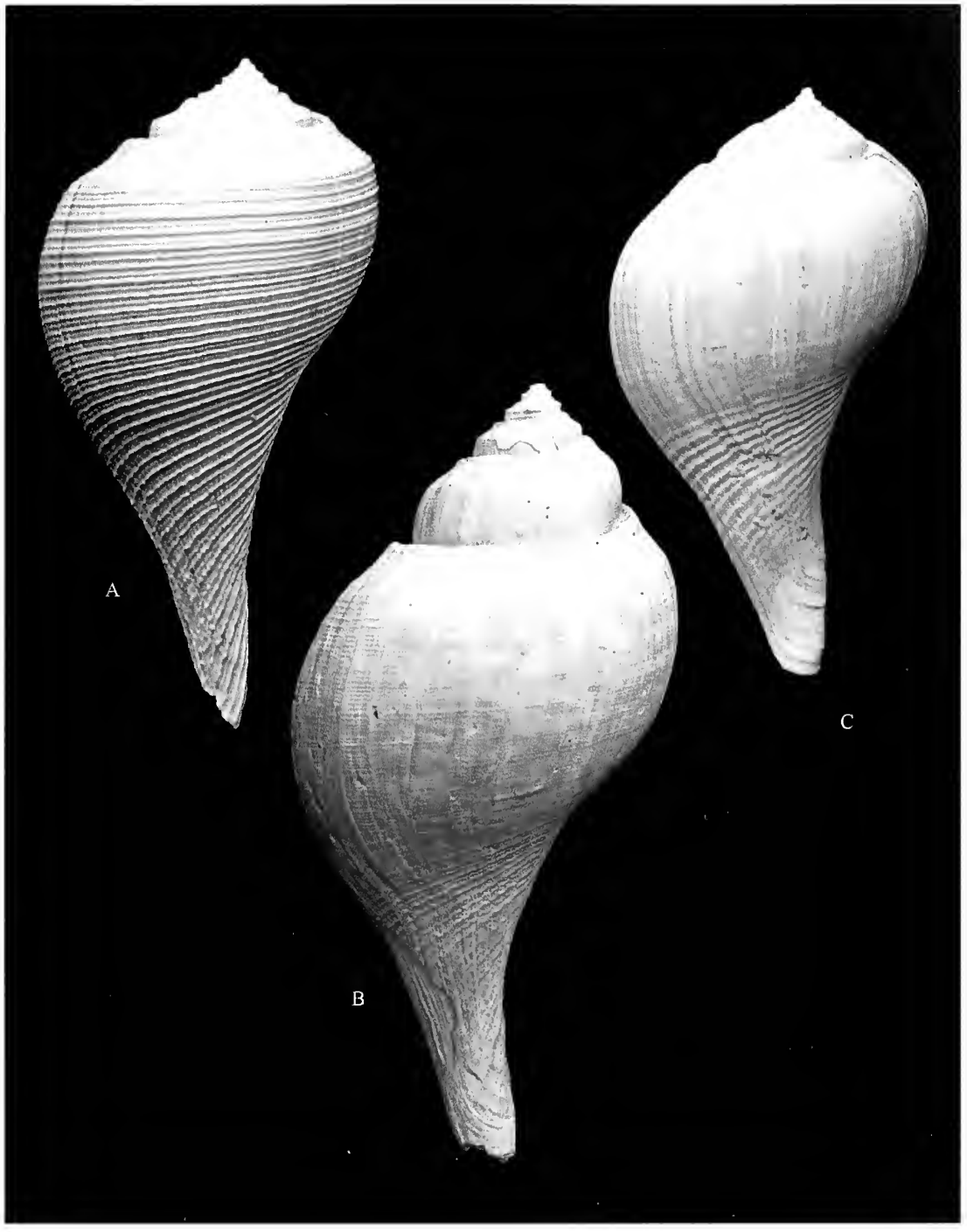


Figure 7.12 Fossil Species in the *Fulguropsis spiratus* Complex.
A= *Fulguropsis radula* Petuch, 1994, length 87 mm, from the fossil coral reef excavations in the Florida Rock Industries Naples Mine (old Mule Pen Quarry), East Naples, Collier County, Florida. Golden Gate Member of the Tamiami Formation; Piacenzian Age of the Pliocene.
B= *Fulguropsis elongatus* (Gill, 1867), length 118 mm, from the Miami Canal excavation south of Lake Harbor, Palm Beach County, Florida. Bee Branch Member of the Caloosahatchee Formation; late Gelasian Age, early Pleistocene.
C= *Fulguropsis evergladesensis* Petuch, 1994, length 60 mm, from the North New River Canal excavation, south of South Bay, Palm Beach County, Florida. Belle Glade Member of the Bermont Formation; Ionian Age of the Pleistocene.

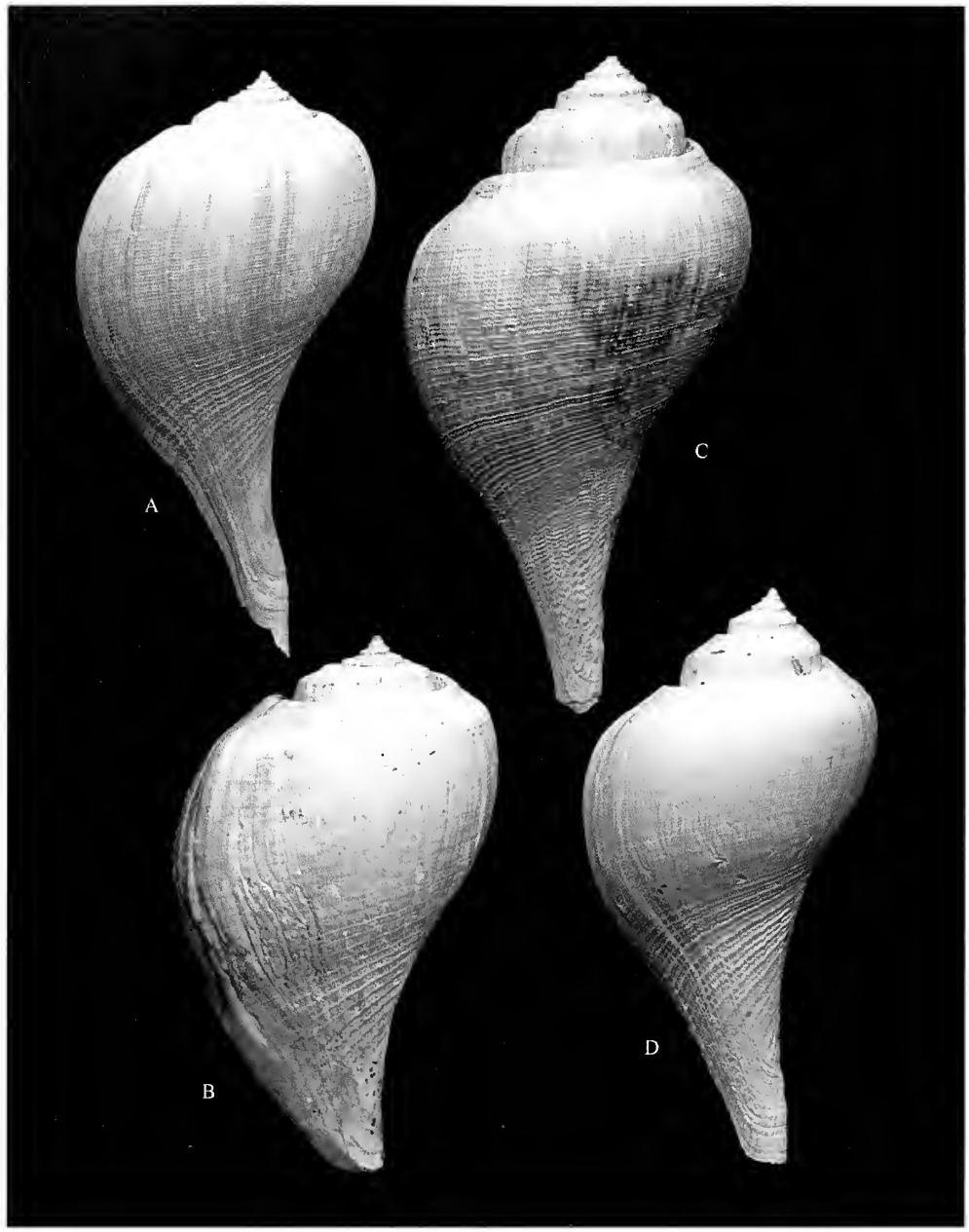


Figure 7.13 Fossil Species in the *Fulguropsis spiratus* Complex.
A= *Fulguropsis floridanum* (Olsson and Harbison, 1953), length 112 mm, from the Miami Canal excavation south of Lake Harbor, Palm Beach County, Florida. Fort Denaud Member of the Caloosahatchee Formation; Gelasian Age, early Pleistocene.
B= *Fulguropsis pyriformis* (Conrad, 1867), length 76 mm, from the upper fossiliferous beds in the Lee Creek Mine, Aurora, Beaufort County, North Carolina. Edenhouse Member, Chowan River Formation, late Piacenzian Age, Pliocene.
C= *Fulguropsis griffini* Petuch, 1994, length 93 mm, collected in the middle shell beds, Bergeron Star Pit, south of South Bay, Palm Beach County, Florida. Ayers Landing Member of the Caloosahatchee Formation, late Gelasian Age of the early Pleistocene.
D= *Fulguropsis pyruloides pahayokee* Petuch, 1994, length 88 mm, found in the upper shell beds of Palm Beach Aggregates Pit #6, Loxahatchee, Palm Beach County, Florida. Okaloacoochee Member of the Fort Thompson Formation, Tarantian Age of the late Pleistocene. This fossil subspecies is the common ancestor of the living western Florida *Fulguropsis pyruloides* and the eastern Florida *Fulguropsis rachelcarsonae*.

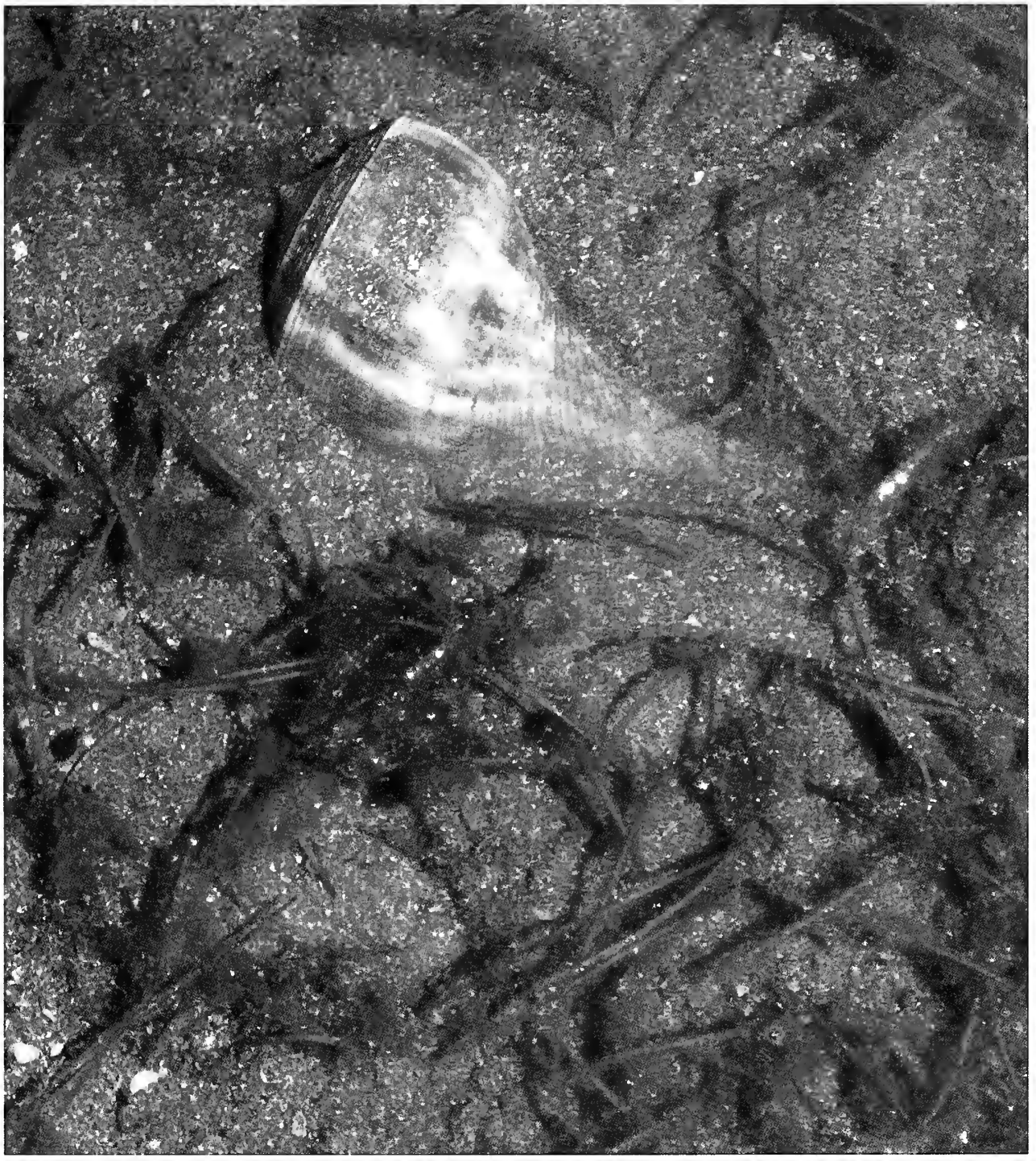


Figure 7.14 Living specimen of a *Fulguropsis rachelcarsonae*.
This shell, from a Shoal Grass bed in the Lake Worth Lagoon off Pine Point, Singer Island, differs from typical specimens of *Fulguropsis rachelcarsonae* in having a flatter spire and a much more sharply-angled shoulder.

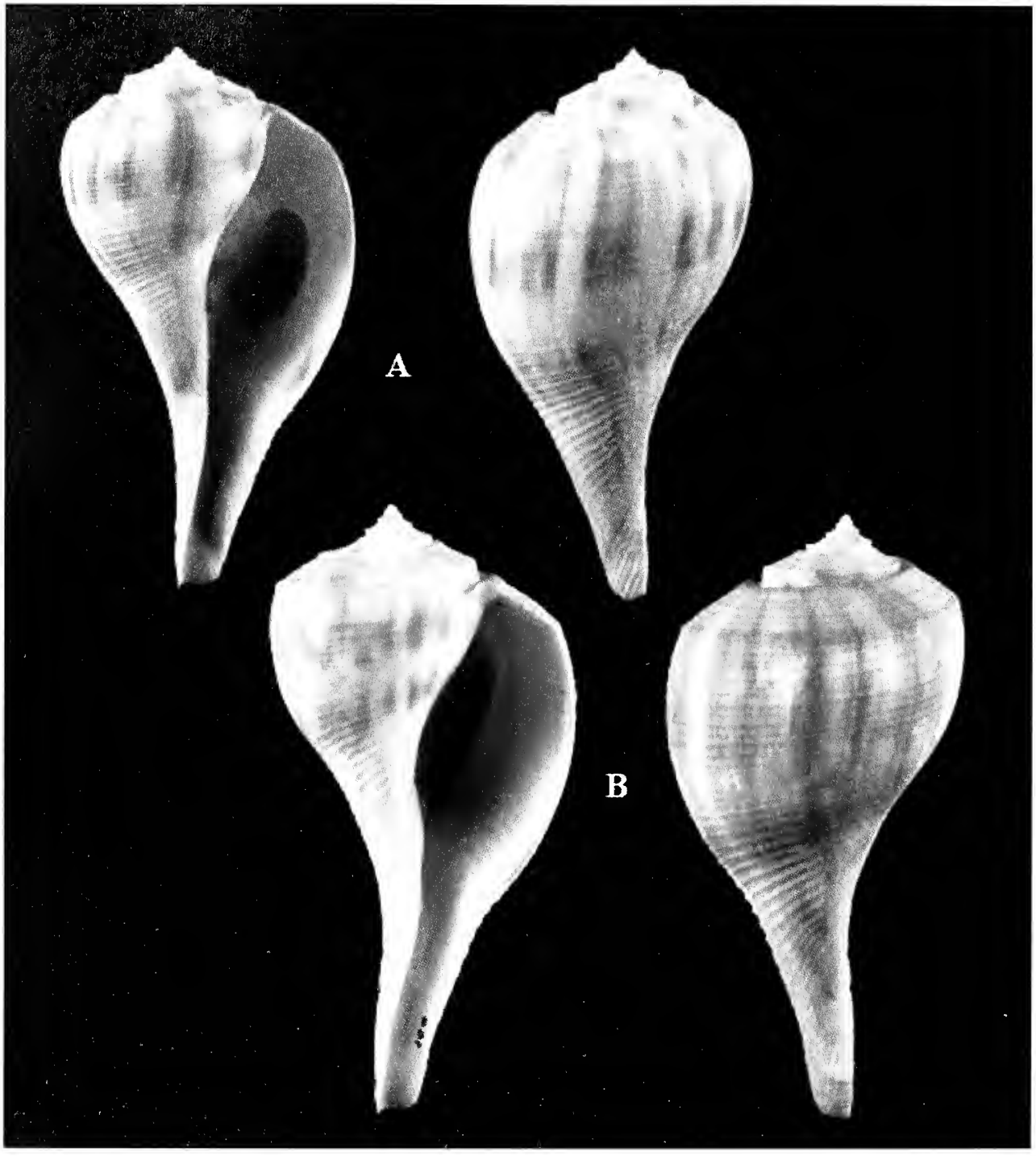


Figure 7.15 Comparison between two specimens of *Fulguropsis pyruloides* and *F. rachelcarsonae*
A= *Fulguropsis pyruloides* (Say, 1822), 67.6mm collected at Panama City, Bay County, Florida. Specimen from the Berschauer Collection. (*see* p. 145)
B= *Fulguropsis rachelcarsonae* Petuch, Myers, and Berschauer, new species, 72.1mm collected in Jupiter Island, Martin County, Florida. Specimen from the Berschauer Collection. Note the prominent shell sculpture composed of strong spiral cords; this differs greatly from the smooth and silky-textured *Fulguropsis pyruloides* of western Florida. (*see* p. 141)

CHAPTER EIGHT

The Keeled Pear Whelks: *Fulguropsis plagosus* Species Complex

The two species and one subspecies that belong to this group of elongated, vase-shaped Pear Whelks all have a sharply-angled shoulder and a prominent shoulder carina. Because of these distinctive characters, they are referred to as the "Keeled Pear Whelks" and are easily differentiated from the more round-shouldered and pyriform species of the *Fulguropsis spiratus* complex. Unlike the members of that group, which are found throughout the entire Carolinian Province, the Keeled Pear Whelks of the *Fulguropsis plagosus* species complex are confined to the northern, western, and southern Gulf of Mexico. Besides having a well-developed shoulder carina, members of this species group all have deeper and more pronounced sutural channels than do the Pear Whelks of the *Fulguropsis spiratus* complex. In cross section, these sutural channels have straight sides and a flat base and resemble miniature versions of the channels seen in the genus *Busycotypus*. Because of this distinctive channel shape, Hollister (1958: 95-99) placed *Fulguropsis plagosus* in the genus *Busycotypus (Busycotypus)*, along with *B. canaliculatus*, and considered it to be distinct from members of his subgenus *Pyrofulgur* (=*Fulguropsis*).

Along the Florida Panhandle, Alabama, Mississippi, southern Texas, and the western Campeche Banks, the ranges of the *Fulguropsis plagosus* and *Fulguropsis spiratus* complexes overlap, but they are generally not sympatric and are bathymetrically separated. Along northwestern Florida and Alabama, *F. plagosus* lives in deeper, offshore waters while *F. pyruloides* is found in intertidal depths. A similar pattern is seen along the western Campeche Banks off the Yucatan Peninsula, where *F. texanus* and *F. plagosus* live in offshore environments and *F. spiratus* lives in shallower near-shore environments. A flat-spired and highly-carinated *Fulguropsis* has also been dredged from deep water north of the Dry Tortugas and this shell may represent either a previously-unknown southern population of *F. plagosus* or a new subspecies. The living Keeled Pear Whelks are discussed here and illustrated, along with the known fossil species, in the iconography at the end of this chapter.

Family Busyconidae
Subfamily Busycotypinae
Genus *Fulguropsis* Marks, 1950

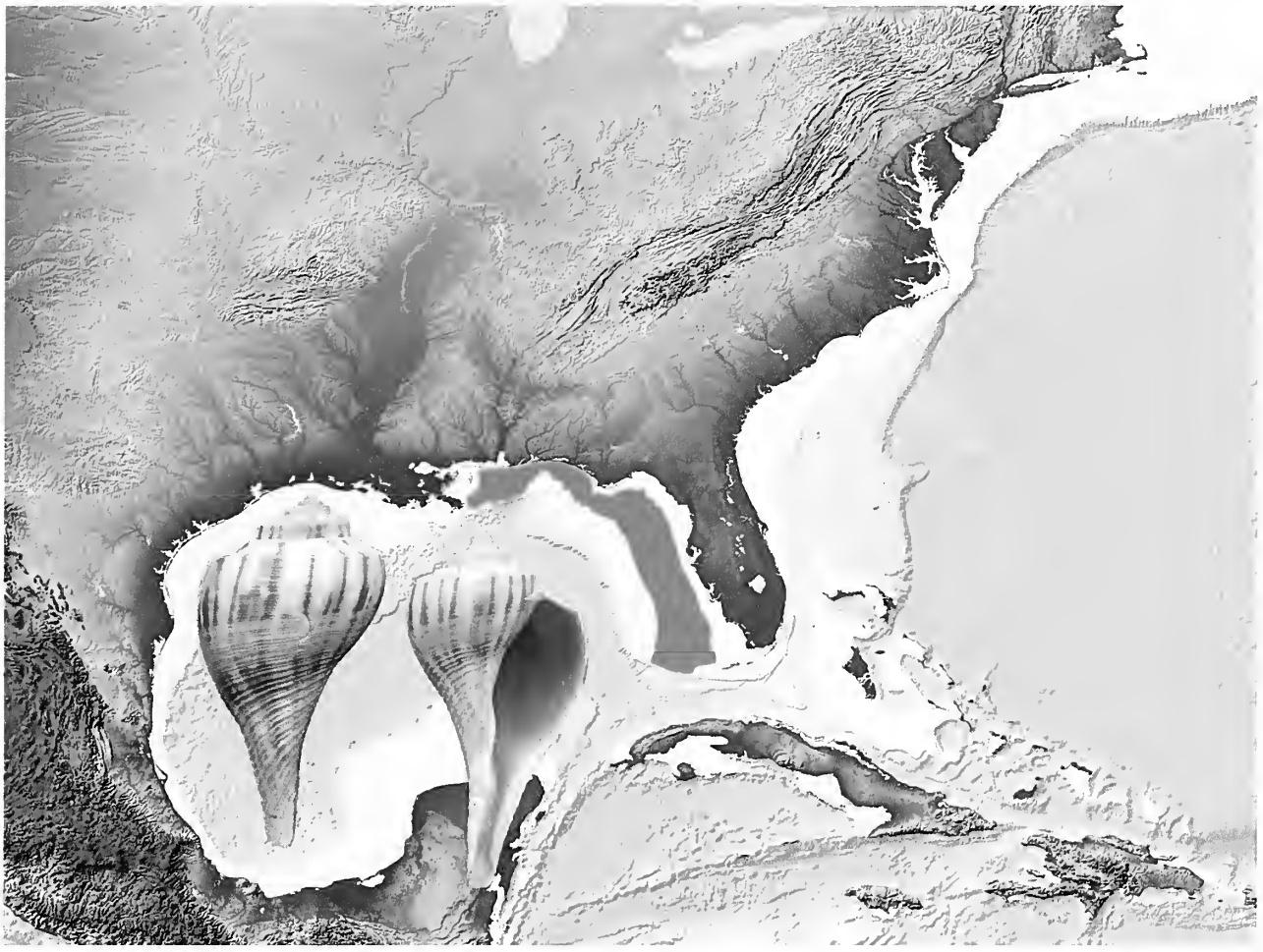
***Fulguropsis plagosus* (Conrad, 1863)**
(Figures 8.1 and 8.2)

Synonymy:
Busycon plagosum Conrad, 1863
Busycotypus (Busycotypus) plagosus (Conrad) Hollister, 1958
Busycon (Fulguropsis) spiratum plagosum (Conrad) Abbott, 1974
Busycotypus plagosus (Conrad) Tunnell, *et al.*, 2010
Fulguropsis plagosus (Conrad) Petuch, 2013

Description: Shell thin and inflated, distinctly vase-shaped, with a wide, broad shoulder and only slightly rounded sides; shoulder sharply-angled, with a large prominent shoulder carina; spire low, scalariform, distinctly stepped; spire whorls flattened, only slightly sloping; suture bordered by a proportionally wide and deep channel, which has straight sides and a flat base; the squared-off channel base is most pronounced on the early whorls; body whorl and spire whorls sculptured with very numerous, extremely fine spiral threads, giving the shella silky texture; siphonal canal tapering directly from body whorl, without an obvious constriction, roughly equal in length to the body whorl, ornamented with numerous strong and prominent spiral cords; shell base color white or yellow-white, overlaid with 2 wide bands of large, reddish-brown rectangular patches, one above the shell mid-body and one below the shell mid-body; spiral bands overlaid with numerous closely-packed reddish-brown thin longitudinal lines and flammules; spire whorls marked with thin, evenly-spaced reddish-brown flammules arranged in a radial pattern; siphonal canal pale reddish-orange with a distinct white anterior tip; aperture wide and flaring, oval shaped, with small, poorly-developed cords, dark reddish-brown within the interior; protoconch composed of one and one-half whorls, rounded, domelike, white or pale tan in color; periostracum thick and fuzzy, with a velvet-like texture.

Discussion: Because of its preference for deeper water, offshore environments, *Fulguropsis plagosus* is rarely seen in shell collections, with most specimens having been found washed up on beaches after storms. The species seems to be most common in the area extending from Apalachicola, Florida to Mobile Bay, Alabama and Biloxi, Mississippi, where it is frequently taken by commercial shrimpers working at 20-30 m depths.

Biogeographical Range: As shown on Map 15, *Fulguropsis plagosus* is found from the Mississippi River Delta, westward along the Florida Panhandle, and southward off western Florida as far as the Dry Tortugas. It is an offshore species and frequently taken by commercial shrimpers working at 20-30 m depths.



Map 15. The biogeographical range of *Fulguropsis plagosus* extends from the Mississippi River Delta, westward along the Florida Panhandle, and southward off western Florida as far as the Dry Tortugas.

Fulguropsis plagosus galvestonensis (Hollister, 1958) (Figures 8.3 and 8.4)

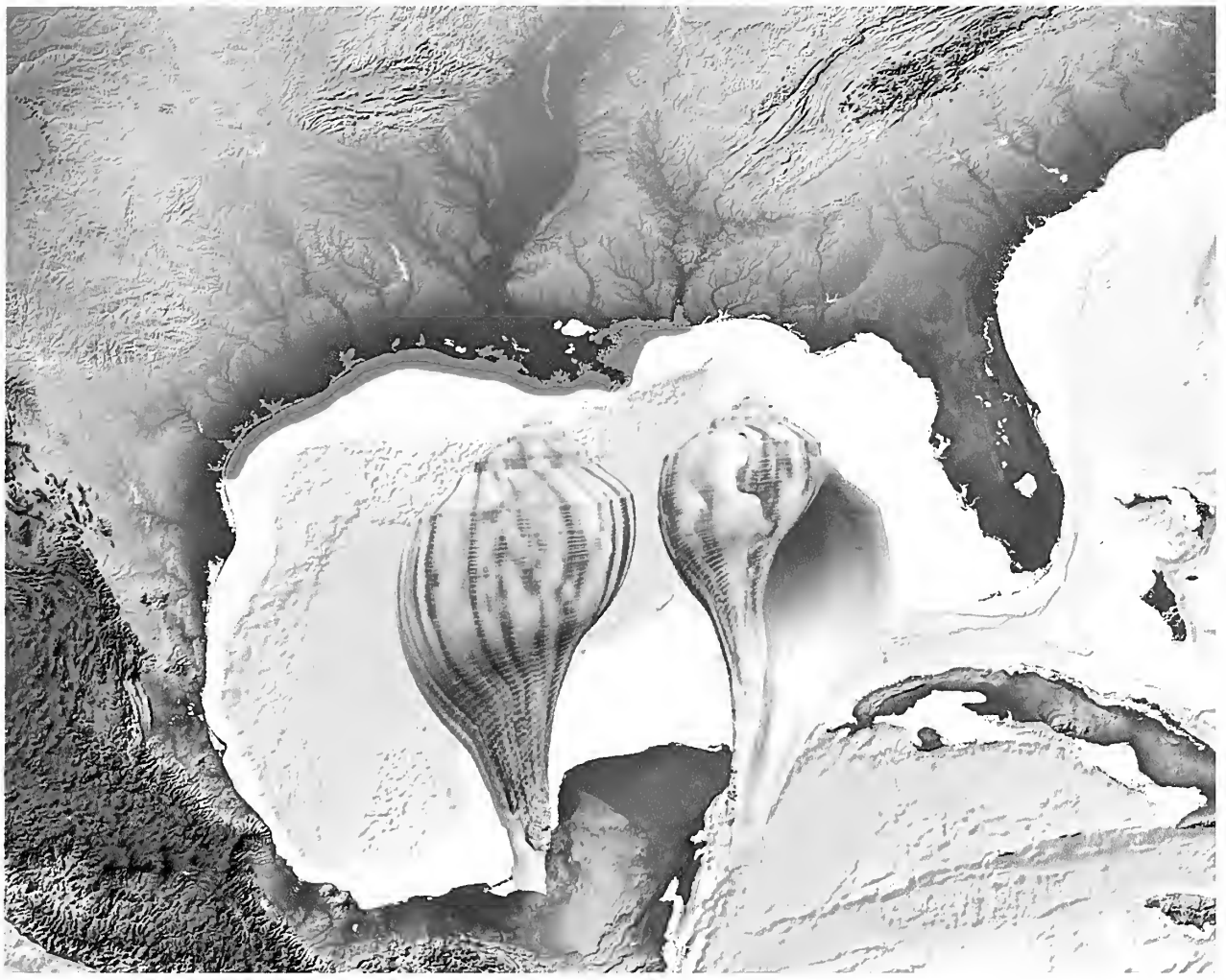
Synonymy:
Busycotypus (Busycotypus) plagosus galvestonensis Hollister, 1958
Busycon (Fulguropsis) spiratum plagosum (Conrad) "minor colonial variant", Abbott, 1974
Fulguropsis plagosus galvestonense (Hollister) Petuch, 2013

Description: Shell very elongated and vase-shaped, proportionally narrow, with only slightly rounded sides; shoulder very sharply-angled, bordered with a very large, prominent, thick carina; spire high and pyramidal, with slightly stepped whorls; spire whorls and subsutural areas distinctly sloping; suture bordered by a deep and proportionally wide channel which has straight sides and a flat base; body whorl, spire whorls, and siphonal canal ornamented with numerous fine spiral cords and threads, with the cords on the siphonal canal being larger and coarser; shell base color yellow-white, overlaid with numerous, closely-packed reddish-brown longitudinal flammules, often arranged in a zebra stripe-like pattern, which are sometimes arranged in 2 wide bands, one above the shell mid-body and one below-the shell mid-body; the siphonal canal is long and straight and grades directly into the body whorl without a distinct constriction, and is

bands, one above the shell mid-body and one below-the shell mid-body; the siphonal canal is long and straight and grades directly into the body whorl without a distinct constriction, and is roughly equal in length to the body whorl; the spire whorls are marked with evenly-spaced thin reddish-brown flammules arranged in a radial pattern; the aperture is wide and flaring, distinctly oval in shape, with numerous weak cords and ribs, pure white within the interior; protoconch yellow-white, composed of 2 rounded and domelike whorls; periostracum thick, light brown in color, with a velvet-like texture.

Discussion: Although generally considered to be a subspecies of the widespread *Fulguropsis plagosus*, this unusual northwestern Gulf of Mexico whelk may eventually prove to be a full species all to itself. *Fulguropsis plagosus galvestonensis* (named for Galveston, Texas) differs from the nominate subspecies in several major ways: in being consistently a much larger and more elongated shell; in having a higher, less stepped, and more pyramidal spire; in having distinctly more sloping spire whorls; in having a proportionally smaller and shallower sutural channel; and a coarser body whorl and spire whorl sculpture, giving the shell a rougher texture. To date, no intergrades in shell form and sculpture are known between true *F. plagosus* (as shown here) and *F. plagosus galvestonensis*. Although this distinctive subspecies lives just offshore and is rarely collected, it occasionally washes ashore during strong storms. While the nominate subspecies prefers cleaner sand sea floors in deeper water, the subspecies *galvestonensis* prefers muddy substrates in shallower areas all along the Mississippi River Delta.

Biogeographical Range: As shown on Map 16, *Fulguropsis plagosus galvestonensis* ranges from Mobile Bay, Alabama and the Mississippi River Delta westward to near Galveston, Texas and appears to be most common in the Bolivar Peninsula and Sabine Pass areas. This unusual Keeled Pear Whelk has the smallest geographical distribution of all the *Fulguropsis* species. Throughout its range, *F. plagosus galvestonensis* is found in much shallower water than typical *F. plagosus plagosus*, where it occurs on organic-rich mud substrates in deltaic and lagoonal areas.



Map 16. The biogeographical range of *Fulguropsis plagosus galvestonensis* extends from Mobile Bay, Alabama and the Mississippi River Delta westward to near Galveston, Texas. This subspecies of *Fulguropsis plagosus* prefers much shallower depths than does the nominate subspecies, being found from intertidal areas to depths of 5 to 10 m.

Fulguropsis texanus (Hollister, 1958)
(Figures 8.5 and 8.6)

Synonymy:
Busycotypus (Busycotypus) plagosus texanus Hollister, 1958
Busycon (Fulguropsis) spiratum plagosum (Conrad) "minor colonial variant", Abbott, 1974
Fulguropsis plagosus texanum (Hollister) Petuch, 2013

Description: Shell very elongated, protracted, narrow, and vase-shaped, with proportionally straight sides; shoulder sharply-angled, ornamented with a small but prominent, carina; spire high and pyramidal, with slightly stepped whorls; spire whorls and subsutural areas distinctly and sharply sloping; suture bordered by a deep and proportionally wide channel which has straight sides and a flat base; body whorl, spire whorls, and siphonal canal ornamented with numerous strong spiral cords and ribs, creating a rough shell texture; the cords on the siphonal

canal are larger and coarser; shell base color white, overlaid with numerous, closely-packed reddish-brown longitudinal lines and flammules, arranged in a zebra stripe-like pattern; a wide band of a fainter color is present around the mid-body of the shell; the siphonal canal is long and straight and grades directly into the body whorl without a distinct constriction, and is roughly equal in length to the body whorl; the spire whorls are marked with evenly-spaced thin reddish-brown flammules arranged in a radial pattern; the aperture is wide and flaring, distinctly oval in shape, with numerous strong cords and lirae, pure white within the interior; protoconch white, composed of 2 rounded and dome-like whorls; periostracum thick, light brown in color, with a velvet-like texture.

Discussion: Although originally described as a subspecies of *Fulguropsis plagosus*, this distinctive and beautiful whelk is here considered to be a full species that is endemic to the western Gulf of Mexico. Of the *Fulguropsis* species known from that area, *F. texanus* is most similar to *F. plagosus galvestonensis*, especially in overall shape, but differs in being a larger and less inflated shell, in having a lower and less stepped spire, in being a far more ornamented shell with a sculpture pattern composed of large spiral cords and ribs, and in having stronger and more numerous lirae within the aperture. *Fulguropsis texanus* differs greatly from the widespread *F. plagosus*, primarily in being a much larger shell, in having a lower spire with almost no scalariformation, in having more distinctly sloping spire whorls, and in being a much more sculptured shell, having numerous strong and prominent spiral cords covering the spire and body whorl.

Biogeographical Range: As shown on Map 17, *Fulguropsis texanus* has a wide range along the western Gulf of Mexico, extending from Mobile Bay, Alabama and the eastern side of the Mississippi River Delta westward along the entire coast of Texas, and the Yucatan Peninsula as far as the western side of the Campeche Banks.

Map 17. The biogeographical range of *Fulguropsis texanus* extends from Mobile Bay, Alabama and the eastern side of the Mississippi River Delta, westward along the entire coast of Texas, and the Campeche Bank off the Yucatan Peninsula, Mexico.

Iconography of Living and Fossil Keeled *Fulguropsis* Species (*Fulguropsis plagosus* Species Complex)

The following sets of figures illustrate both typical specimens and variations of the three members of the *Fulguropsis plagosus* species complex. Besides the living *Fulguropsis* species, all of the named fossil taxa are also illustrated in the following iconography.

Figure 8.1 *Fulguropsis plagosus* Typical Specimen.
A, B= *Fulguropsis plagosus* (Conrad, 1863), length 72 mm, trawled by commercial shrimpers, from 25 m depth off Biloxi, Harrison County, Mississippi. This specimen is very similar to the lectotype that is deposited in the Academy of Natural Sciences of Philadelphia. (p. 163)

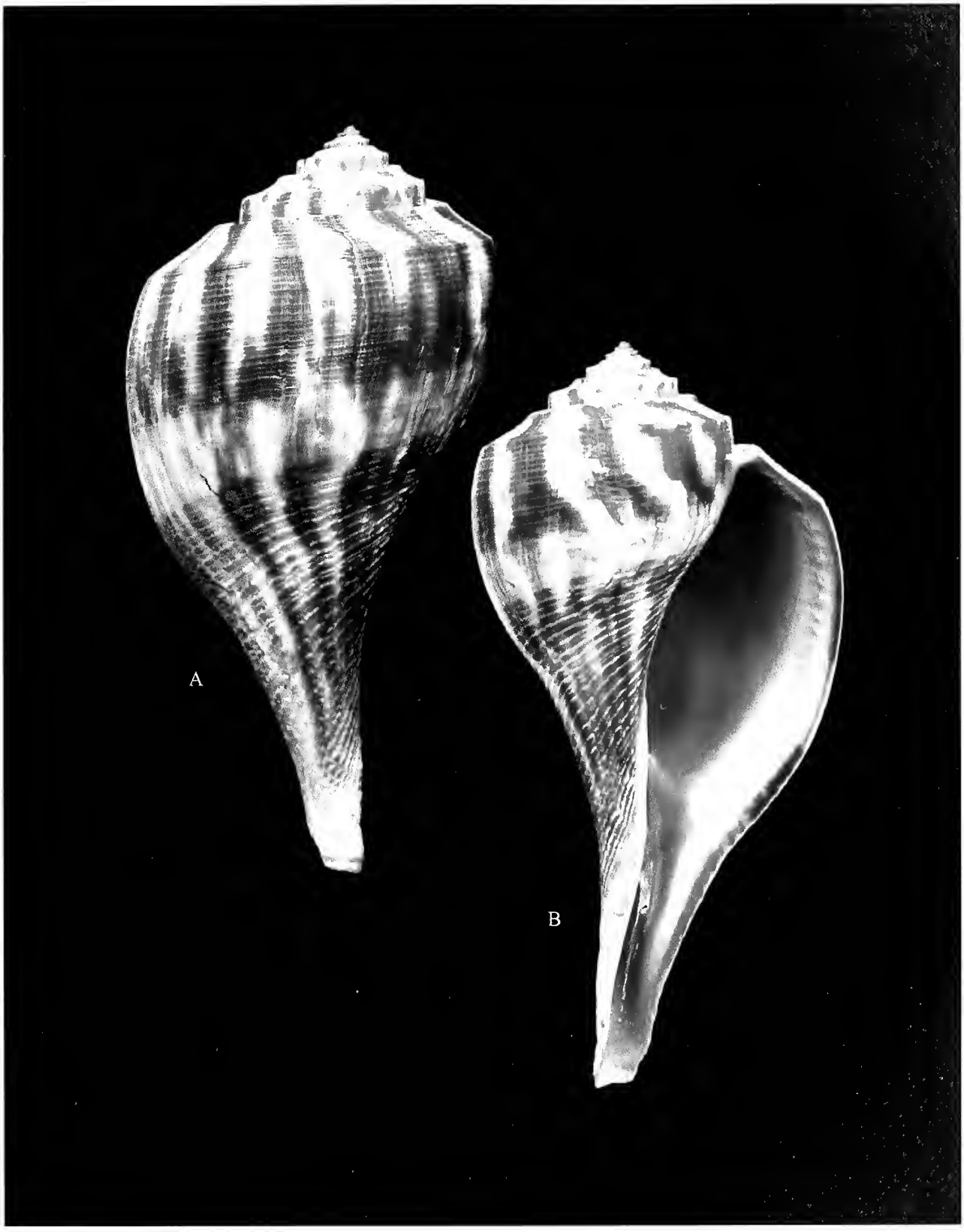


Figure 8.2 *Fulguropsis plagosus* Dark-Colored Variant
A, B= *Fulguropsis plagosus* (Conrad, 1863), length 104 mm, found dead with hermit crab, 20 m depth off Bald Point, Ochlockonee Bay, Franklin County, Florida. (p. 163)

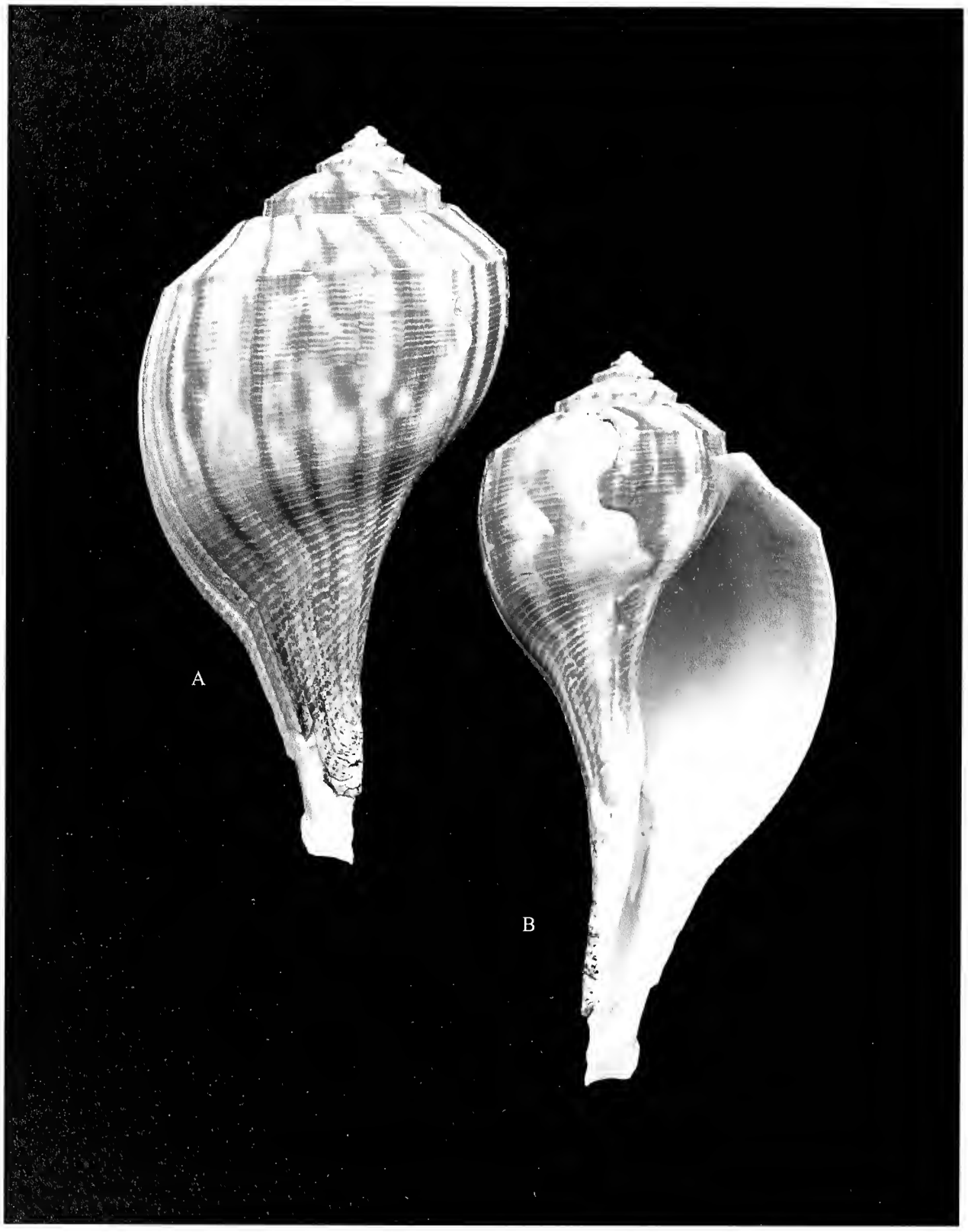


Figure 8.3 *Fulguropsis plagosus galvestonensis*, Typical Specimen.
A, B= *Fulguropsis plagosus galvestonensis* (Hollister, 1958), length 114 mm, found in 3 m depth in mud, off Anahuac, Bolivar Peninsula, Chambers County, Texas. Note the elevated, and distinctly sloping, spire whorls.
(p. 165)

Figure 8.4 *Fulguropsis plagosus galvestonensis* Low-Spired Variant.
A, B= *Fulguropsis plagosus galvestonensis* (Hollister, 1958), length 65 mm, found on the beach after a strong storm, at the mouth of the Sabine Pass, Jefferson County, Texas. Note the low spire whorls, which are more depressed than those seen on typical specimens. (p. 165)

Figure 8.5 *Fulguropsis texanus*, Typical Specimen.
A, B= *Fulguropsis texanus* (Hollister, 1958), length 90 mm, trawled by commercial fishermen from 20 m depth off Matagorda Island, Calhoun County, Texas. Note the distinctive shell sculpture composed of strong spiral cords. (p. 167)

Figure 8.6 *Fulguropsis texanus* Variant.
A, B= *Fulguropsis texanus* (Hollister, 1958), length 113 mm, found on the beach after a strong storm, on South Padre Island, Cameron County, Texas. This specimen represents a large inflated variant with a low, pyramidal spire. (p. 167)

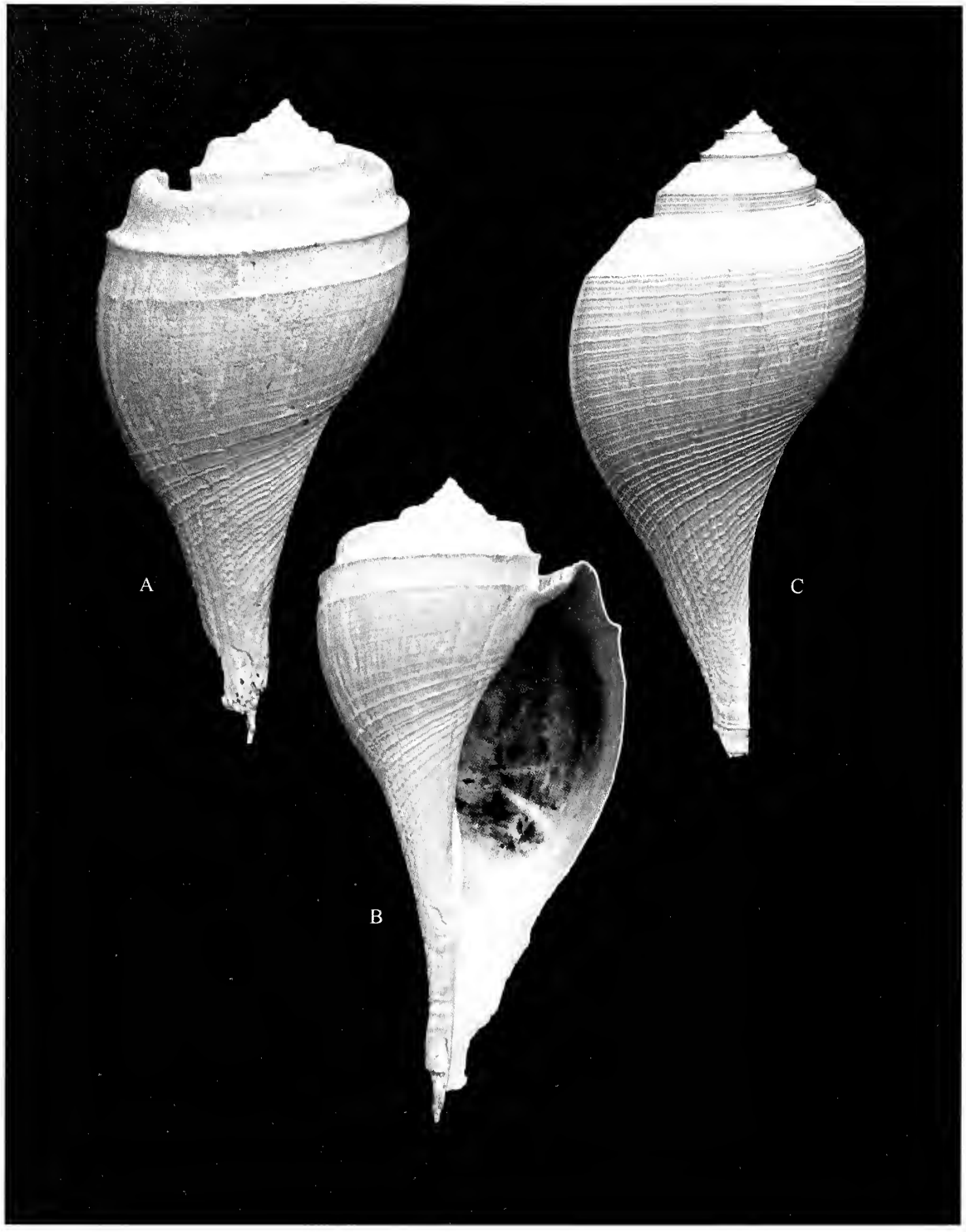


Figure 8.7 Fossil Species in the *Fulguropsis plagosus* Complex.
A, B= *Fulguropsis carolinensis* (Tuomey and Holmes, 1856), length 121 mm, from Unit 10 in Quality Aggregates Pit #6, Sarasota, Sarasota County, Florida. Buckingham Member of the Tamiami Formation; early Piacenzian (or late Zanclean) Age of the Pliocene. Also found in the contemporaneous Duplin Formation of the Carolinas. This is the oldest-known species of *Fulguropsis*.
C= *Fulguropsis capelettii* Petuch, 1994, length 122 mm, found in Palm Beach Aggregates Pit #9, Loxahatchee, Palm Beach County, Florida. Holey Land Member of the Bermont Formation; Calabrian Age of the early Pleistocene.

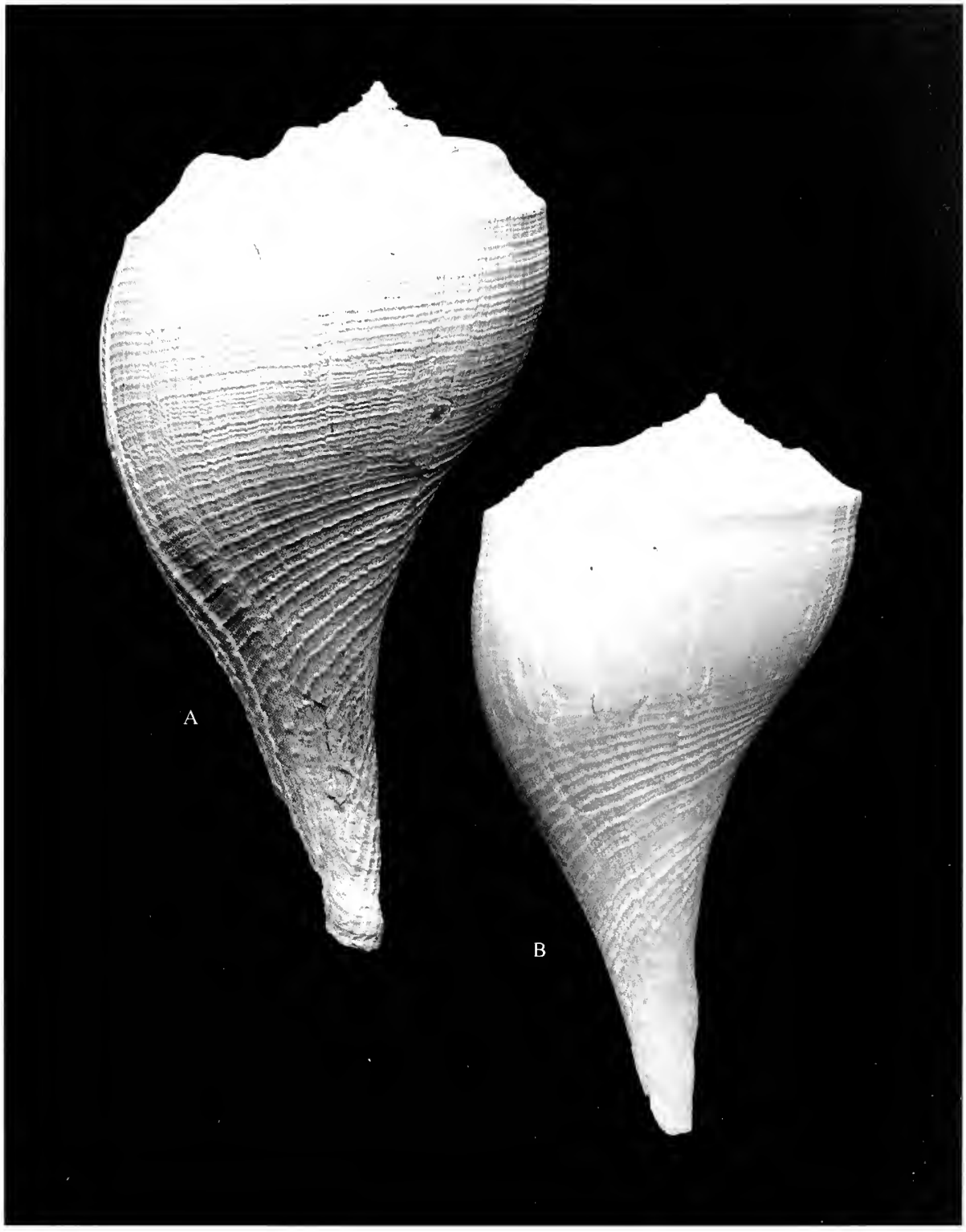


Figure 8.8 Fossil Species in the *Fulguropsis plagosus* Complex.
A= *Fulguropsis excavatum* (Conrad, 1839), length 104 mm, from the Lakes of the Meadows housing excavation off Bird Road, Miami, Dade County, Florida. Golden Gate Member of the Tamiami Formation, Piacenzian Age, Pliocene. Also found in the contemporaneous Yorktown and Duplin Formations.
B= *Fulguropsis feldmanni* Petuch, 1991, length 72 mm, found in Capeletti Brothers Pit #11, Miami, Dade County, Florida. Holey Land Member of the Bermont Formation; Calabrian Age of the early Pleistocene.

Image of a live Left-Handed Whelk *Sinistrofulgur sinistrum* crawling on sand in sea grass off Knight's Key, Monroe County, Florida; photo by Anton Oleinik, with permission.

APPENDIX 1.
LIST OF DESCRIBED FOSSIL SPECIES OF BUSYCONIDAE

Family Busyconidae Wade, 1917
Subfamily Busyconinae Petuch, 1994

Genus *Busycon* Röding, 1798 (Type: *B. carica*)

Busycon alumense (Mansfield, 1930) (Jackson Bluff Formation, early Piacenzian Pliocene)
Busycon auroraensis Petuch, 1994 (Chowan River Formation, late Piacenzian Pliocene)
Busycon burnsi (Dall, 1890) (Chipola Formation, Burdigalian Miocene)
Busycon diegelae Petuch, 2004 (Chipola Formation, Burdigalian Miocene)
Busycon duerri Petuch, 1994 (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Busycon filosum (Conrad, 1862) (Duplin Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Busycon filosum (Conrad, 1862) form *tritonis* Conrad, 1863 (Duplin Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Busycon gilmorei Petuch, 1994 (James City Formation, Gelasian Pleistocene)
Busycon maximus (Conrad, 1839) (Yorktown and Duplin Formations, Piacenzian Pliocene)
Busycon montforti Aldrich, 1909 (Shoal River Formation, Serravallian Miocene)
Busycon pachyus Petuch, 1994 (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Busycon radix Gardner, 1944 (Oak Grove Formation, Langhian Miocene)
Busycon rucksorum Petuch, 1994 (Nashua Formation, Gelasian Pleistocene)
Busycon titan Petuch, 1994 (Golden Gate Member, Tamiami Formation, Piacenzian Pliocene)

Genus *Sinistrofulgur* Hollister, 1958 (Type: *S. sinistrum*)
Sinistrofulgur adversarium (Conrad, 1862) (Chowan River Formation and Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)
Sinistrofulgur caloosahatcheensis Petuch, 1994 (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Sinistrofulgur contrarium (Conrad, 1839) (Yorktown and Duplin Formations, Piacenzian Pliocene)
Sinistrofulgur grabaui Petuch, 1994 (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Sinistrofulgur holeylandicum Petuch, 1994 (Holey Land Member, Bermont Formation, Calabrian Pleistocene)
Sinistrofulgur hollisteri Petuch, 1994 (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Sinistrofulgur labelleensis Petuch, 1994 (Bee Branch Member, Caloosahatchee Formation, Gelasian Pleistocene)
Sinistrofulgur palmbeachensis Petuch, 1994 (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Sinistrofulgur pamlico Petuch, 1994 (James City Formation, Gelasian Pleistocene)
Sinistrofulgur perversum okeechobeensis Petuch, 1994 (Okaloacoochee Member, Fort

Thompson Formation, Tarantian Pleistocene)
Sinistrofulgur robesonense (Gardner, 1948) (Duplin and Bear Bluff Formations, Piacenzian Pliocene)
Sinistrofulgur roseae Petuch, 1991 (Belle Glade Member, Bermont Formation, Ionian Pleistocene)
Sinistrofulgur yeehaw Petuch, 1994 (Nashua Formation, Gelasian Pleistocene)

Genus *Lindafulgur* Petuch, 2004 (Type: *L. lindajoyceae*)
Lindafulgur alencasterae (Perrilliat, 1963) (Agueguexquite Formation, Messinian Miocene of Veracruz State, Mexico)
Lindafulgur lindajoyceae (Petuch, 1991) (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Lindafulgur miamiensis (Petuch, 1991) (Golden Gate Member, Tamiami Formation, Piacenzian Pliocene)

Genus *Busycoarctum* Hollister, 1958 (Type: *B. coarctatum*)
Busycoarctum rapum (Heilprin, 1886) (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Busycoarctum superbus (Petuch, 1994) (Golden Gate Member, Tamiami Formation, Piacenzian Pliocene)
Busycoarctum tropicalis (Petuch, 1994) (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Busycoarctum tudiculatum (Dall, 1890) (lower beds, Jackson Bluff Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)

Genus *Spinifulgur* Petuch, 1994 (Type: *S. spiniger*)
Spinifulgur armiger Petuch, 2004 (Chipola Formation, Burdigalian Miocene)
Spinifulgur epispiniger (Gardner, 1944) (Chipola Formation, Burdigalian Miocene)
Spinifulgur gemmulatum Petuch, 1997 (Suwannee Formation, Rupelian Oligocene)
Spinifulgur nodulatum (Conrad, 1849) (Mint Springs Formation, Rupelian Oligocene)
Spinifulgur onslowensis (Kellum, 1926) (Belgrade Formation, Chattian Oligocene)
Spinifulgur perizonatum (Dall, 1890) (Tampa Member, Arcadia Formation, Chattian Oligocene)
Spinifulgur proterum (Gardner, 1944) (Flint River Formation, Rupelian Oligocene)
Spinifulgur spiniger (Conrad, 1848) (Vicksburg Group, Rupelian Oligocene)
Spinifulgur stellatum (Dall, 1890) (Tampa Member, Arcadia Formation, Chattian Oligocene)
Spinifulgur tampaensis (Dall, 1890) (Tampa Member, Arcadia Formation, Chattian Oligocene)

Genus *Sycopsis* Conrad, 1867 (Type: *S. tuberculatum*)
Sycopsis carinatum (Conrad, 1862) (Cove Point Member, St. Mary's Formation, Tortonian Miocene)
Sycopsis lindae Petuch, 1988 (Choptank Formation, Serravallian Miocene)
Sycopsis tuberculatum (Conrad, 1839) (Windmill Point Member, St. Mary's Formation, Tortonian Miocene)

Genus *Turrifulgur* Petuch, 1988 (Type: *T. fusiforme*)
Turrifulgur aldrichi (Gardner, 1944) (Shoal River Formation, Serravallian Miocene)
Turrifulgur atractoides (Gardner, 1944) (Oak Grove Formation, Langhian Miocene)
Turrifulgur covepointensis Petuch, 2004 (Cove Point Member, St. Mary's Formation, Tortonian Miocene)
Turrifulgur dasum (Gardner, 1944) (Shoal River Formation, Serravallian Miocene)
Turrifulgur foerstei (Gardner, 1944) (Oak Grove Formation, Langhian Miocene)
Turrifulgur fusiforme (Conrad, 1839) (Windmill Point Member, St. Mary's Formation, Tortonian Miocene)
Turrifulgur marylandicum Petuch, 1993 (Plum Point Member, Calvert Formation, Langhian Miocene)
Turrifulgur prunicola Petuch, 1993 (Plum Point Member, Calvert Formation, Langhian Miocene)
Turrifulgur turriculus Petuch, 1988 (Chancellor Point Sandstone, St. Mary's Formation, Tortonian Miocene)

Subfamily Busycotypinae Petuch, 1994

Genus *Busycotypus* Wenz, 1943 (Type: *B. canaliculatum*)
Busycotypus bicoronatum (Tripp, 1988) (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Busycotypus concinnum (Conrad, 1975) (Chowan River Formation and Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)
Busycotypus incile (Conrad, 1833) (Yorktown and Duplin Formations, Piacenzian Pliocene; *B. conradi* of Tuomey and Holmes is a synonym)
Busycotypus libertiense (Mansfield, 1930) (lower beds, Jackson Bluff Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Busycotypus mansfieldi Petuch, 1994 (upper beds, Jackson Bluff Formation, Piacenzian Pliocene)
Busycotypus scotti Petuch, 1994 (Nashua Formation, Gelasian Pleistocene)

Genus *Coronafulgur* Petuch, 2004 (Type: *C. coronatum*)
Coronafulgur calvertensis (Petuch, 1988) (Plum Point Member, Calvert Formation, Langhian Miocene)
Coronafulgur chesapeakensis (Petuch, 1988) (Cove Point Member, St. Mary's Formation, Tortonian Miocene)
Coronafulgur coronatum (Conrad, 1839) (Windmill Point Member, St. Mary's Formation, Tortonian Miocene)
Coronafulgur kendrewi Petuch, 2004 (Cobham Bay Member, Eastover Formation, Messinian Miocene)
Coronafulgur propecoronatum (Mansfield, 1935) (Red Bay Formation, Messinian Miocene)

Genus *Sycofulgur* Marks, 1950 (Type: *S. rugosum*)
Sycofulgur asheri (Petuch, 1988) (Chancellor Point Sandstone, St. Mary's Formation, Tortonian Miocene)
Sycofulgur choptankensis (Petuch, 1993) (Drumcliff Member, Choptank Formation,

Serravallian Miocene)
Sycofulgur martini (Petuch and Drolshagen, 2010) (Cove Point Member, St. Mary's Formation, Tortonian Miocene)
Sycofulgur rugosum (Conrad, 1843) (Windmill Point Member, St. Mary's Formation, Tortonian Miocene)
Sycofulgur scalaspirus (Conrad, 1863) (Plum Point Member, Calvert Formation, Langhian Miocene)

Genus *Brachysycon* Petuch, 1994 (Type: *B. amoenum*)
Brachysycon amoenum (Conrad, 1875) (James City and Nashua Formations, Gelasian Pleistocene)
Brachysycon canaliferum (Conrad, 1862) (Chowan River Formation and Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)
Brachysycon kissimmeensis Petuch, 1994 (Pinecrest Member (Kissimmee facies), Tamiami Formation, Piacenzian Pliocene)
Brachysycon propeincile (Mansfield, 1930) (lower beds, Jackson Bluff Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)

Genus *Fulguropsis* Marks, 1950 (Type: *F. pyrum*)
Fulguropsis aepynotum (Dall, 1890) (lower beds, Jackson Bluff Formation, early Piacenzian Pliocene)
Fulguropsis capelettii Petuch, 1994 (Holey Land Member, Bermont Formation, Calabrian Pleistocene)
Fulguropsis carolinensis (Tuomey and Holmes, 1856) (lower beds, Duplin Formation and Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Fulguropsis elongatus (Gill, 1867) (Bee Branch Member, Caloosahatchee Formation, Gelasian Pleistocene)
Fulguropsis evergladesensis Petuch, 1994 (Belle Glade Member, Bermont Formation, Ionian Pleistocene)
Fulguropsis excavatum (Conrad, 1839) (Yorktown and Duplin Formations and Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Fulguropsis feldmanni Petuch, 1991 (Holey Land Member, Bermont Formation, Calabrian Pleistocene)
Fulguropsis floridanum (Olsson and Harbison, 1953) (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Fulguropsis griffini Petuch, 1994 (Ayers Landing Member, Caloosahatchee Formation, latest Gelasian Pleistocene)
Fulguropsis pyruloides pahayokee Petuch, 1994 (Okaloacoochee Member, Fort Thompson Formation, Tarantian Pleistocene)
Fulguropsis pyriformis (Conrad, 1867) (Chowan River Formation and the Fruitville Member of the Tamiami Formation)
Fulguropsis radula Petuch, 1994 (Golden Gate Member, Tamiami Formation, Piacenzian Pliocene)

Genus *Pyruella* Petuch, 1982 (Type: *P. harasewychi*)
Pyruella basingerensis Petuch, 1994 (Fruitville Member (Kissimmee facies), Tamiami

Formation, late Piacenzian Pliocene)
Pyruella bladenense (Gardner, 1948) (James City, Waccamaw, and Nashua Formations, Gelasian Pleistocene) ("*Busycon*" *kerrii* Conrad, 1875 may be an earlier name)
Pyruella blountense (Mansfield, 1935) (Red Bay Formation, Messinian Miocene)
Pyruella carraheri Petuch, 1994 (Pinecrest Member, Kissimmee Facies, Tamiami Formation, Piacenzian Pliocene)
Pyruella eismonti Petuch, 1994 (Ayers Landing Member, Caloosahatchee Formation, late Gelasian Pleistocene)
Pyruella federicoae Petuch, 1994 (Unit 3, Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)
Pyruella harasewychi Petuch, 1982 (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Pyruella miccosukee Petuch, 1991 (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Pyruella osceola Petuch, 1982 (Pinecrest Member, Unit 8, Tamiami Formation, Piacenzian Pliocene)
Pyruella ovoidea (Petuch, 1994) (Ayers Landing Member, Caloosahatchee Formation, late Gelasian Pleistocene)
Pyruella rugosicostata Petuch, 1982 (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Pyruella sarasotaensis Petuch, 1982 (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Pyruella schmidti Petuch, 1994 (Unit 4, Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)
Pyruella seminole Petuch, 1982 (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Pyruella sicyoides (Gardner, 1944) (Chipola Formation, Burdigalian Miocene)
Pyruella streami Petuch, 1994 (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Pyruella tomeui Petuch, 2004 (Holey Land Member, Bermont Formation, Calabrian Pleistocene)
Pyruella waltfrancei Petuch, 1994 (Buckingham Member, Tamiami Formation, early Piacenzian Pliocene)
Pyruella willcoxi (Gardner, 1948) (Waccamaw Formation, Gelasian Pleistocene)

Genus *Laevisycon* Petuch, Myers, and Berschauer new genus (Type: *L. laevis*)
Laevisycon demistriatum (Petuch, 1982) (Pinecrest Member, Tamiami Formation, Piacenzian Pliocene)
Laevisycon laevis (Petuch, 1982) (Unit 4, Fruitville Member, Tamiami Formation, Piacenzian Pliocene)
Laevisycon planulatum (Dall, 1890) (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Laevisycon soror (Petuch, 1994) (Fort Denaud Member, Caloosahatchee Formation, Gelasian Pleistocene)
Laevisycon turbinalis (Petuch, 1982) (Unit 3, Fruitville Member, Tamiami Formation, late Piacenzian Pliocene)

Image of a live Left-Handed Whelk *Sinistrofulgur sinistrum* eating a *Mercenaria campechensis* found at low tide on Marco Island, Collier County, Florida; photo by Anton Oleinik, with permission.

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LIST OF ILLUSTRATED SPECIES

Only species and subspecies that were illustrated in the previous chapters are listed here. These are arranged by genus and include both living and fossil forms of the families Echinofulguridae and Busyconidae.

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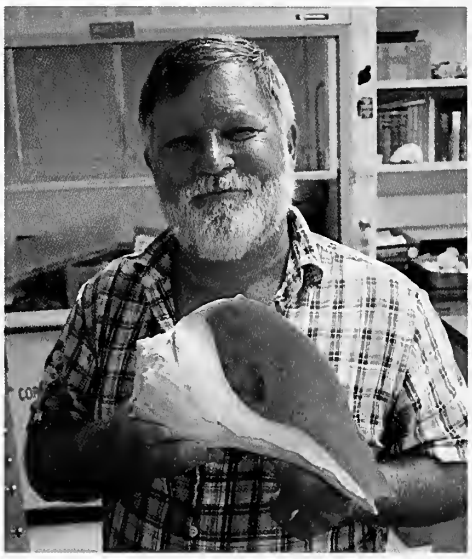
ABOUT THE AUTHORS



Edward J. Petuch was born in Bethesda, Maryland in 1949. Raised in a Navy family, he spent many of his childhood years collecting living and fossil shells in such varied localities as Chesapeake Bay, California, Puerto Rico and Wisconsin. His early interests in malacology and oceanography eventually led to BA and MS degrees in zoology from the University of Wisconsin-Milwaukee. While in Wisconsin, his thesis worked concentrated on the molluscan biogeography of West Africa. There, he collected mollusks and traveled extensively in Morocco, Western Sahara, the Canary Islands, Senegal, Gambia, Sierra Leone, Ivory Coast, and the Cameroons. At this time, he also made frequent research trips to both coasts of Mexico and the Barrier Reef of Belize.

Continuing his education, Petuch studied marine biogeography and malacology under Gilbert Voss and Donald Moore at the Rosenstiel School of Marine and Atmospheric Sciences at the University of Miami. During this time, his dissertation work involved intensive collecting and fieldwork in Colombia, Venezuela, Barbados, the Grenadines, and Brazil. After receiving his Ph.D. in oceanography in 1980, Petuch undertook two years of postdoctoral research, sponsored by the National Science Foundation, with Geerat Vermeij at the University of Maryland. While there, he also held a research associateship with the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution (under the sponsorship of Thomas Waller) and conducted fieldwork on the Plio-Pleistocene fossil beds of Florida and North Carolina and the Miocene fossil beds of Maryland and Virginia.

Petuch has also collected and studied living mollusks in Australia, Papua-New Guinea, the Fiji Islands, French Polynesia, Japan, the Bahamas, Nicaragua, Costa Rica, and Uruguay. This research has led to the publication of almost 200 scientific papers and the descriptions of over 1000 new species of mollusks and 60 new genera. His previous 17 books are well-known reference texts in the malacological and paleontological communities, and some of the better known include *Biogeography and Biodiversity of Western Atlantic Mollusks* (2013), *Cenozoic Seas: The View From Eastern North America* (2004), *The Geology of the Everglades and Adjacent Areas* (with Charles Roberts, 2007), *Molluscan Paleontology of the Chesapeake Miocene* (with Mardie Drolshagen, 2010), *Molluscan Communities of the Florida Keys and Adjacent Areas: Their Ecology and Biodiversity* (with Robert Myers, 2014), *New Caribbean Molluscan Faunas* (1987), *Cone Shells of the Okeechobean Sea* (with Mardie Drolshagen and Gunther Herndl, 2015), and *Atlas of Florida Fossil Shells* (1994).

Currently, Petuch is a professor of geology in the Department of Geosciences at Florida Atlantic University in Boca Raton, Florida, where he teaches classes in oceanography, paleontology, and physical geology. When not collecting and studying mollusks in Palm Beach and the Florida Keys, Petuch leads an active career as a musician, giving regular concerts on the pipe organ and playing the recorder and harpsichord in university chamber ensembles.

Robert F. Myers was born in 1953 and spent much of his childhood in southeastern Asia, where he developed an intense interest in natural history. His diving and passion for marine life took hold during his early high school years in Hong Kong and continued at the University of Hawaii. There, he assisted well-known ichthyologist John E. Randall by collecting fishes for both ciguatera research and fish population surveys. After earning a BA degree in zoology, Myers moved to Guam to pursue graduate studies and underwater photography. There, he earned an MS degree in biology from the University of Guam Marine Laboratory, worked as a fisheries biologist for the government of Guam, and founded Coral Graphics.

Myers retired from the government in 1995 and now pursues photography, writing, research, and consulting. He has written or coauthored numerous scientific papers and popular articles on western Pacific fishes and several books. Some of these include *Micronesian Fishes* (three editions, 1989-1999), *Coral Reef Fishes* (with Lieske, 1993), *Coral Reef Guide Red Sea* (with Lieske, 2004), and *Dangerous Marine Animals* (with Bergbauer and Kirschner, 2009). He has developed an application for iphones and ipads on Florida-Caribbean reef fish identification. Now residing in Wellington, Florida, Myers is currently working on a field guide to Florida and Caribbean marine life and serves on the coral reef fishes Species Survival Commission (SSC) of the International Union for the Conservation of Nature (IUCN).

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David P. Berschauer was born in Rockville Center, New York in 1964, and spent his childhood years collecting shells in such varied localities as California, New York, Florida, Washington, and Mexico. His early interests in natural history, malacology and marine biology eventually led to a BS degree in biology at the University of California Irvine, an advanced marine invertebrate zoology course at Washington State University's Friday Harbor Marine Lab, and studies towards the pursuit of a graduate degree in marine biology at Florida State University in Tallahassee, Florida. While still an undergraduate he performed field biology research and published a number of research papers and gave scientific presentations at national conferences. Thereafter, he determined to keep malacology as a lifetime avocation, switched career paths and went to Southwestern University School of Law in Los Angeles, California, earning his Juris Doctorate in 1991. He is a licensed California attorney and has practiced law full time for over twenty years in the southern California region.

During this entire time Berschauer continued to pursue his interests in marine biology, collecting and studying mollusks and marine life. In his spare time he has developed and published a relational database software program to organize and maintain a systematic

collection; originally designed for malacology the program is equally effective in entomology or other fields. Now residing in Laguna Hills, California, Berschauer has accumulated a substantial collection of mollusks over more than a forty year period, is an active member of the San Diego Shell Club, and is the Co-Editor of its long published malacological journal, *The Festivus*. When not collecting, studying and photographing mollusks he has been engaged as an adult leader in his children's activities as a baseball coach, soccer coach, umpire, youth mentor, and Scout leader during which time has led natural history tours, hikes, and backpacking trips.

David P. Berschauer and Edward J. Petuch during an expedition to the Ten Thousand Islands in August 2015 studying busycon whelk habitats. Photo by "Kenny" Brown, with permission.

Geological Time Scale

Era	Epoch	Age	Time Range
Cenozoic			
	Holocene		11,700 YA to present
	Pleistocene	Tarantian	12,600 to 11,700 YA
		Ionian	78,100 to 12,600 YA
		Calabrian	1.8 MYA to 78,100 YA
		Gelasian	2.58 to 1.8 MYA
	Pliocene	Piacenzian	3.6 to 2.58 MYA
		Zanclean	5.3 to 3.6 MYA
	Miocene	Messinian	7.3 to 5.3 MYA
		Tortonian	11.6 to 7.3 MYA
		Serravallian	13.8 to 11.6 MYA
		Langhian	16.0 to 13.8 MYA
		Burdigalian	20.4 to 16.0 MYA
		Aquitanian	23.0 to 20.4 MYA
	Oligocene	Chattian	28.1 to 23.0 MYA
		Rupelian	33.9 to 28.1 MYA
	Eocene		56 to 33.9 MYA
	Paleocene		66 to 56 MYA

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