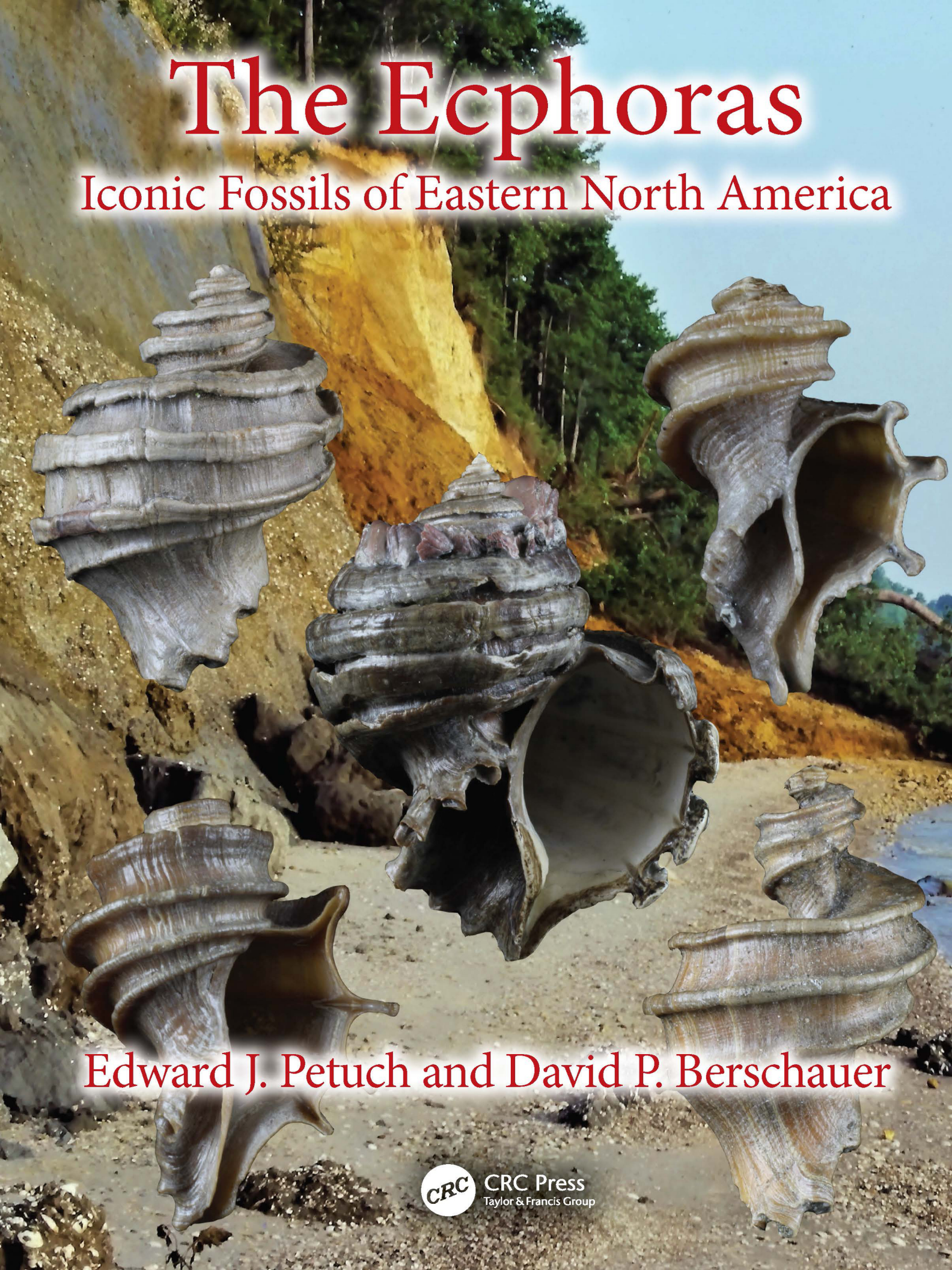
The Ecphoras

Iconic Fossils of Eastern North America



Edward J. Petuch and David P. Berschauer

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The Ecphoras

In the Miocene and Pliocene fossil shell beds of the eastern United States, the single most spectacular molluscan species radiation is seen in the ecphora shells (the Tribe Ecphorini). These bizarrely shaped gastropods, with their distinctive ribbed shell sculpture, represent a separate branch of the Subfamily Ocenebridae, Family Muricidae. Characteristically, these muricid gastropods are heavily ornamented with spiral ribs and cords and are considered some of the most beautiful and interesting groups of fossil mollusks found along the Atlantic Coastal Plain and Floridian Peninsula. The ecphoras are greatly sought after by fossil collectors.

The ecphora faunas, and their individual species and subspecies, are illustrated and described in detail in *The Ecphoras: Iconic Fossils of Eastern North America,* along with photographs of ecphora-bearing geological units and in situ specimens. The authors list the 67 known species and subspecies that are recognized as valid, arranged by the eight genera and five subgenera that encompass these taxa

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Iconic Fossils of Eastern North America

Edward J. Petuch
David P. Berschauer

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Dedication

This book is dedicated to the following:

Linda J. Petuch, Eric and Rasa Petuch,

Brian Petuch and Kendra Berentsen, and Jennifer Petuch

and

Felicia Weisbrot Berschauer, Morgan, Jeremy, Lincoln and Brantley Coker,

Jonathon, Tawni, Nora and Emmett Berschauer

THE ECPHORAS: ICONIC FOSSILS OF EASTERN NORTH AMERICA

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Ecphora (Powhatan) gardnerae unnamed subspecies, length 92 mm, from the base of the Eastover Formation near St. Inigoes Creek, St. Mary's County, Maryland. Specimen collected by the senior author and now in the collection of the Academy of Natural Sciences of Drexel University, Catalog No. ANSP IP 52868.

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Ecphora roxaneae dalli Petuch and Berschauer n. subsp., length 111 mm, Goose Creek Formation, South Carolina.

INTRODUCTION. The Ecphoras: Eastern North America's Iconic Fossils

In the Miocene and Pliocene fossil shell beds of the eastern United States, from southern New Jersey south to southern Florida, the single most spectacular molluscan species radiation is seen in the ecphora shells (vernacular usage for any member of the Tribe Ecphorini). These bizarrely-shaped gastropods, with their distinctive ribbed shell sculpture, represent a separate branch of the Subfamily Ocenebridae, Family Muricidae. Characteristically, these muricid gastropods are heavily ornamented with spiral ribs and cords and are considered to be some of the most beautiful and interesting groups of fossil mollusks found along the Atlantic Coastal Plain and Floridian Peninsula. Because of their exotic shell sculpture, large size, and intrinsic beauty, the ecphoras are greatly sought after by fossil collectors and are second only to shark teeth as prized collector's items in the Chesapeake Miocene formations of Maryland, Virginia, and northern North Carolina.

The intrinsic beauty and unusual appearance of ecphora shells have been known since the first European naturalists began exploring North America, and a specimen of an unidentified ecphora (probably *Ecphora quadricostata*) was the first American fossil gastropod to be illustrated in a natural history text (the 1770 Huddesford Edition of Martin Lister's *Historiae sive Synopsis Methodique Conchyliorum*). Since then, an additional 66 species have been discovered and named by several molluscan paleontologists, demonstrating that the ecphora shells were a more important and diverse part of the American paleofauna than was previously thought. Of the Atlantic Coastal Plain areas where there are exposures of sediments containing ecphoras, the Calvert Cliffs area of western Chesapeake Bay contains the largest number of collectible species and encompasses faunas from three separate geological formations: the **Calvert Formation**, the **Choptank Formation**, and the **St. Mary's Formation**. These formations and their component ecphoras are discussed, in detail, in the following chapters.

Although originally thought to be classic fossils for only the Miocene of the eastern United States, the ecphoras actually survived into the subsequent Pliocene Epoch and are well represented by a large number of species in Virginia, the Carolinas, and Florida. Indeed, the very last-living ecphora, *Latecphora hertwecki*, inhabited the late Pliocene **Myakka Lagoon System** off southwestern Florida, long after all the other ecphoras had become extinct elsewhere in eastern North America (see Petuch and Berschauer, 2021: 68-69, 121-131). Interestingly, the oldest-known ecphora, the Aquitanian Miocene *Ecphorosycon tampaensis*, was first discovered in southwestern Florida, the same area where the last ecphora species lived its final days. Southern Florida, then, can be seen to have been both the birthplace of the ecphoras and also the place of their death.

We here list the 67 known species and subspecies of ecphoras that are recognized as valid and which are discussed in the following chapters of this book. These are arranged by the eight genera and five subgenera that encompass these taxa.

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1913
Tribe Ecphorini Petuch and Berschauer, new tribe
Genus *Ecphorosycon* Petuch, 1988
Ecphorosycon tampaensis (Dall, 1890)
Ecphorosycon pamlico (Wilson, 1987)
Ecphorosycon lindajoyceae (Petuch, 1993)
Ecphorosycon kalyx (Petuch, 1988)
Genus *Siphoecphora* Petuch, 1988
Siphoecphora aurora (Wilson, 1987)
Siphoecphora gerrardi new species
Genus *Chesathais* Petuch, 1988
Chesathais ecclesiasticus (Dall, 1915)
Chesathais whitfieldi Petuch, 1988
Chesathais pungoensis new species
Chesathais donaldasheri Petuch, 1988
Chesathais lindae Petuch, 1988
Chesathais drumcliffensis Petuch, 1988
Genus *Trisecphora* Petuch, 1988 sensu stricto
Trisecphora precursor new species
Trisecphora tricostata (Martin, 1904)
Trisecphora governorensis new species
Trisecphora scientistensis (Petuch, 1992)
Subgenus *Recurvecphora* Petuch and Berschauer, new subgenus
Trisecphora (Recurvecphora) recurvicostata new species
Trisecphora (Recurvecphora) schmidti (Petuch, 1988)
Trisecphora (Recurvecphora) martini (Petuch, 1988)
Subgenus *Eccentrella* Petuch and Berschauer, new subgenus
Trisecphora (Eccentrella) chamnessi (Petuch, 1988)
Trisecphora (Eccentrella) eccentrica (Petuch, 1988)
Subgenus *Matoaka* Petuch and Berschauer, new subgenus
Trisecphora (Matoaka) prunicola (Petuch, 1988)
Trisecphora (Matoaka) carolinensis (Petuch, 1988)
Trisecphora (Matoaka) bartoni Petuch and Drolshagen, 2010
Trisecphora (Matoaka) smithae (Petuch, 1988)
Trisecphora (Matoaka) patuxentia (Petuch, 1988)
Trisecphora (Matoaka) shattucki (Petuch, 1988)
Genus *Ecphora* Conrad, 1843 sensu stricto
Ecphora wardi Petuch, 1988
Ecphora mattinglyi Petuch, 2004
Ecphora sandgatesensis Petuch, 1988
Ecphora meganae Ward and Gilinsky, 1988
Ecphora amyae Petuch and Drolshagen, 2010

Ecphora kochi Ward and Gilinski, 1988
Ecphora roxaneae Petuch, 1991
Ecphora roxaneae dalli Petuch and Berschauer, new subspecies
Ecphora leecreekensis Petuch, 1988
Ecphora quadricostata (Say, 1824)
Ecphora quadricostata striatula Petuch, 1986
Ecphora quadricostata umbilicata (Wagner, 1839)
Ecphora quadricostata rachelae Petuch, 1988
Subgenus *Rhombecphora* Petuch and Berschauer, new subgenus
Ecphora (Rhombecphora) harasewychi Petuch, 1988
Ecphora (Rhombecphora) rikeri Petuch, 1988
Subgenus *Powhatan* Petuch and Berschauer, new subgenus
Ecphora (Powhatan) calvertensis Petuch, 1988
Ecphora (Powhatan) chesapeakensis Petuch, 1988
Ecphora (Powhatan) williamsi Ward and Gilinsky, 1988
Ecphora (Powhatan) conoyensis Petuch, 2004
Ecphora (Powhatan) asheri Petuch, 1988
Ecphora (Powhatan) germonae Ward and Gilinski, 1988
Ecphora (Powhatan) gardnerae Wilson, 1987
Ecphora (Powhatan) gardnerae angusticostata Petuch, 1988
Ecphora (Powhatan) grulkei new species
Ecphora (Powhatan) whiteoakensis Ward and Gilinski, 1988
Ecphora (Powhatan) whiteoakensis hopei Petuch, 1991
Ecphora (Powhatan) pachycostata Petuch, 1988
Genus *Planecphora* Petuch, 2004
Planecphora turneri (Petuch, 1992)
Planecphora vokesi (Petuch, 1988)
Planecphora choptankensis (Petuch, 1988)
Planecphora delicata (Petuch, 1988)
Planecphora hertweckorum (Petuch, 1987)
Planecphora mansfieldi (Petuch, 1988)
Genus *Globecphora* Petuch, 1994
Globecphora floridana (Petuch, 1988)
Globecphora floridana streami (Petuch, 1994)
Globecphora parvicostata (Pilsbry, 1911)
Globecphora mardieae new species
Genus *Latecphora* Petuch, 1988
Latecphora violetae (Petuch, 1988)
Latecphora bradleyae (Petuch, 1987)
Latecphora hertwecki (Petuch, 1988)

These beautiful and unusual murex shells are shown in the iconographies at the end of each of the following chapters. It is our hope that this book will serve as a field guide for amateur and professional paleontologists alike, and will give new insights into the evolutionary history and stratigraphy of eastern North America's most iconic group of fossil shells, the ecphoras. In the predecessor to this book, the 1988 *Field Guide to the Ecphoras*, a point of confusion as to the actual date of publication was inadvertently introduced. Projecting when the book might be published, the senior author stated that the date of publication was "15 February 1989". Since the book was actually published a few months earlier, in late 1988 (as stated in the front matter, "Copyright 1988 by the Coastal Education and Research Foundation"), all the taxa proposed in that monographic work should have publication dates of 1988, not 1989. This discrepancy in publication dates has been corrected in this subsequent volume.

Edward J. Petuch, Ph.D. and David P. Berschauer, J.D., 2022

View of a prime *Chesathais* collecting locality, along the Calvert Cliffs south of Governor Run, near St. Leonards, Calvert County, Maryland. Here, the highly-fossiliferous Shattuck Zone 18, Drumcliff Member of the Choptank Formation can be seen to overlay the darker and less-fossiliferous Shattuck Zone 17, St. Leonards Member of the Choptank Formation (at the base of the cliff). Eleven different ecphoras have been collected at this locality, including the most desirable species, the rare and beautiful rapaniform ecphora, *Chesathais lindae.*

CHAPTER 1. Systematics and Classification of the Ecphoras

The senior author (Petuch, 1988) originally considered the ecphoras to belong in their own extinct subfamily of the Muricidae (Murex Shells), the Ecphorinae. Because of the similarities in size and shell morphology, Bouchet *et al*. (2017) synonymized the Subfamily Ecphorinae with the Subfamily Ocenebrinae (the Ecphorini), as representing an extinct eastern North American clade of the worldwide subfamily. The living western North American genus *Forreria* appears to represent the closest group of extant ocenebrines to the extinct clade that we describe in the following section. This is especially apparent when considering that both *Forreria* and the ecphora shells have a two-layered mineralogical shell structure, with an inner layer of aragonite and an outer layer of calcite. The higher-order systematic classification scheme for our new clade, the Tribe Ecphorini, is arranged as follows:

Class Gastropoda Cuvier, 1797
Subclass Orthogastropoda Ponder and Lindberg, 1995
Superorder Caenogastropoda Cox, 1960
Order Sorbeoconcha Ponder and Lindberg, 1997
Infraorder Neogastropoda Wenz, 1938
Superfamily Muricoidea Rafinesque, 1815
Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903
Tribe Ecphorini Petuch and Berschauer, new tribe

Description: (originally described as a subfamily of the Family Thaididae; now considered to be a tribe within the Subfamily Ocenebrinae, Family Muricidae; see Petuch, 1988: 29-30) “Shells inflated, globose, generally thickened and heavy; all genera with flaring, wide apertures and open umbilici; parietal shields either adherent **or** only partially attached to earlier whorl; siphonal canals generally elongated, well developed in most genera; almost all genera heavily sculptured with prominent raised cords or ribs, numbering three, four, five, or more; ribs may be simple and bladelike in form or complex, with flaring edges, producing ‘T’-shaped cross section.”

Morphological Characters of the Ecphorini

Shells of the Ecphorini characteristically are composed of two distinct calcium carbonate layers, with an outer layer of resistant calcite and an inner layer of softer aragonite. The outer calcite layer is frequently stained red, brown, or yellow and is often extremely well preserved. The inner aragonite layer, exposed within the aperture, is white in color but is often dissolved away in specimens from leached sedimentary layers. The 67 known species and subspecies of ecphoras cover a wide variety of morphological types and these taxa can be distinguished from each other by the examination and comparison of the following eight shell characters.

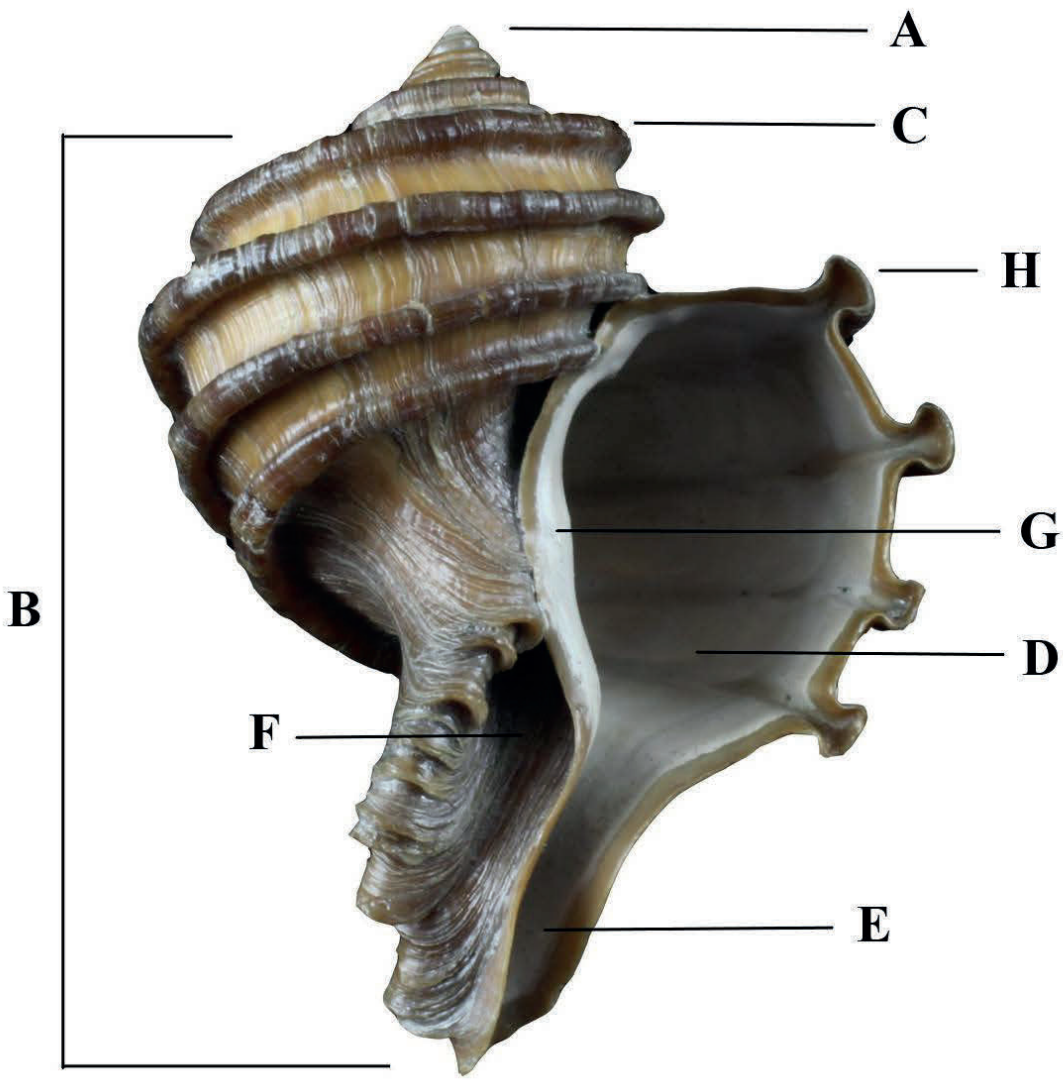

ILLUSTRATION OF A TYPICAL ECPHORA SHELL AND ITS PARTS
A= apex; **B=** body whorl; **C=** shoulder; **D=** aperture; **E=** siphonal canal; **F=** umbilicus; **G=** parietal wall; **H=** rib.

These important morphological characters are:

1. SHELL SHAPE: The shape of the shells, particularly that of the shell's body whorl, differs greatly between the various genera and subgenera of ecphoras. Some, such as the five-ribbed *Globecphora floridana*, are highly inflated and globose, often being the shape and size of a cantaloupe or small melon. Other species, such as *Ecphora mattinglyi*, are highly elongated and protracted, with extremely protracted and fragile spire whorls. The main types of ecphora shell shapes include the following, with an example of each form:

- **Globose** (*Globecphora floridana*); shells highly inflated with greatly expanded body whorls.

- **Cylindrical** (*Ecphora sandgatesensis*); shells round in cross section but straight-sided and narrow.
- **Pyriform (Pear-Shaped)** (*Siphoecphora aurora*); shells with rounded body whorls and elongated siphonal canals.
- **Vermiform** (*Trisecphora (Eccentrella) eccentrica*); shells extremely protracted and wormlike, with uncoiled, detached spire and body whorls.
- **Fusiform** (*Chesathais lindae*); spindle-shaped shells with high spires, narrow body whorls, and elongated siphonal canals.
- **Vase-Shaped (Vasiform)** (*Trisecphora (Matoaka) bartoni*); shells with broad shoulder areas, tapering quickly to the anterior end, producing a vase-like shape.
- **Turbinate** (*Latecphora bradleyae*); shells broad and inflated, with rounded shoulders and low spire whorls, having the shape of an inverted cone.

2. SHELL SIZE: The range in size among the ecphoras is substantial, with some species, such as *Ecphorosycon tampaensis*, being very small and delicate and others, such as the giant *Ecphora (Powhatan) gardnerae*, reaching the size of a small melon. The range of sizes, over the entire evolutionary history of the Tribe, extends from 15-20 mm for *E. tampaensis* to over 150 mm for *E. (Powhatan) gardnerae*. The older, early Miocene species are generally quite small, averaging lengths of only around 30 mm, with the only exception being the large pyriform genera, *Siphoecphora* and *Ecphorosycon*, which can reach lengths of 75 mm. The late Miocene and Pliocene ecphoras all are much larger than their early Miocene ancestors, with most taxa averaging over 90 mm in length.

3. SPIRE HEIGHT: The spire whorls differ greatly between genera and subgenera, with some species having low, nearly flattened spire whorls, such as *Globecphora parvicostata* and *Ecphora (Powhatan) pachycostata*, while others have greatly elevated and protracted spire whorls, such as *Ecphorosycon kalyx* and *Chesathais whitfieldi*. These differences in spire height and structure are important diagnostic features for separating subgenera and species complexes.

4. RIB COUNT: Although the general perception of ecphoras, by collectors and non-malacologists, is that they are four-ribbed shells, all resembling the well-known *Ecphora quadricostata*, a detailed review of the family shows that rib count is specific to each genus and subgenus. The six types of rib counts include the following (with an example of a species for each count):

- **Multiple Cords** (*Chesathais ecclesiaticus*); shells with as many as eight main cords on the body whorl, of variable size, with some being larger than others.
- **Three Main Ribs** (*Trisecphora (Matoaka) carolinensis*); shells with only three equal-sized ribs around the body whorl and no other primary ornamentation.
- **Three Main Ribs with Fourth Smaller Rib** (*Trisecphora tricostata*); shells with three main ribs around the body whorl and a fourth smaller subsidiary cordlike rib around the siphonal canal-body whorl juncture.
- **Four Main Ribs** (*Planecphora choptankensis*); shells with only four equal-sized ribs around the body whorl.

- **Four Main Ribs with Fifth Smaller Rib** (*Ecphora (Powhatan) whiteoakensis hopei*); shells with four main ribs around the body whorl and a fifth smaller subsidiary cordlike rib around the siphonal canal-body whorl juncture.
- **Five Main Ribs** (*Ecphora (Powhatan) asheri*); shell with five equal-sized ribs.

5. RIB STRUCTURE: The shape of the ribs is the single most important morphological criterion for differentiating the species, genera, and subgenera of ecphoras. This character is relatively invariant, with each taxon consistently having a set type of rib and showing little variation. The rib types include:

- **Rounded Cord** (*Globecphora floridana*); ribs that are directly adherent to the body and spire whorls, only slightly raised and rounded in cross section.
- **Low Cord with Flattened Edge** (*Ecphora (Rhombecphora) rikeri*); ribs that are directly adherent to the body and spire whorls, slightly raised, with a flattened edge and rectangular in cross section.
- **Thin Blade with Rounded Edge** (*Planecphora mansfieldi*); ribs that are very thin, delicate, and bladelike, often noticeably projecting outward from the body whorl and with rounded edges.
- **Thin Rib with Upturned, Cuplike Edge** (*Trisecphora (Recurvecphora) schmidti*); ribs that are thin and bladelike, but curl upward (posteriorward), producing a distinct trough-like channel.
- **Thin Rib, Slightly "T"-Shaped** (*Ecphora quadricostata*); ribs that are thickened, with distinctly flattened edges that are slightly "T"-shaped in cross section.
- **Thick Rib, Distinctly "T"-Shaped** (*Ecphora (Powhatan) gardnerae*); ribs that are thickened, with wide flanges on the edges and are strongly "T"-shaped in cross section. Ribs of this type frequently are sculpted with one or two deeply-incised cords.
- **Wide Rib, Extremely "T"-Shaped** (*Latecphora bradleyae*); ribs that are extremely wide and flattened, with very wide flanges on the rib edges; on advanced forms, the edges are almost in contact and the rib is broadly "T"-shaped. Ribs of this type frequently are sculpted with two, three, or four deeply-incised cords.

6. SHELL SCULPTURE: This morphological character refers to the texture of the shell surface that is exposed between the ribs and cords. These intracostal areas can be smooth and polished (as on *Globecphora parvicostata*); sculpted with fine spiral threads, which give the shell a silky appearance (as on *Ecphora wardi*); ornamented with numerous fine spiral cords and threads (as on *Ecphora quadricostata striatula*); or ornamented with very strong spiral ribs, some of which may be almost as large as the main ribs (as seen on *Chesathais drumcliffensis*). The shell sculpture is very consistent within any given species or subspecies and can be used to determine individual taxa.

7. SIPHONAL CANAL STRUCTURE: Both the length and the structure of the siphonal canal in the Tribe Ecphorini is variable between genera and subgenera. Some genera, such as *Siphoecphora* and *Ecphorosycon*, have very long, narrow siphonal canals that approximate those seen in the gastropod Family Busyconidae and the living Eastern

Pacific ocenebrine muricid genus *Forreria*. Other genera, such as *Latecphora* and *Globecphora*, have proportionally very short and broad canals, resembling those seen on smaller ocenebrine groups such as *Ocenebra*, *Ocenebrina*, and *Urosalpinx*. Genera such as *Ecphora* and *Planecphora* have siphonal canals that fall between these two extremes; being intermediate in both length and width.

8. STRUCTURE AND FORM OF THE UMBILICUS: The umbilical area, adjacent to the aperture, also varies in shape, size, and structure. Some genera, such as *Latecphora* and *Globecphora*, have extremely wide, open, and flaring umbilici while other genera, such as *Siphoecphora* and *Chesathais*, have very narrow, slot-like umbilici. The genera *Ecphora* and *Trisecphora* fall between these two extremes in umbilical form.

These eight morphological criteria, when studied and applied in consort, demonstrate that the Tribe Ecphorini is actually much more species-rich than previously thought and that its 67 species and subspecies belong to eight separate higher taxa. These include the following genera:

Ecphorosycon (Figure 1.1 A)
Siphoecphora (Figure 1.1B)
Chesathais (Figure 1.1C)
Trisecphora (Figure 1.1D)
Ecphora (Figure 1.2A)
Planecphora (Figure 1.2B)
Globecphora (Figure 1.2C)
Latecphora (Figure 1.2D)

Five evolutionary offshoots (subclades) are also known and these are described here as subgenera of *Trisecphora* and *Ecphora*. These include:

Eccentrella (subgenus of *Trisecphora*; Figure 1.3A)
Recurvecphora (subgenus of *Trisecphora*; Figure 1.3B)
Matoaka (subgenus of *Trisecphora*; Figure 1.3C)
Rhombecphora (subgenus of *Ecphora*; Figure 1.3D)
Powhatan (subgenus of *Ecphora*; Figure 1.3E)

All of these genera and subgenera are described in the following chapters of this book.

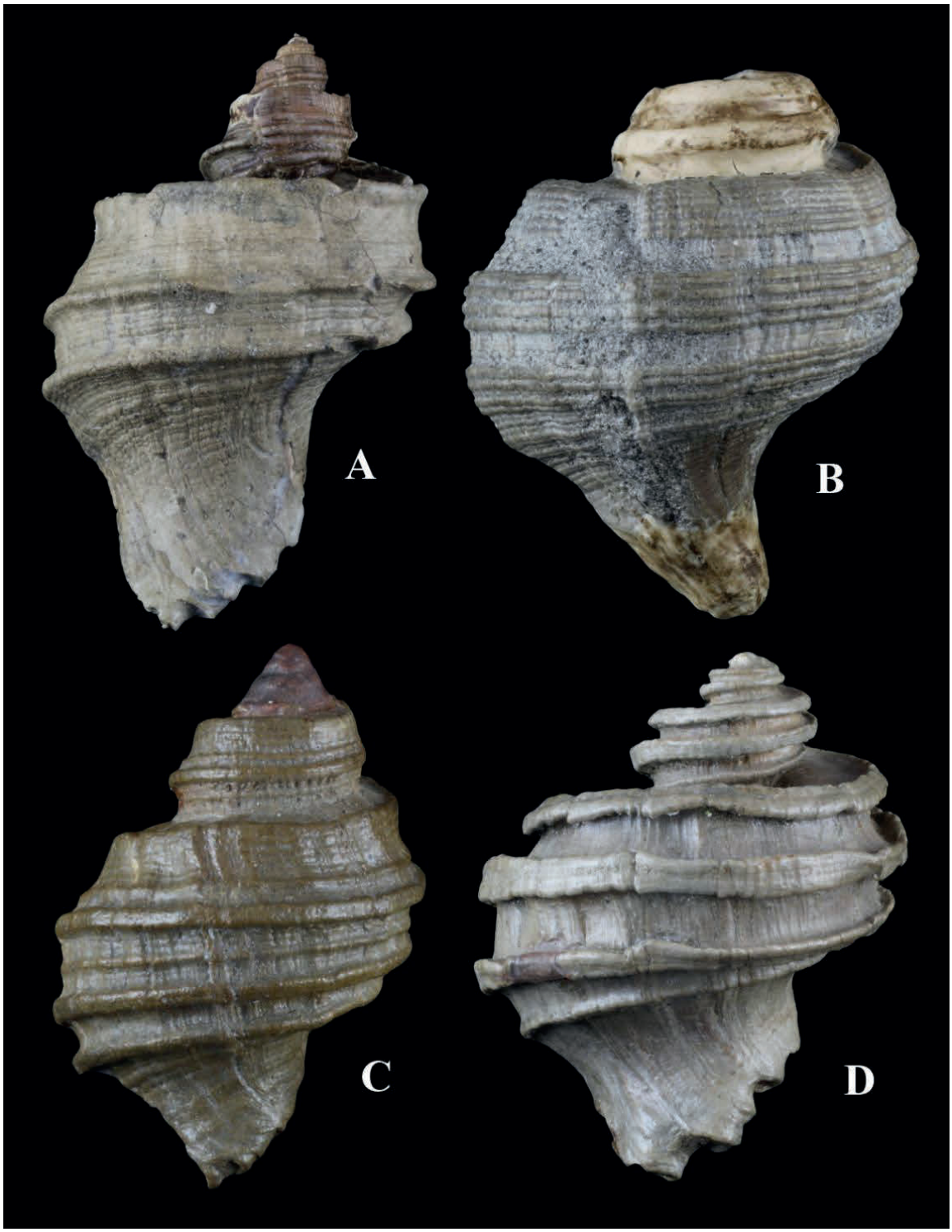

Figure 1.1 Genera of the Tribe Ecphorini.
A= *Ecphorosycon* Petuch, 1988 (*Ecphorosycon pamlico* (Wilson, 1987), length 74 mm); **B= *Siphoecphora* Petuch, 1988** (*Siphoecphora aurora* (Wilson, 1987), length 70 mm); **C= *Chesathais* Petuch, 1988** (*Chesathais ecclesiasticus* (Dall, 1915), length 50 mm); **D= *Trisephora* Petuch, 1988** (*Trisecphora tricostata* (Martin, 1904), length 35 mm).

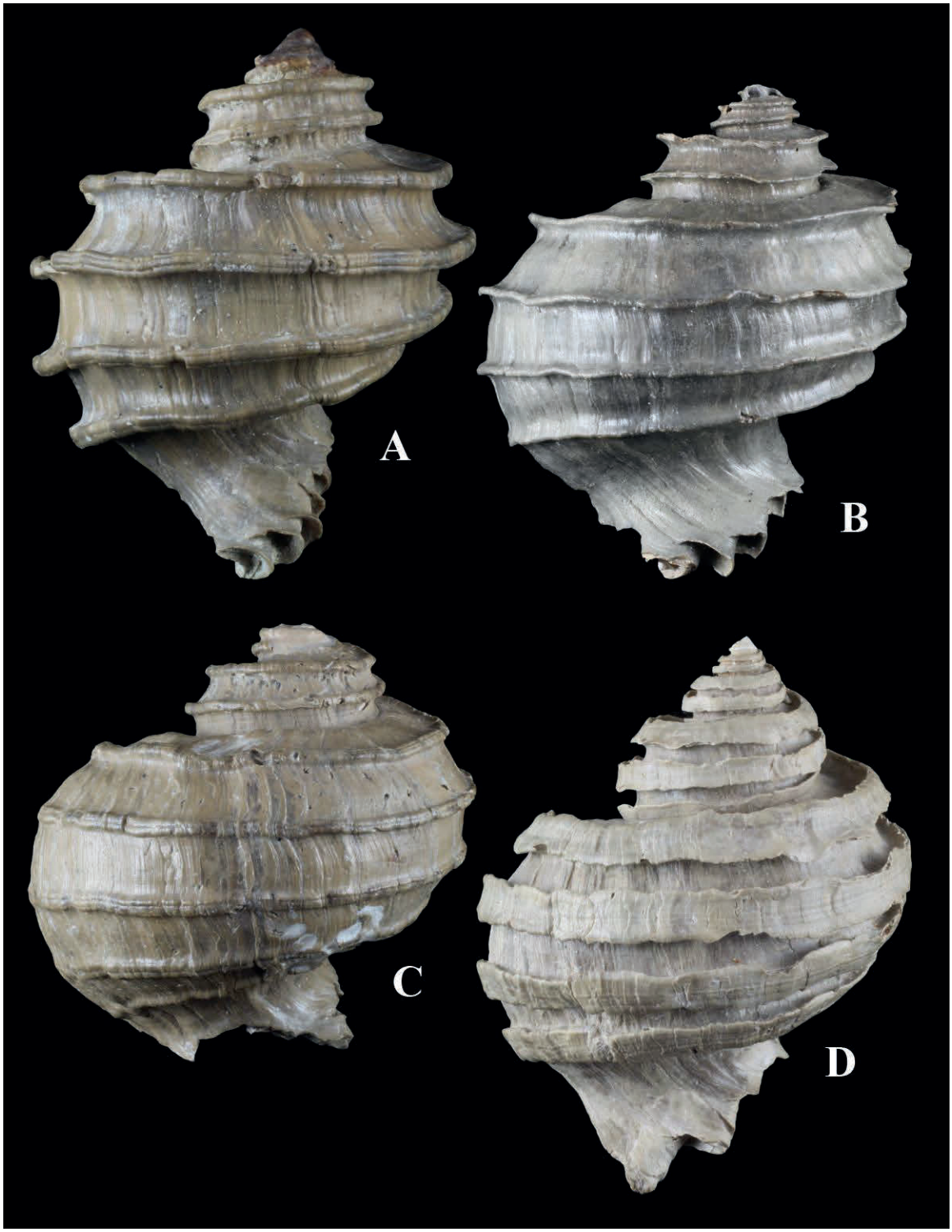

Figure 1.2 Genera of the Tribe Ecphorini.
A= *Ecphora* Conrad, 1843 (*Ecphora quadricostata* (Say, 1824), length 60 mm); **B= *Planecphora* Petuch, 2004** (*Planecphora mansfieldi* (Petuch, 1988), length 85 mm); **C= *Globecphora* Petuch, 1994** (*Globecphora floridana* (Petuch, 1988), length 110 mm); **D= *Latecphora* Petuch, 1988** (*Latecphora bradleyae* (Petuch, 1987), length 93 mm).

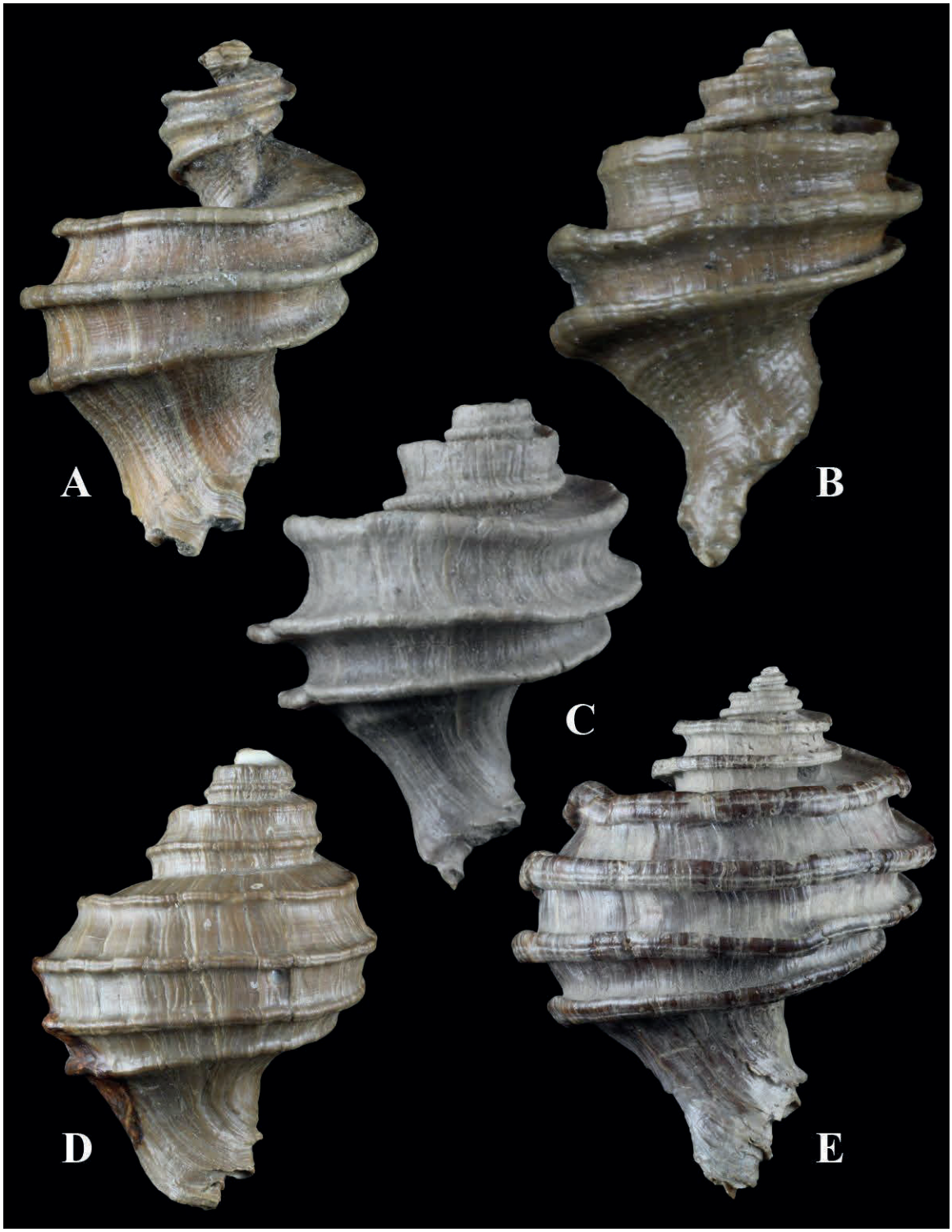

Figure 1.3 Subgenera of the Tribe Ecphorini.
A= *Eccentrella* new subgenus of *Trisecphora* (*Trisecphora (Eccentrella) eccentrica* Petuch, 1988), length 56 mm); **B= *Recurvecphora* new subgenus of *Trisecphora*** (*Trisecphora (Recurvecphora) schmidti* (Petuch, 1988), length 30 mm); **C= *Matoaka* new subgenus of *Trisecphora*** (*Trisecphora (Matoaka) patuxentia* (Petuch, 1988), length 37 mm); **D= *Rhombecphora* new subgenus of *Ecphora*** (*Ecphora (Rhombecphora) rikeri* Petuch, 1988, length 80 mm); **E= *Powhatan* new subgenus of *Ecphora*** (*Ecphora (Powhatan) gardnerae* Wilson, 1987, length 120 mm).

Ecology of the Ecphora Shells

Since the entire Tribe Ecphorini is extinct, the ecologies of the various genera can only be partially reconstructed from inferences in the fossil record. As in all the living members of the muricid Subfamily Ocenebrinae, ecphoras were carnivorous gastropods that fed by drilling holes in the shells of other mollusks, mostly bivalves, and rasping out the exposed flesh. This feeding style is readily seen in large bivalves collected from the St. Mary's Formation (Tortonian Miocene) along the St. Mary's River in Maryland. Many of the single valves of the large venerid clams *Mercenaria tetrica* and *Mercenaria mortoni* are found with over-sized holes drilled near the hinges. Some of these holes are over 5 mm in diameter, and are all of the typical muricid-type, straight-sided form. With the exception of one large muricid, *Ecphora (Powhatan) gardnerae*, all the other St. Mary's muricoideans, which include species of *Mariasalpinx*, *Urosalpinx*, *Scalarispira*, *Chesatrophon*, and *Laevityphis* are small, under 25 mm in length, and were incapable of drilling a 5 mm-diameter hole in a thick *Mercenaria* valve. This leaves only one possibility; *Ecphora (Pohatan) gardnerae* was the culprit and was the apex predator on large bivalves such as *Mercenaria*, *Dosinia*, and *Dallarca* (see Petuch and Drolshagen, 2010: 41-43: figure 3.3).

While the St. Mary's Formation contained only one species of ecphora that had virtually no competition for its food resource, the older Calvert and Choptank Formations (Langhian and Serravallian Miocene) contain molluscan assemblages with as many as five contemporaneous and sympatric ecphoras. A good example is Shattuck Zone 19, Boston Cliffs Member of the Choptank Formation, where five species occur together. To avoid competition, these species evolved different-sized shells and accordingly, preyed upon different size classes of bivalves. Small species, such as *Ecphora amyae* and *Trisecphora (Matoaka) delicata*, probably preyed upon small, thin-shelled bivalves such as *Aligenia*, *Diplodonta*, *Abra*, and *Paramya*. Larger ecphora species, such as *Ecphora (Powhatan) williamsi* and *Chesathais drumcliffensis*, would have had an abundance of large bivalve prey, including *Mercenaria capax*, *M. plena*, and *Marvacrassatella marylandica*, as these large clams form solid beds in Shattuck Zone 19; attesting to the immense biomass available to the resident ecphoras. The five Shattuck Zone 19 ecphoras make up the bulk of muricoidean predation, since only one small species of *Urosalpinx* and one *Laevityphis* are found along with the ecphoras.

While living on soft substrates on the open sea floor, and while feeding on shallow infaunal bivalves, the ecphoras were, themselves, vulnerable to molluscivore predators. Primary among these were crabs of the genera *Menippe* (Stone Crabs) and *Calappa* (Box Crabs), who used their claws to peel back the shell from the aperture and expose the unprotected snail. Ecphoras with large healed breaks are common (see Figure 1.4 A, B) and testify to the high frequency of crab attacks. Ecphoras were also often victims of drilling predation, mostly from Moon Snails of the family Naticidae. Conically-shaped, beveled naticid drill holes are commonly seen on ecphora shells, such as the one shown