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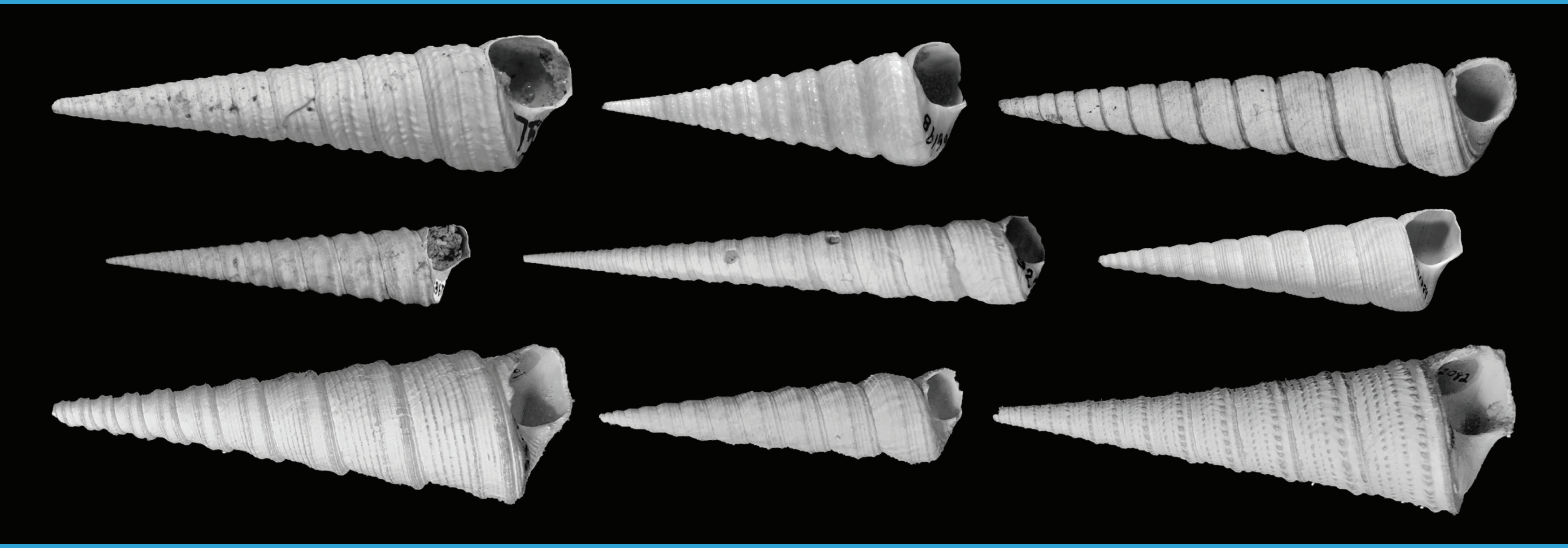

Systematics and Phylogeny of Plio-Pleistocene Species of Turritellidae (Gastropoda) from Florida and the Atlantic Coastal Plain

Dana S. Friend, Brendan M. Anderson, Elizabeth Altier, Stephanie Sang, Elizabeth Petsios, Roger W. Portell, and Warren D. Allmon

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Cover image: Plio-Pleistocene turritellid fossils (not shown at scale). Top row: *Torcula apicalis*, "*Turritella*" *miamiensis*, and *Caviturritella magnasulcus*. Middle row: *Caviturritella alumensis*, *Caviturritella etiwanensis*, *Caviturritella mansfieldi*. Bottom row: "*Turritella*" *pontoni*, "*Turritella*" *perexilis*, and "*Turritella*" *gladeensis*.

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SYSTEMATICS AND PHYLOGENY OF PLIO-PLEISTOCENE SPECIES OF TURRITELLIDAE (GASTROPODA) FROM FLORIDA AND THE ATLANTIC COASTAL PLAIN

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ABSTRACT

Turritellid gastropods are among the most widespread, abundant, and diverse mollusks in Plio-Pleistocene deposits of the Atlantic coastal plain and Florida, with at least 46 species and subspecies described over almost two centuries. Yet the systematic status of these common fossil species and their phylogenetic relationships—to each other and to turritellids living today in the western Atlantic—have never been investigated in detail. We make use of recent molecular phylogenetic work on living turritellids and new analyses of shell characters to review the group from this time interval to the present in a comprehensive phylogenetic analysis and assessment of their evolutionary history in the region. We conclude that 20 fossil and two Recent species are valid. Four of these species are placed in the genus *Torcula* Gray, 1847; five in *Caviturritella* new genus, and eleven in "*Turritella*" *sensu lato*. We identify *Torcula perattenuata* as the likely direct ancestor of one of the two turritellid species living today off the southeastern U.S. coast, *Torcula exoleta*, and we elucidate the fossil record of the other extant species, "*Turritella*" *perexilis* (senior synonym of *Turritella acropora*). We show that *Caviturritella* was extirpated from the United States Gulf and Atlantic coastal plains in the Early Pleistocene but is still represented in the western Atlantic by the living species *C. variegata* in the southern Caribbean. We also present the first detailed treatment of Plio-Pleistocene turritellid fossils from Georgia. Our analysis shows that the Plio-Pleistocene Pinecrest beds of Florida contain 18 co-occurring turritellid species, which is the highest turritellid species diversity in one formation known in the fossil record.

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INTRODUCTION

"In the Pliocene the conditions of existence for the Turritellas seem to have been particularly favorable."
- Dall (1892, pp. 314–316)

Turritellid gastropods (family Turritellidae Lovén, 1847, *sensu* Marwick, 1957) originated in the Jurassic (Das et al., 2018). They are common components of many benthic marine assemblages of Early Cretaceous to Recent age worldwide (Allmon, 1988, 2007, 2011a), and they are among the most biostratigraphically important molluscan groups for this time interval (e.g., Kauffman, 1977; Sohl, 1977; Squires, 1988). They are especially abundant and diverse in Plio-Pleistocene sediments of the United States Atlantic coastal plain and Florida (e.g., Allmon, 1992a; Allmon et al., 1995; Fallon et al., 2014), where at least 46 fossil and two Recent species and subspecies have been named over almost 200 years. In this paper, we report the results of a detailed analysis of these forms, and find that only 20 fossil and two Recent species should be recognized as valid species (Table 1).

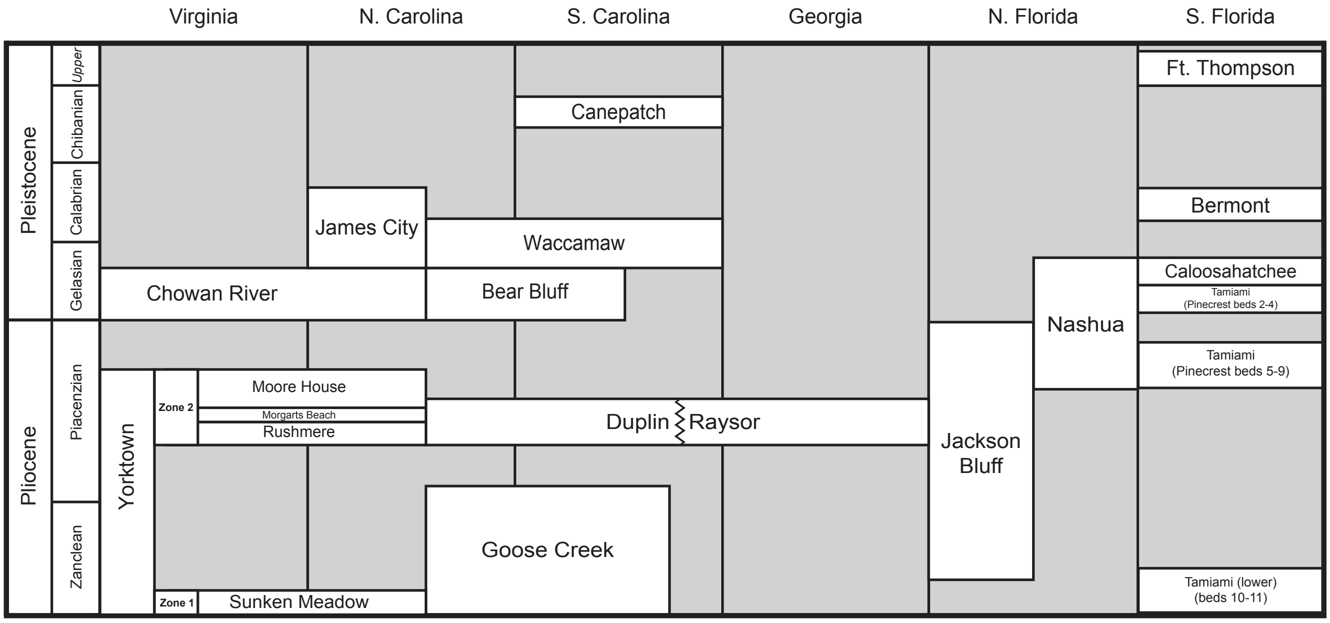
Phylogenetic analysis in extant and fossil turritellids has long been difficult due to a lack of molecular data, a paucity of shell characters, presumed widespread homoplasy, and nomenclatural confusion (Allmon, 1996; Beu, 2010). This has begun to change with more recent work, and the present paper is the first analysis of these fossil turritellids to take recent molecular phylogenetic analyses into account (Anderson, 2018; Sang et al., 2019). The use of morphological characters can provide support for molecular phylogenies, often resolving internal nodes not recovered by means of molecular data (e.g., Walberg et al., 2005). With this in mind, we provide a hypothesis based on a parsimony analysis of morphological (conchological) data. Our results provide a framework of morphological characters that can serve as a basis for a more comprehensive understanding of fossil and Recent turritellid evolutionary relationships in other regions of the world. We present here the first-ever phylogenetic analyses of Neogene North American turritellids, and we connect living North American species to fossil lineages present in the southeastern United States. During this study, we observed in some turritellids a shell character previously unnoted: an opening in the base of the shell where an umbilicus is sometimes located. We have named this feature a hollow newel (Friend et al., 2023), and it is an important synapomorphy for recognizing a clade in these turritellids, for which we herein propose the genus *Caviturritella* Friend and Anderson. Our analysis does not include species assigned to the turritellid genus *Vermicularia* Lamarck, 1799, which are treated comprehensively elsewhere (Anderson, 2018).

Our results have important implications for phylogenetic analysis of other fossil turritellids worldwide. We also present a general discussion of the complex and topic of turritellid genera, which has bedeviled systematists for decades and hindered a general understanding of the evolution of this important group of gastropods. As the first large-scale phylogenetic analysis of fossil and Recent turritellids using both molecular data and a large number of conchological characters, this study provides a basis for similar analyses of turritellids elsewhere, including attempts to place other species into appropriate genera.

GEOLOGICAL SETTING

The Plio-Pleistocene stratigraphic record of the U.S. Atlantic coastal plain is a complex horizontal and vertical mosaic of mostly unlithified, variously fossiliferous sands, silts, and clays, which accumulated in a series of embayments during sea level highstands (Ward and Strickland, 1985; Ward and Blackwelder, 1987; Ward et al., 1991; Ward, 1992). Exposures are present along rivers and creeks, and in quarries. Geological and paleontological studies of the region date back to colonial times (Ward and Allmon, 2019). Although stratigraphic relationships began to be well-understood in the mid-twentieth century, correlations of certain units have continued to improve since then (Ward and Blackwelder, 1987; Ward et al., 1991) and chronostratigraphic relationships continue to be refined to the present day (e.g., Saupe et al., 2014; Sime and Kelley, 2016; Johnson et al., 2019; Dowsett et al., 2021). The correlations presented in Text-fig. 1 represent a summary of the most recent stratigraphic interpretations.

The Plio-Pleistocene stratigraphic record of Florida is an even more complex mosaic of variously fossiliferous siliciclastic sands and siliciclastic-bearing carbonates (shell beds) (Jones, 1997; Lyons, 1991; Scott, 1997). In northern Florida (i.e., the central panhandle), this record is exposed at a few long-studied riverbank exposures, such as Alum Bluff (Liberty County) and Jackson Bluff (Leon County) (Puri, 1966; Means, 2010). In southern Florida (i.e., south of the latitude of Tampa Bay), the record is known principally from sections temporarily exposed in quarries ("pits") and canals, and from cores and a few riverbanks (Scott, 1992, 1997). Although stratigraphic and paleontological works date back more than a century (e.g., Heilprin, 1886; Dall, 1892), both biostratigraphy and lithostratigraphy have suffered from considerable confusion and instability in terminology, especially in the southern part of the peninsula. This has been due to a combination of factors, including paucity of explicit biostratigraphic analyses, ephemeral outcrops, and extreme lateral variability of facies (Lyons, 1991; Scott, 1992, 1997, 2001; Allmon, 1993; Jones, 1997). Only in the last 20 years have stratigraphic nomenclature and biostratigraphic correlations begun to stabilize.



Text-fig. 1. Stratigraphic nomenclature and generalized correlation of Plio-Pleistocene geologic units discussed in this study. The Yorktown Formation of Virginia and North Carolina includes (from youngest to oldest) the Moorehouse, Mogarts Beach, and Rushmere members (also known as Zone 2) and the Sunken Meadow Member (also known as Zone 1). The Tamiami Formation of Florida includes (from youngest to oldest) the Pinecrest beds (upper = units 2–4, lower = 5–9), the Ochopee Limestone Member, and the Buckingham Limestone Member. As stated by Hendricks (2009: p. 9), "Absolute ages for most formations and/or their boundaries are controversial" (also see Lyons, 1991; Campbell et al., 1993; Ward and Gilinsky, 1993; Allmon et al., 1996; Hendricks, 2009; Kittle et al., 2013; Saupe et al., 2014; Dowsett et al., 2021; and references therein).

In Florida, the Plio-Pleistocene Tamiami Fm. is a poorly-defined lithostratigraphic unit containing a wide range of mixed carbonate-siliciclastic facies and associated fossil assemblages (Missimer, 1992; Scott, 1992, 1997, 2001; Portell et al., 2012). It is present in the subsurface across most of the southern part of the peninsula, but natural surface exposures are few. Many named and unnamed subunits have been recognized within the Tamiami Fm. (see, e.g., Petuch and Roberts, 2007), but not all have achieved widespread acceptance or use. Subunits include the Buckingham Limestone; Ochopee Limestone; Bonita Springs Marl; several unnamed sands and limestone facies; Golden Gate Reef Member; an oyster (*Hyotissa* Stenzel, 1971) facies; and the Pinecrest Sand or Pinecrest beds. The Pinecrest beds, which are a particular focus of the present paper, are the best-known and perhaps most widespread facies in the Tamiami Fm. They contain abundant, diverse, and well-preserved fossil mollusks (Allmon, 1993; Allmon et al., 1996; Portell et al., 2012). Petuch (1982) divided the Tamiami Fm. at Sarasota, Florida into 11 numbered biostratigraphic units, and this scheme has been used with modifications by most subsequent workers. Today Petuch's unit 1 is placed in the Caloosahatchee Fm., units 2–9 are placed in the Pinecrest beds, and units 10 and 11 are considered lower Tamiami Fm. (Portell et al., 2012). Based on $^{87}Sr/^{86}Sr$ isotope dating of bivalves, paleomagnetism, and invertebrate and vertebrate biochronology, Jones et al. (1991) estimated the age of units 2 through 4 at Sarasota as being 2.25 (± 0.25) Ma and units 5 through 10 as being 3.0 (+0.5) Ma. The boundary between Pliocene and Pleistocene is set at 2.588 Ma (Gradstein et al., 2020). Therefore, given the minimum age of 2.0 Ma and maximum age of 2.5 Ma, units 2–4 fall within the Early Pleistocene. Units 5–10, with a minimum age of 2.5 Ma and a maximum age of 3.5 Ma, straddle the Pliocene-Pleistocene boundary, and the underlying unit 11 is probably Late Pliocene in age. Ongoing research may alter some of these dates.

The Plio-Pleistocene fossiliferous sands and limestones overlying the Pinecrest beds have long been referred to as "formations" (e.g., Cooke, 1945; Puri and Vernon, 1964; Vernon and Puri, 1964; Brooks, 1982), but most are probably biostratigraphic units (Scott, 1992, 2001). Scott (1992) suggested grouping the latest Pliocene through Late Pleistocene Caloosahatchee, Bermont, and Fort Thompson "formations" into a single lithostratigraphic unit, the Okeechobee Fm. This proposal has not been widely adopted, however, and the traditional units continue to be treated as separate formal or informal stratigraphic units in recent literature (e.g., Harper, 2002; Dietl et al., 2004; Knowles et al., 2009; Portell and Kittle, 2010; Tao and Grossman, 2010; Scott, 2011; Stringer et al., 2017; Johnson et al., 2019) (Text-fig. 1).

Table 1. Previously described turritellid taxa (other than *Vermicularia*) from the Pliocene–Recent of the Atlantic Coastal Plain, and their designations in this paper.

Original species/subspecies name	**Assigned to this species herein**
acropora Dall, 1889	"*Turritella*" *perexilis* Conrad, 1875
alaquaensis Mansfield, 1935	*Torcula cookei* (Mansfield, 1930)
alticostata Conrad, 1834	"*Turritella*" *alticostata* Conrad, 1834
alumensis Mansfield, 1930	*Caviturritella alumensis* (Mansfield, 1930)
apicalis Heilprin, 1886	*Torcula apicalis* (Heilprin, 1886)
beaufortensis Ward and Blackwelder, 1987	"*Turritella*" *alticostata* Conrad, 1834
bipertita Conrad, 1844	*nomen nudum*
burdenii Tuomey and Holmes, 1856	*nomen nudum*
burnsii Dall, 1892	"*Turritella*" *perexilis* Conrad, 1875
buckinghamensis Mansfield, 1939	*nomen nudum*
carolinensis Conrad, 1875	*nomen nudum*
cingulata Heilprin, 1886	"*Turritella*" *gladeensis* Mansfield, 1931
clarksvillensis Mansfield, 1930	*Torcula clarksvillensis* (Mansfield, 1930)
cookei Mansfield, 1930	*Torcula cookei* (Mansfield, 1930)
duplinensis Gardner and Aldrich, 1919	"*Turritella*" *fluxionalis* Rogers and Rogers, 1837
etiwanensis Tuomey and Holmes, 1856	*Caviturritella etiwanensis* (Tuomey and Holmes, 1856)
exaltata Tuomey and Holmes, 1856	*nomen nudum*
exoletus Linnaeus, 1758	*Torcula exoleta* (Linnaeus, 1758)
fluxionalis Rogers and Rogers, 1837	"*Turritella*" *fluxionalis* Rogers and Rogers, 1837
gardnerae Mansfield, 1930	*Caviturritella alumensis* (Mansfield, 1930)
gladëensis Mansfield, 1931	"*Turritella*" *gladeensis* Mansfield, 1931
harveyensis Mansfield, 1930	*Torcula cookei* (Mansfield, 1930)
holmesii Dall, 1892	*Caviturritella mansfieldi* (Olsson, 1967)
intermedia Dall, 1892	"*Turritella*" *perexilis* Conrad, 1875
jacksonensis Mansfield, 1930	"*Turritella*" *perexilis* Conrad, 1875
jacula Gardner, 1947	"*Turritella*" *jacula* Gardner, 1947
leonensis Mansfield, 1930	"*Turritella*" *perexilis* Conrad, 1875
magnasulcus Petuch, 1991	*Caviturritella magnasulcus* (Petuch, 1991)
mansfieldi Olsson, 1967	*Caviturritella mansfieldi* (Olsson, 1967)
mediosulcata Dall, 1892	*Torcula apicalis* (Heilprin, 1886)
miamiensis Petuch, 1994	"*Turritella*" *miamiensis* (Petuch, 1994)
obsoleta Dall, 1892	*Torcula perattenuata* (Heilprin, 1886)
ochlockoneensis Mansfield, 1930	"*Turritella*" *perexilis* Conrad, 1875
perattenuata Heilprin, 1886	*Torcula perattenuata* (Heilprin, 1886)
perexilis Conrad, 1875	"*Turritella*" *perexilis* Conrad, 1875
perincisa Dall, 1892	"*Turritella*" *perexilis* Conrad, 1875
permenteri Mansfield, 1935	*Torcula cookei* (Mansfield, 1930)
pilsbryi Gardner, 1928	"*Turritella*" *pilsbryi* Gardner, 1928
pontoni Mansfield, 1931	"*Turritella*" *pontoni* Mansfield, 1931
seminole Petuch, 1994	"*Turritella*" *seminole* Petuch, 1994
striata Tuomey and Holmes, 1856	*nomen nudum*

Table 1, continued.

Original species/subspecies name	Assigned to this species herein
subannulata Heilprin, 1886	"*Turritella*" *perexilis* Conrad, 1875
tensa Dall, 1892	*Torcula apicalis* (Heilprin, 1886)
terebriformis Dall, 1892	*nomen nudum*
terstriata Rogers and Rogers, 1837	*Caviturritella terstriata* (Rogers and Rogers, 1837)
undula Dall, 1892	*Torcula perattenuata* (Heilprin, 1886)
vaughanensis Mansfield, 1935	*Torcula cookei* (Mansfield, 1930)
virginica Campbell, 1993	"*Turritella*" *virginica* Campbell, 1993
wagneriana Olsson and Harbison, 1953	"*Turritella*" *wagneriana* Olsson and Harbison, 1953

TAXON SAMPLING AND SPECIMEN REPOSITORIES

This paper treats only species that lived during the Pliocene and later. This was an arbitrary decision driven by the need to circumscribe the project. Post-Miocene faunas have traditionally been studied separately from older assemblages, and significant unconformities are present between the Pliocene and Miocene units across much of the coastal plain. It is clear, however, that some Pliocene and later turritellid species either occur or have obvious close relatives in older deposits, and these should be the focus of future detailed analyses.

Turritellid taxa used for this study are listed in Table 1 and the geographic locations of examined material are illustrated in Text-fig. 2 and listed in Appendix 1. *Turritella* species names have been used with widely varying accuracy in the Atlantic coastal plain and Florida over almost two centuries, and the appearance of a particular name in a list that has not been verified is therefore of uncertain value. We primarily relied on fossil specimens in collections for occurrence data. For literature occurrences without referenced specimens or illustrations, we annotate with a "?" before the reference. We have chosen to omit locality records reported in some publications that were not subject to peer-review (Petuch, 1994, 2004; Petuch and Roberts, 2007) because previous experience has suggested these may be unreliable (Allmon, 2005, 2011b). In addition, the quality of illustrations in some of these publications makes verification of species identifications difficult or impossible.

Most of the studied material is held in collections at the Paleontological Research Institution (PRI) and the Florida Museum of Natural History, University of Florida (UF). Additional material, mainly type and figured specimens, is deposited in the following institutions: American Museum of Natural History (Fossil Invertebrates), New York (AMNH FI); Academy of Natural Sciences of Drexel University, Philadelphia (ANSP); Carnegie Museum of Natural History, Pittsburgh (CM); Departments of Invertebrate Paleontology

Text-fig. 2. Geographic distribution of localities referenced in the present manuscript. For a complete list of locality information see Appendix 1.

and Mollusks, Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZIP, MCZM); Department of Geology, University of North Carolina, Chapel Hill (UNC); National Museum of Natural History (Invertebrate Paleontology and Mollusk Collections), Smithsonian Institution, Washington, DC (USNM IP, USNM MO); Virginia Museum of Natural History, Martinsville (VMNH); Natural History Museum of Los Angeles County Malacology Collection, Los Angeles, CA (LACM); and the Wagner Free Institute of Science, Philadelphia (WFI).

TAXONOMIC CONCEPTS

Species Concept

In this paper, we use the conception of fossil species advocated by Allmon (1996, p. 13): "fossil species are groups of morphologically distinct populations within which variation is of the magnitude displayed by closely-related living species and their local populations, and between which the differences are of the kind and degree expected to result from reproductive isolation of populations in such related or analogous species" (see also Allmon, 2016). Almost all modern turritellid gastropod species are based exclusively on shell characters (e.g., Ryall and Vos, 2010; Herbert, 2013), but there are unfortunately no detailed studies of genetic, anatomical, or behavioral differences between species or populations defined by differences in shell form. We therefore use ranges of conchological variation observed in most traditionally recognized modern turritellid species (e.g., Charles, 1977; Allmon, 1996) as a guide for ranges of variation in fossil species.

Genus Concept

Turritellid genus-level systematics has long been unclear in regards to how species should be assigned to genera and how many genera should be recognized (Allmon, 1996). It is commonly accepted that most species placed in the genus *Turritella s.s.* (*sensu stricto*) Lamarck, 1799 do not belong there, but lacking a comprehensive revision of the group, the name remains in widespread use for most turritellid species. For this reason, *Turritella* has frequently been considered a classic example of a "wastebasket taxon" (Allmon, 1996; Plotnick and Wagner, 2006). Genera are of course constructed arbitrarily (Allmon 1992b; Hendricks et al., 2014; Garbino, 2015; Villmoare, 2018), but should represent monophyletic clades and thereby convey hypothesized evolutionary relationships (Hennig, 1965, 1966; Dubois, 1982; Hendricks et al., 2014; Villmoare, 2018). The frequent use of a single *sensu lato* genus "*Turritella*" existing from the Jurassic–Recent obscures biogeographic, biostratigraphic, and phylogenetic patterns in anciently diverging clades and limits our ability to use these extremely abundant fossils in macroevolutionary studies (Harzhauser and Landau, 2019). Numerous genus names have been proposed for clades within the family (Allmon, 2011a), but few are widely used for extant species beyond *Maoricolpus* Finlay, 1926, *Mesalia* Gray, 1847, *Protoma* Baird, 1870, *Turritella* Lamarck, 1799, and *Vermicularia* Lamarck, 1799. This is in part because the shell features that have been used to identify turritellid genera frequently require either the preservation of the protoconch and early neanic whorls or are subtle combinations of growth line and/or sculpture features that require careful examination for proper assessment (Marwick, 1957; Garrard, 1972; Allmon, 1992b).

We propose that turritellid genera should be erected when biogeographically plausible clades are typified by characters or combinations of characters that are rare across turritellids as a whole (also see Harzhauser and Landau, 2019). The unique appearance of a particular characteristic feature (e.g., hollow newel morphology; see Friend et al., 2023) in several species in one region strongly implies that those species are likely to be each other's closest relatives. The genus-rank clades discussed herein appear to have originated in or prior to the Miocene and are therefore comparable in age to clades given generic rank in recent molecular phylogenies of other gastropod families (e.g., 10–55 my divergence times of clades within Conidae, Muricidae, and Littorinidae; Castelin et al., 2012; Claremont et al., 2013; Puillandre et al., 2014; Reid et al., 2012). Recently, multi-gene molecular phylogenies for turritellids have become available—with particular emphasis on western Atlantic/eastern Pacific species—allowing an informed assessment of how well particular morphological characters may correspond to phylogenetic relationships (Anderson, 2018; Sang et al., 2019).

Where morphological features, or unique combinations of features, can be found to consistently describe clades—even if these features are limited in number or require experience to properly assess—we argue that turritellid species should be assigned membership in genera to convey important information about their relationships and evolutionary history. For example, the two extant species *Turritella exoleta* Linnaeus, 1758 and *Turritella radula* Kiener, 1843 are both consistent with the morphological definition of *Torcula* Gray, 1847. These form a clade that is itself more distant from the remaining extant neotropical American turritellids than those non-*Torcula* American species are from southeast Asian forms assigned to *Turritella sensu stricto* (Sang et al., 2019). Therefore, referring to all of these species as *Turritella sensu lato* is less informative of evolutionary history than assigning each of these clades to its own genus. Yet when species cannot be confidently assigned to a turritellid genus, we resort to the convention of naming them to "*Turritella*" *sensu lato* (e.g., Allmon, 1996; DeVries, 2007; Anderson and Allmon, 2020), largely because we are cautious in assigning species to genera with no morphological synapomorphies. To be clear, we do not believe these are closely related to *Turritella s.s.* (i.e., *sensu* Marwick, 1957), which is biogeographically implausible for the Americas, being restricted to the tropical Indo-Pacific.

MORPHOLOGICAL FEATURES OF TURRITELLID GASTROPODS

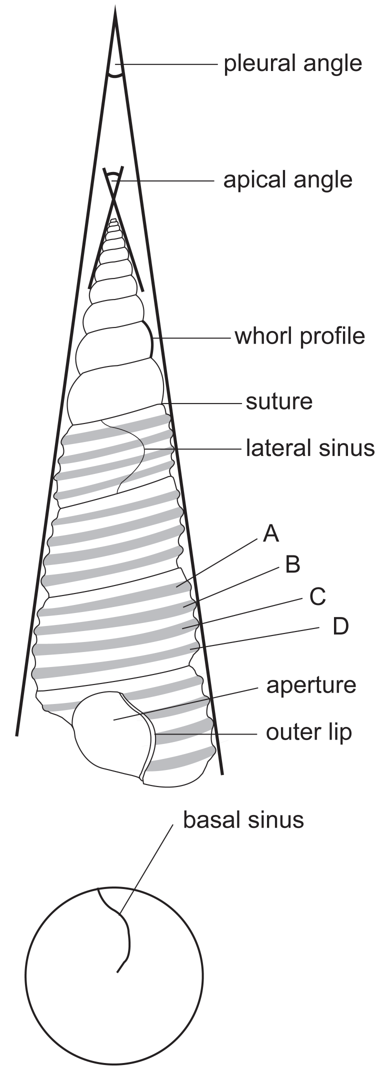
For descriptions of shell morphology we follow Allmon (1996) and Harzhauer and Landau (2019). We recognize several principal sources of morphological information available to help in describing and delineating species: (1) gross morphology (i.e., size, angles of growth, whorl profile, suture depth); (2) protoconch form and number of whorls; (3) apical spiral sculpture ontogeny; (4) teleoconch sculpture; (5) basal and lateral growth lines (sinus); and (6) aperture.

Gross Morphology

In describing gross morphology we provide measurements of maximum length (ML), maximum width (MW), pleural angle (PA), and apical angle (AA) (Text-fig. 3). Description of shell sizes within species descriptions are relative to the other species included in this paper. Easily observed is whorl profile (shape of an individual whorl) and the depth and/or form of the suture. Allmon (1996) proposed a classification based on whorl profiles, modified from Ida (1952) and Marwick (1971b), which we use here (Text-fig. 4). Both of these characters may change during the course of an individual's life and so may be described in terms of juvenile and mature adult profiles.

Protoconch

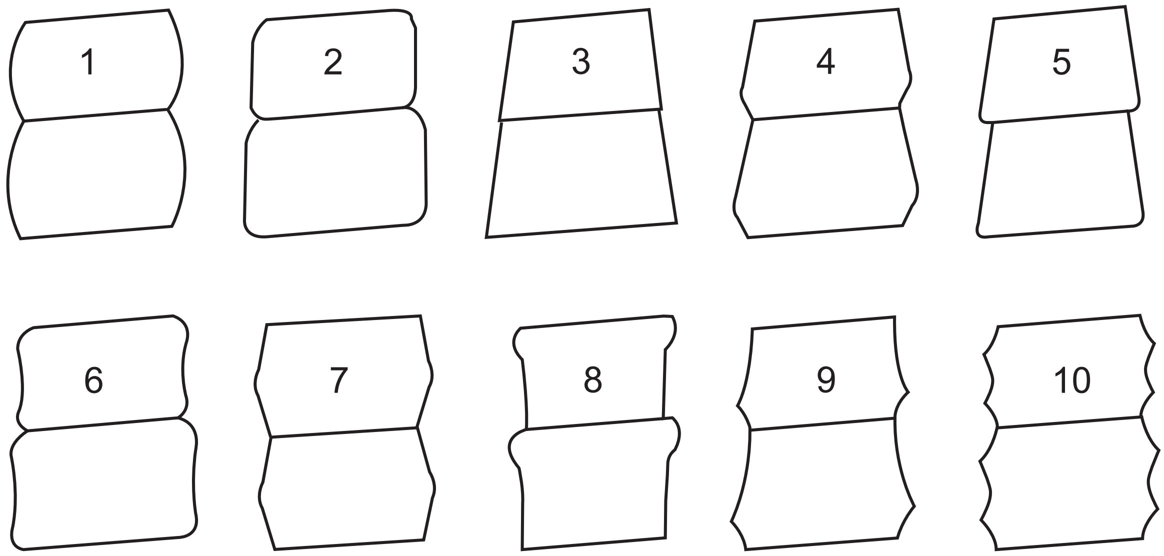
All known turritellid protoconchs consist of between one and four (or rarely five) smooth, unsculptured whorls (Allmon, 1996, 2011). Associated with differences in whorl number and diameter are often differences in overall form, which may vary from having a first whorl well immersed within the others to an erect, high-spired cone. The boundary with the teleoconch is marked only by the development of spiral sculpture, which may be quite faint initially (Text-fig. 5). All protoconchs observed in the present study are similar in form (paucispiral). For those species for which representative protoconchs could be found (15 of the 20 fossil species we accept as valid), the structure was detached from the shell, cleaned in an ultrasonic bath, and mounted on an aluminum stub. The specimens were imaged using the Jeol Scanning Electron Microscope at PRI.



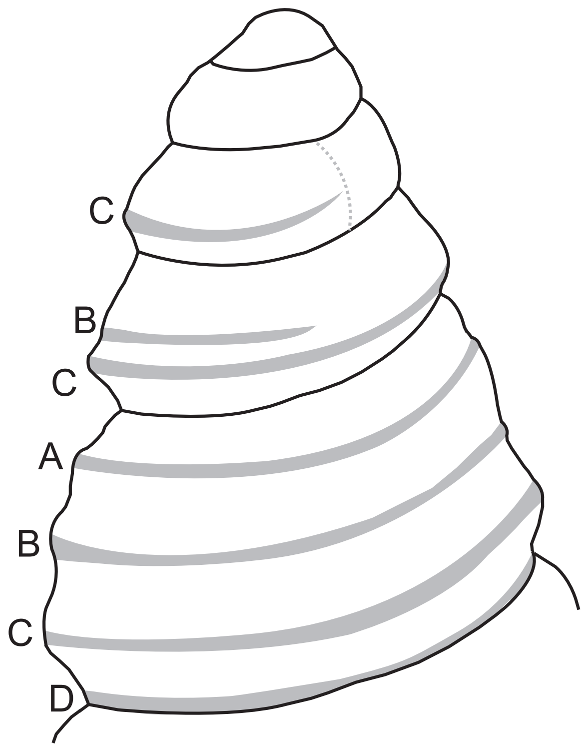
Text-fig. 3. Gross morphological features of adult turritellid shells used in classification and species description. Measurements to describe maximum length (ML), maximum width (MW), pleural angle (PA), and apical angle (AA) (adapted from Harzhauer and Landau, 2019).

Ontogeny of Spiral Sculpture

The order of the development of spiral sculpture at the protoconch-teleoconch boundary is of particular interest (Text-fig. 5) because turritellid systematics depends heavily on recognition of the early ontogenetic sequence of the introduction of spiral cords on the shell (see Allmon, 1996). Marwick (1957) highlighted the importance in the order of appearance of the cords on the neanic whorls and used a lettering system for the spiral cords in which B was the medial primary, D the anterior-most primary generally involved with the suture, A was the first to appear adapical to B, and C the first to appear abapical to B, between B and D (Marwick, 1957, p. 148). The order of introduction of these



Text-fig. 4. Classification of whorl profiles following Allmon (1996) and Harzhauser and Landau (2019). 1, convex, 2 = subquadrate, 3 = flat-sided, 4 = frustate, 5 = imbricate, 6 = concave, 7 = keeled, 8 = telescoped, 9 = campanulate, 10 = double campanulate.

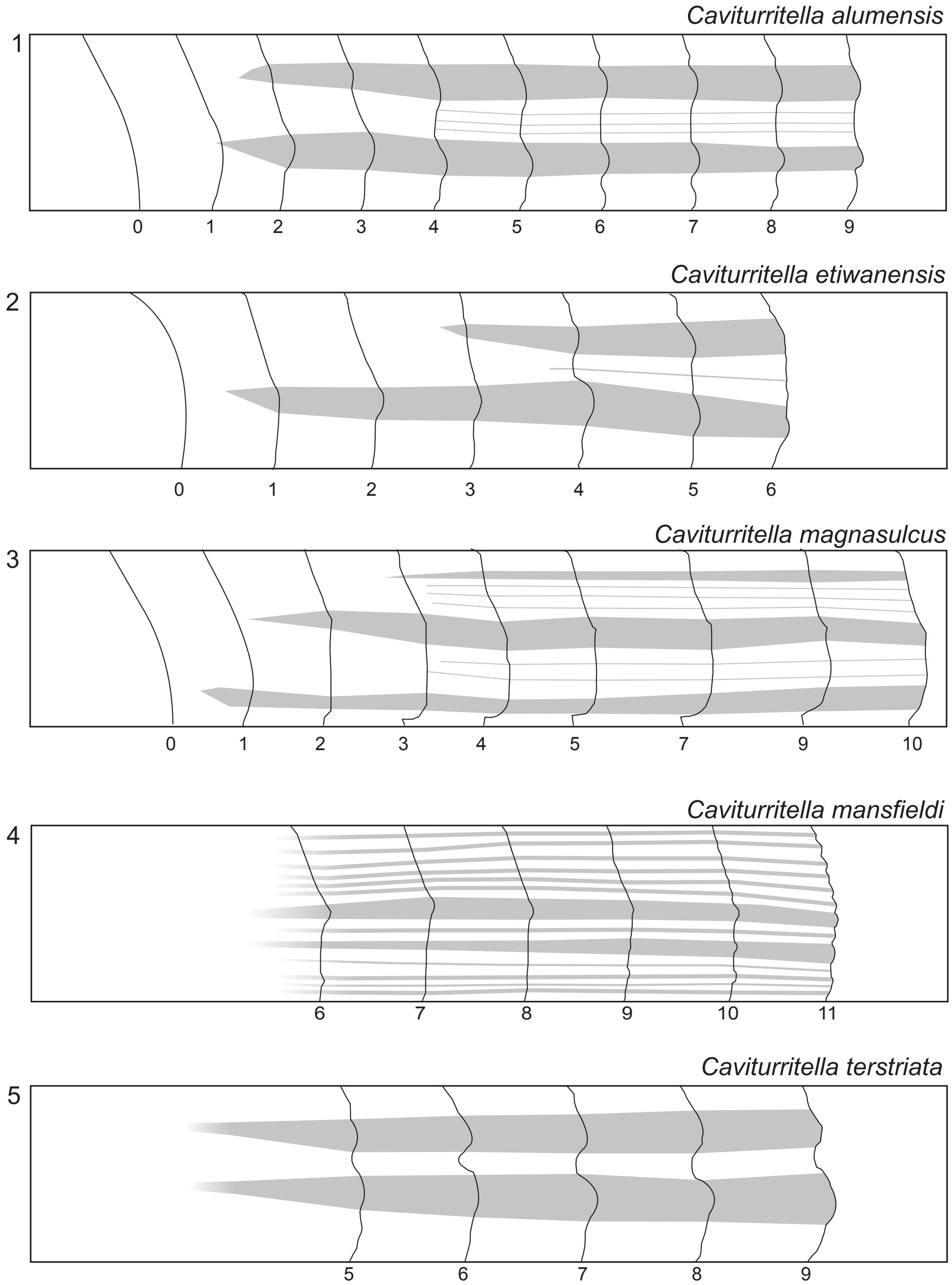


Text-fig. 5. Initiation of primary spiral cords at the protoconch-teleoconch boundary (illustrated above as a dashed line). In this example the C cord appears first, followed by the B cord, and the A cord last. The D cord is the anterior-most primary generally involved in the suture.

spiral cords can be expressed as an "apical sculpture formula"; thus C1B2A3 means that the C cord appears first, followed by the B cord, and then the A cord. This system was also used by Kotaka (1959) and Allmon (1996) and is followed herein. We designate as A' a prominent cord adapical of A that appears in the early teleoconch whorls, within 2–3 whorls of earliest primaries, and retains similar strength as other primaries. Schematic illustrations depicting the ontogenetic development of spiral cords in the species discussed here are shown in Text-figs. 6–9. As in Allmon (1996), we refer to these as "Marwick Diagrams" in recognition of the use of a similar technique for illustrating turritellid ontogeny by Marwick (1971b). Numbers at the bottom represent whorl number, the protoconch and youngest whorls being on the left. All whorl profiles are depicted standardized to the same height. Beaded cords are marked with white dots. We lack protoconchs of several species so beginning whorl number in these species is an approximation.

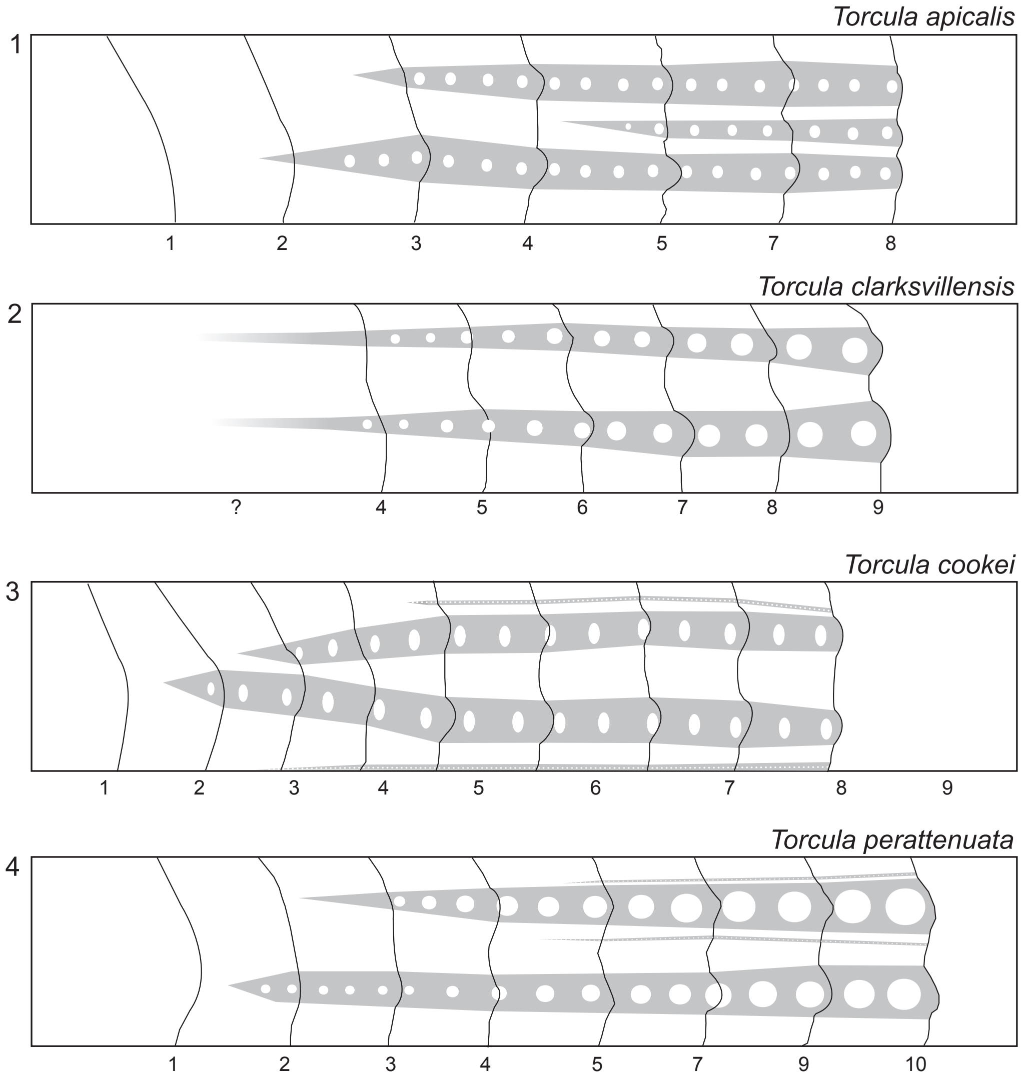
Teleoconch

The turritellid shell is an accretionary structure on which spiral cords are formed at points along the growing edge, and there is usually no clear morphological mark of the border between a given cord and the troughs lying to each side. Our limited understanding of the mechanisms of formation of a shell and its sculpture also restricts our insight on issues of homology regarding spiral cords. For these reasons it has remained unclear whether each spiral cord can be treated as an individualized part (character) of the shell. Moreover, the presence of spiral cords of varying prominence (i.e., primary, secondary, etc.) on the same shell adds complexity



Text-fig. 6. Marwick diagrams depicting the ontogenetic development of spiral cords in *Caviturritella* Friend and Anderson, n. gen. (herein). Numbers at the bottom represent whorl number, the protoconch and youngest whorls being on the left. All whorl outlines are standardized to the same height. Note that *Caviturritella alumensis* cord A does not appear until ~whorl 14 (not shown). We lack protoconchs of *C. terstriata* and *C. mansfieldi* and so therefore the beginning whorl numbers are approximations. See pp. 7, 8 for more information on these schematic diagrams.

to the problem. It is therefore crucial that all assumptions inherent in the use of spiral cords in gastropod systematics are stated clearly. Here we assume that spiral ribs in similar relative vertical position on the whorl, and their order of appearance, represent homologous characters (Text.-fig. 5; see Allmon, 1996). Data on traditional teleoconch characters (the presence, spacing, and relative strength of spiral cords on the whorls) were collected through the observation of the various shell structures, often under a binocular microscope for better accuracy.



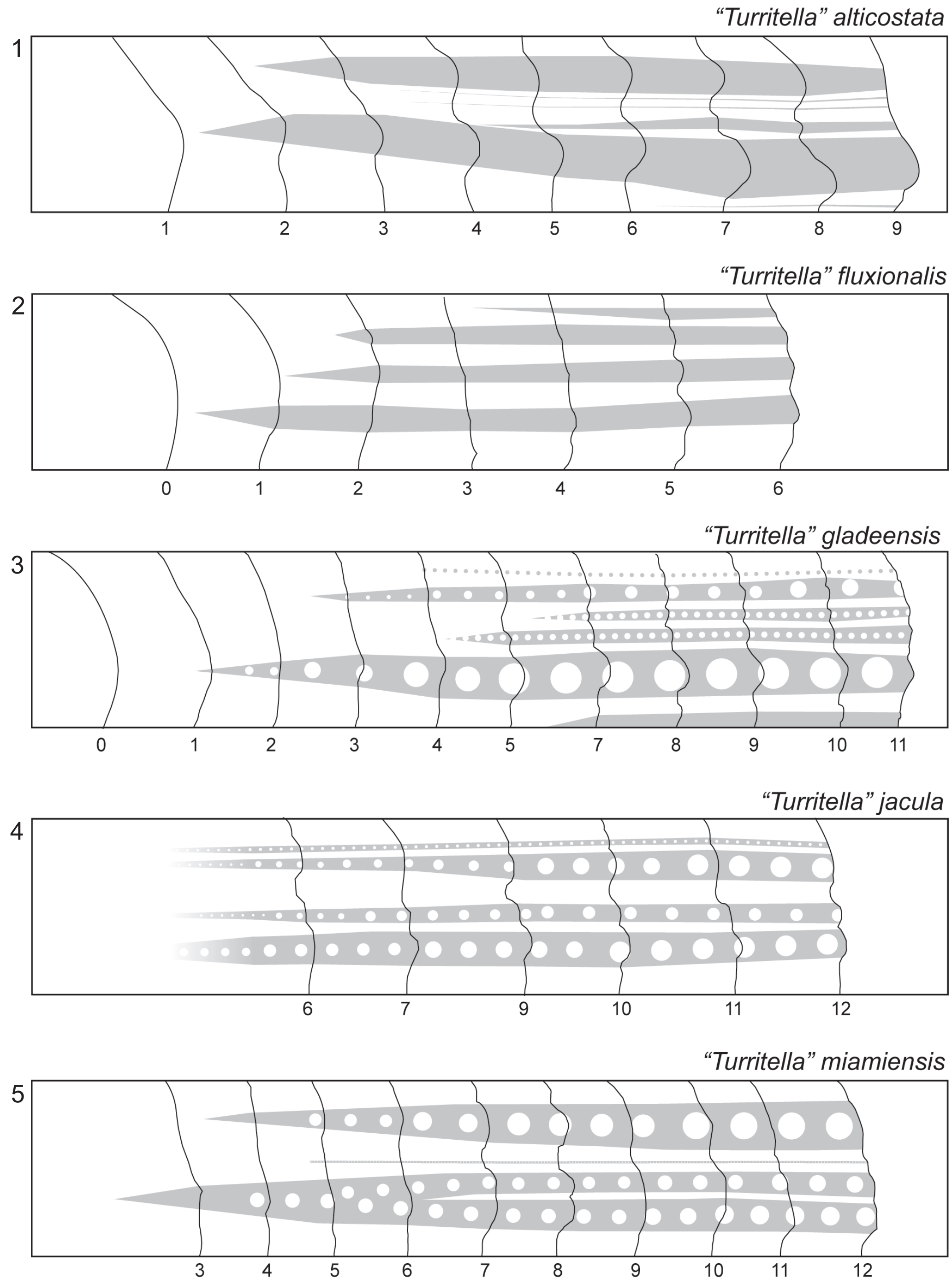
Text-fig. 7. Marwick diagrams depicting the ontogenetic development of spiral cords in *Torcula* Gray, 1847. We lack protoconchs of *Torcula clarksvillensis* so beginning whorl number is an approximation.

Growth Lines

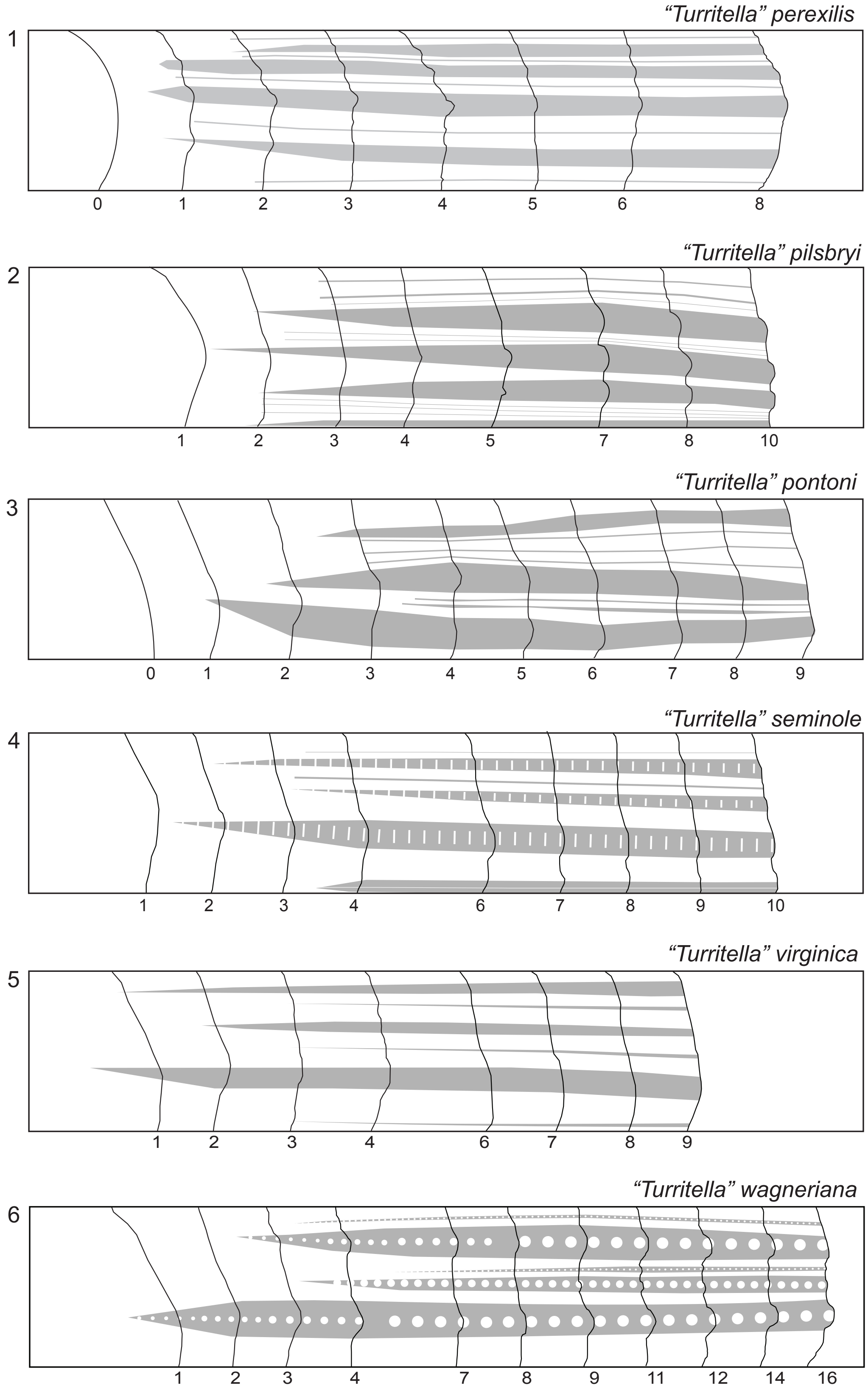
Marwick (1957) drew special attention to the shape of the trace of the outer lip of the aperture (= growth line), using the terms "lateral sinus" for the trace on the whorl sides and the "basal sinus" for the trace on the whorl base (Text-fig. 10). The various types of the growth lines, separated in lateral and basal sinuses, were described by Allmon (1996), emphasizing the depth of the sinus, its relative position within the whorl, and the number of inflection points (see section "Characters and Character States," p. 42). In many cases, growth lines do not develop a full inflection point but display a sinuosity against growth direction close to the adapical and/or abapical suture. We follow Harzhauer and Landau (2019) in describing these as "faint inflection points."

Aperture

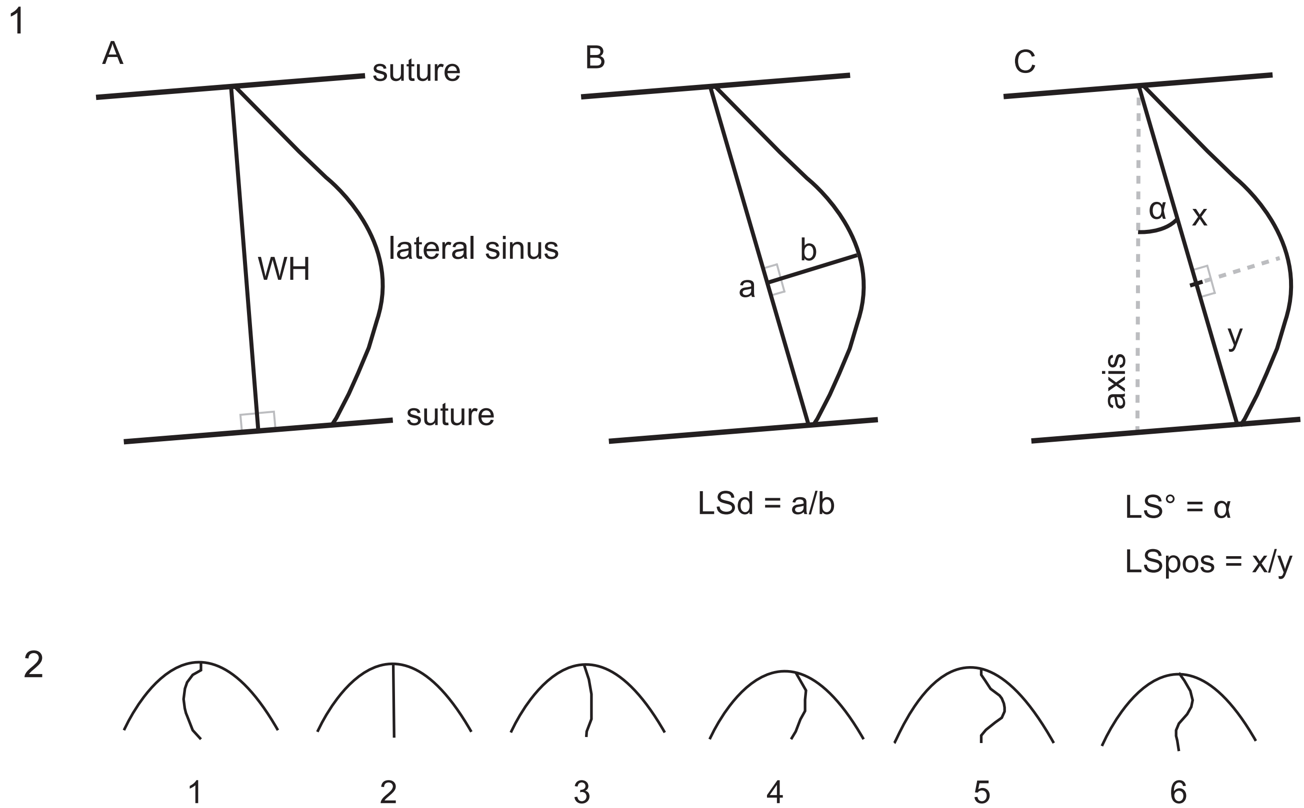
Most turritellids are characterized as having non-entire apertures (Marwick, 1957; Allmon, 1996). Their shells have not previously been reported to possess an umbilicus or other basal axial opening. We have, however, noticed openings in the bases of several of the species discussed here. These openings, visible in both broken and unbroken shells (Text-fig. 11), are not a true umbilicus because they are visible only inside the aperture, and the inner walls of the whorls are not separated from each other to form a space. This feature does not appear to have been recognized or named before. We refer to it as a hollow newel, based on its resemblance to the architecture of spiral staircases, in which a *newel* is the central supporting post or pillar, and a *hollow newel* is the absence of such a structure (Friend et al., 2023). This feature is discussed in greater detail in Friend et al. (2023).



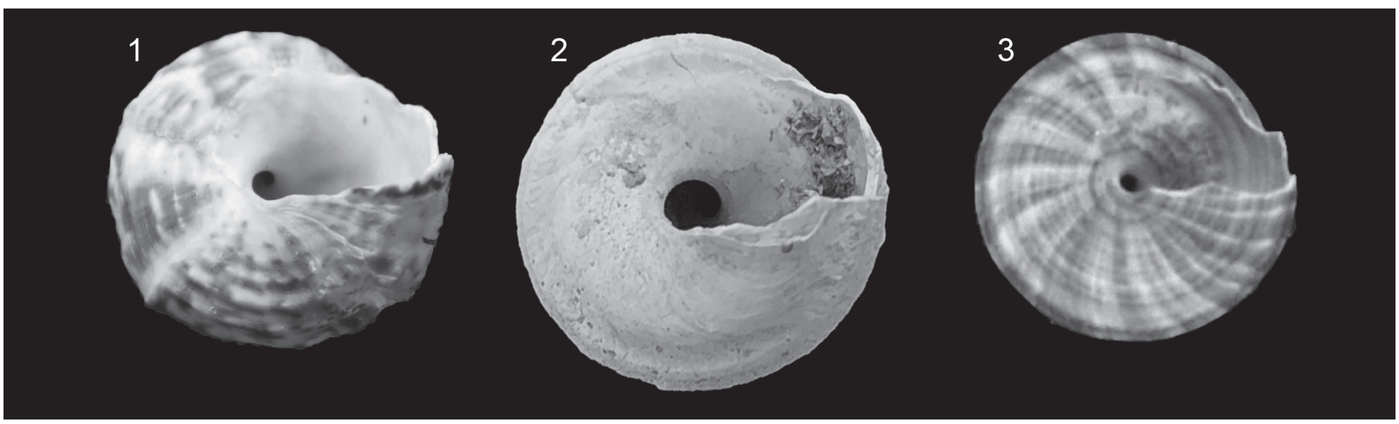
Text-fig. 8. Marwick diagrams depicting the ontogenetic development of spiral cords in "*Turritella*." We lack protoconchs of *Turritella* (s.l.) *jacula* so the beginning whorl number is an approximation.



Text-fig. 9. Marwick diagrams depicting the ontogenetic development of spiral cords in "*Turritella*," continued.



Text-fig. 10. "Lateral and Basal Sinus." 1, the method by which measurements used to classify the morphology of the lateral sinus. WH = whorl height, LS° = lateral sinus angle, LSpos = lateral growth line sinus position, LSd = lateral sinus depth. A, whorl height is the length of a line perpendicular to and between two adjacent sutures. B, to measure lateral sinus depth, we first drew a straight line (a) from the top to the bottom of the lateral sinus. A second line (b) was drawn between the most lateral point of the growth curve to the line (a) mentioned previously (note line b is at a right angle to line a). Line b measures LSd (lateral sinus depth). C, to measure lateral sinus angle (*α*), a vertical line parallel to the coiling axis (gray dashed vertical line) was drawn. To calculate lateral sinus position, line a is divided into x and y based upon its intersection point with line b. (Adapted from Harzhauser and Landau, 2019). 2, classification of basal growth line trace type following Allmon, 1996 (redrawn from Allmon, 1996).



Text-fig. 11. Turritellids with hollow newels. These species lack a columella and instead have cavities visible from the basal surface that opens into the body chamber, facilitating access to the body chamber of more apical whorls than the apertural whorl (e.g., when probed with a pin). 1, *Caviturritella gonostoma*, PRI 104787, Recent, tropical eastern Pacific, diameter 27.5 mm. 2, *Caviturritella alumensis*, PRI 41858, FL-02, diameter 24.1 mm. 3, *Caviturritella magnasulcus*, UF 332525, FL-80, diameter 9.2 mm.

SYSTEMATIC PALEONTOLOGY

In the species accounts below, each unique locality has a code preceded by the state in which it occurs. For details on fossil localities, see Appendix 1.

Phylum **MOLLUSCA** Cuvier, 1795a*
Class **GASTROPODA** Cuvier, 1795b*
Subclass **CAENOGASTROPODA** Cox, 1960
Superfamily **CERITHIOIDEA** Fleming, 1822
Family **TURRITELLIDAE** Lovén, 1847
Subfamily **TURRITELLINAE** Woodward, 1851

CAVITURRITELLA new genus Friend and Anderson

Type species.—*Turritella gonostoma* Valenciennes, 1832. Pliocene–Recent, eastern Pacific Ocean, California to Peru (Text-fig. 12).

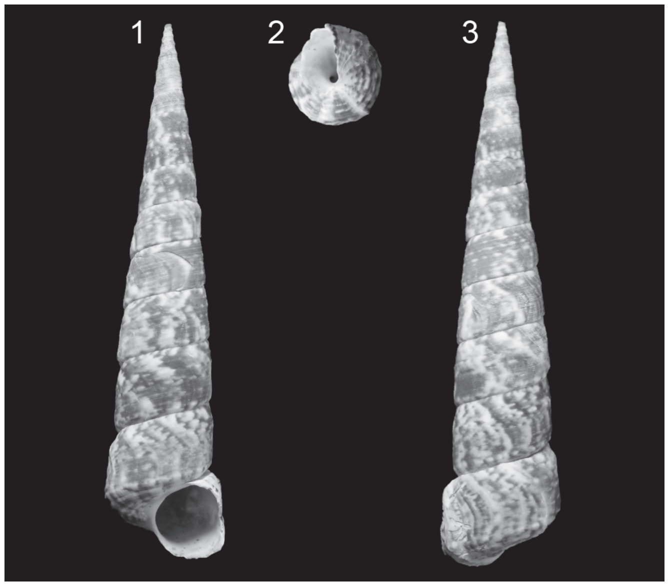
Original species diagnosis.—"Surrounded by thin transverse cords; white at the apex, horn colored below; variegated with dark flammules; flat whorls; (top) whorls halved by carina; angled aperture" (translated from Valenciennes, 1832, p. 275).

Other species referred to this genus.—*Turritella banksii* Gray in Reeve, 1849 (Recent; tropical eastern Pacific). *Turritella leucostoma* Valenciennes, 1832 (Recent; tropical eastern Pacific). *Turritella broderipiana* d'Orbigny, 1840 (Recent; tropical eastern Pacific). *Turritella alumensis* Mansfield, 1930 (Neogene; Florida and the Atlantic coastal plain). *Turritella etiwanensis* (Tuomey and Holmes, 1856) (Neogene; Florida and the Atlantic coastal plain). *Turritella magnasulcus* (Petuch, 1991) (Neogene; Florida and the Atlantic coastal plain). *Turritella terstriata* Rogers and Rogers, 1837 (Neogene; Florida and the Atlantic coastal plain). *Turritella abrupta* Spieker, 1922 (Neogene; tropical and subtropical eastern Pacific and tropical western Atlantic). *Turritella variegata* Linnaeus, 1758 (Recent; tropical western Atlantic).

Diagnosis.—Medium to large turritellines with hollow newels and an apical sculptural formula C1B2A3. Lateral growth lines prosocline, with apex medially located, or located slightly adaperturally of the middle of the whorl. Generally have lineated basal surfaces.

Etymology.—Referring to *Turritella* and the hollow newel cavity.

* See Donovan (1996).



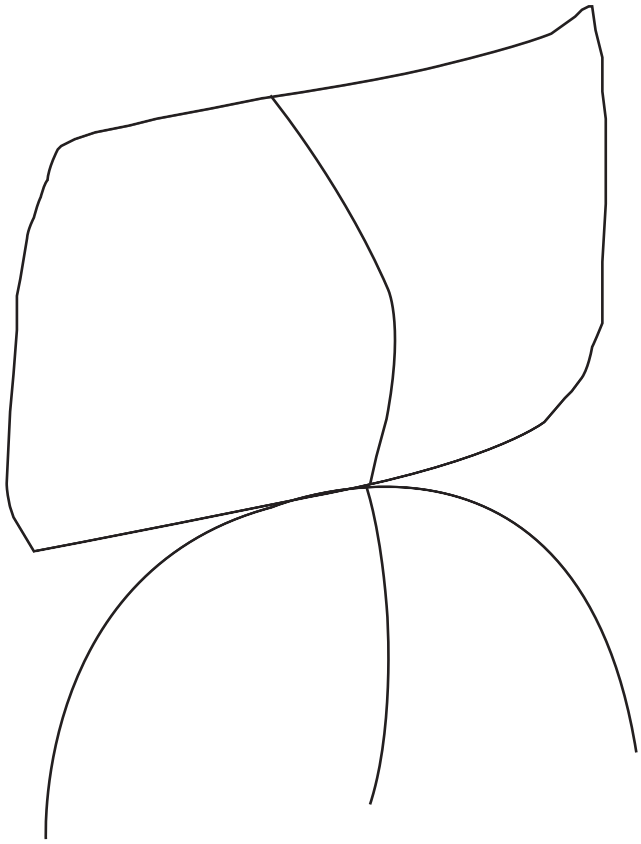
Text-fig. 12. *Caviturritella gonostoma* (Valenciennes, 1832), the type species designated for *Caviturritella* Friend and Anderson, new genus. Specimen PRI 104787 is from an unspecified locality but extant *Caviturritella gonostoma* are found in the eastern Pacific from the Gulf of California to Peru. Specimen length 116.6 mm.

Genus stratigraphic and geographic occurrences.—Miocene–Recent, western Atlantic and eastern Pacific.

Remarks.—Two morphological apomorphies characterize this genus: a C1B2A3 apical sculpture formula and the hollow newel character state. The lateral growth line trace is prosocline, but there is some variability among species with respect to the location of the apex and whether there is a weak inflection point present (Text-fig. 13). The genus name is attributed herein to Friend and Anderson.

Allmon (1988) and Allmon et al. (1992) recorded ecological information regarding habitat, feeding, growth, and reproduction of *Caviturritella gonostoma.* No information about the radulae or detailed soft anatomy have previously been published for the genus.

We are not the first to suggest a potential relationship among the species referred here to *Caviturritella*. The new genus encompasses several modern species that Olsson (1964) assigned to the subgenus *Broderiptella* Olsson, 1964 (*C. broderipiana* d'Orbigny, 1840, *C. banksii* Gray in Reeve, 1849, *C. gonostoma* Valenciennes, 1832, and *C. variegata* Linnaeus, 1758), and to which Olsson also referred *C. mansfieldi* (Olsson, 1967). This subgeneric assignment was based on early whorls sharing a medial spiral keeled appearance, medium to large size, similar growth line trace, and an abundance of fine spiral ornaments on adult whorls, and a "backwards inclined aperture," (Olsson, 1964: p. 188) which may have been an alternate terminology for hollow newel morphology. However,



Text-fig. 13. Lateral and basal sinus shape traced from *Caviturritella gonostoma*, the type species of *Caviturritella* Friend and Anderson, new genus.

Olsson did not make reference to order of appearance of spiral ornamentation and did not refer other hollow newel-bearing taxa (e.g., *C. leucostoma* Valenciennes, 1832, *C. abrupta* Spieker, 1922) to *Broderiptella*, as they lacked the *Broderiptella*-defining characteristic of a single medially-placed spiral keel in early whorls (Olsson, 1964, p. 189). Additional neotropical American species, especially Oligocene-Miocene species which have been at times referred to *Broderiptella* (e.g., *Turritella bifastigata* Nelson, 1870 and *Turritella mimetes* Brown and Pilsbry, 1911) should be examined for potential placement in *Caviturritella*, but a complete treatment of Cenozoic–Recent North and South American turritellids is beyond the scope of this manuscript.

Species of *Caviturritella* have the same apical sculpture formula as those assigned to *Haustator* Montfort, 1810, but have hollow newels, typically lineated basal surfaces, and minimal inflection points of the lateral sinus. *Caviturritella* is distinguished from *Oligodia* Handmann, 1882 by hollow newels and a C-B-A apical formula, while *Oligodia* is characterized by B–D succession of ornamentation (Harzhauser and Landau, 2019). Most members of *Caviturritella* are also generally large for turritellids, while *Oligodia* are medium sized.

Caviturritella alumensis (Mansfield, 1930)
Text-figs. 6.1, 14, Table 2

Turritella alumensis Mansfield, 1930: p. 105, pl. 15, figs. 1, 2, 5.
Turritella alumensis gardnerae Mansfield, 1930: p. 106, pl. 15, fig. 4.
Eichwaldiella alumensis (Petuch, 1994): p. 66, pl. 13, figs. C, D.
Eichwaldiella gardnerae (Petuch, 1994): pl. 13, fig. E.
Torcula alumensis (Petuch, 2004): p. 160, pl. 50, fig. G.
Not *T. gardnerae* LeBlanc in Barry and LeBlanc, 1942; see Allmon (1996, p. 84).

Type material.—Lectotype of *T. alumensis* (Mansfield, 1930) (herein designated), USNM 370319; paralectotype of *T. alumensis* Mansfield, 1930, USNM 370321; holotype of *T. alumensis gardnerae* Mansfield, 1930, USNM 370328.

Other material examined.—See Appendix 2.

Measurements.—See Table 2.

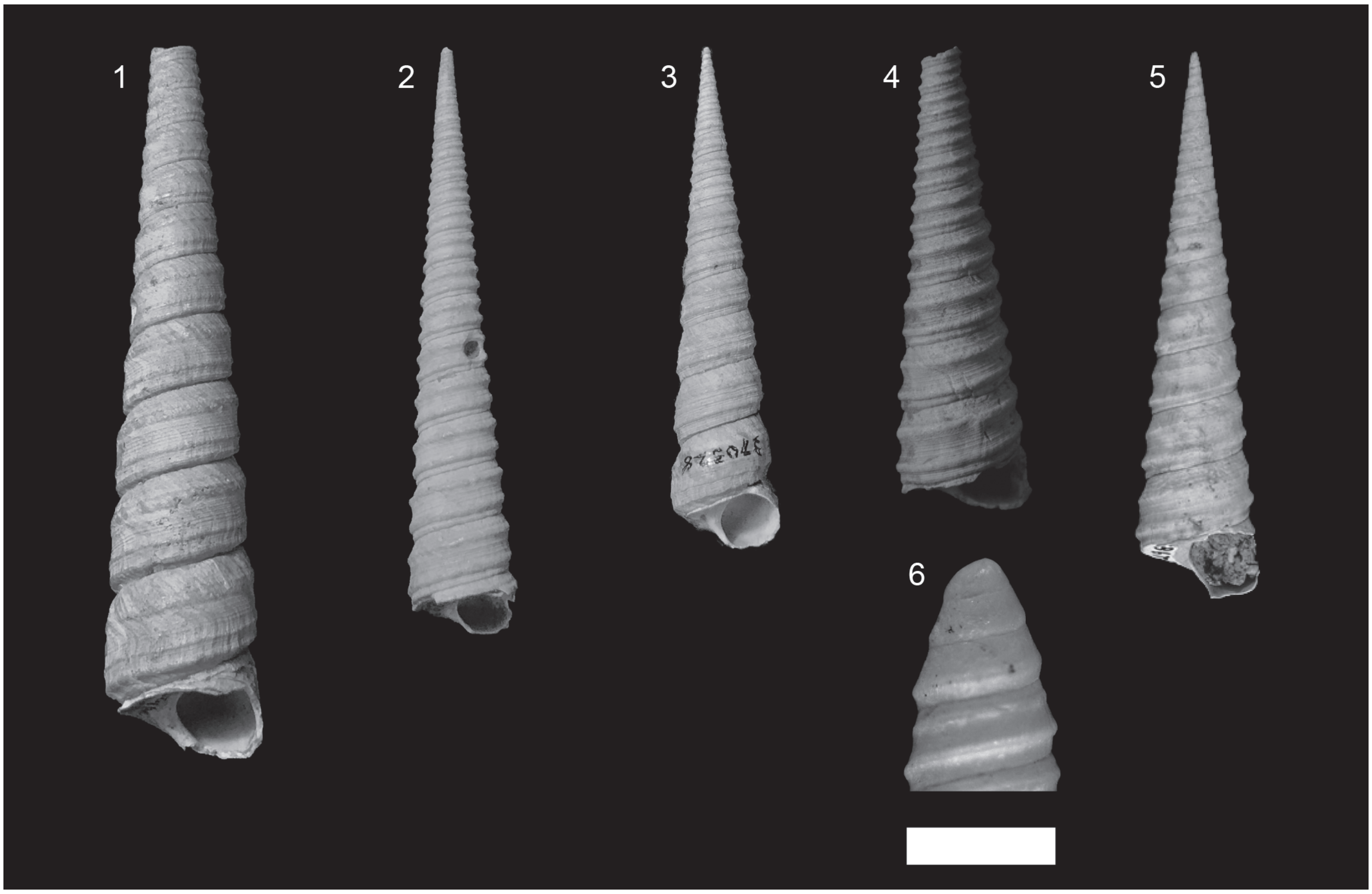
Stratigraphic and geographic occurrences.— Virginia: Yorktown Fm. (Pliocene). South Carolina: Duplin/Raysor Fm. (Pliocene). Georgia: Duplin/Raysor Fm. (Pliocene). Florida: Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Upper bed at Alum Bluff, Liberty County, Florida.

Other localities.—VA-09, VA-13, SC-05, SC-07, GA-01 to GA-02, FL-01 to FL-04, FL-06, FL-07, FL-09, FL-10, FL-15, FL-17, FL-19, FL-33, FL-39, FL-41, FL-46, FL-50, FL-57, FL-68, and FL-69.

Original description.—"Shell large, solid, moderately stout, probably of about 25 whorls on complete specimens. Suture impressed. Whorls nearly flat, medially depressed between primary spirals, upper whorls more so than later. Apical whorl rather large, flatly coiled, tip shallowly immersed. Spiral sculpture, on the earliest whorls, of a sharp basal keel. On ascending the whorl, another spiral begins below the suture, weak at first but later nearly equals in strength the basal one. Sculpture on later whorls of 3 primary spirals, one at the upper fourth and two at the anterior fourth and base. The basal spiral is weakest, the other two being of about equal strength. Aside from the primaries, flat secondary threads, usually intercalated by threadlets, overrun the surface" (Mansfield, 1930: p. 105).

Revised description.—Large shell with a pleural angle of 13.5°. Protoconch with a large first whorl flatly coiled (tip shallowly immersed). Apical sculpture formula C1B2A3. Spiral sculpture on the earliest whorls appears first as a sharp



Text-fig. 14. *Caviturritella alumensis* (Mansfield, 1930). 1, lectotype, USNM 370319, FL-76, 114.3 mm. 2, paralectotype, USNM 370321, FL-76, 68.5 mm. 3, holotype of *C. alumensis gardnerae*, USNM 370328, FL-76, 50.9 mm. 4, *C. alumensis* (*Turritella terebriformis* of Harris), PRI 104759, NC-07, 46.6 mm. 5, UF 329858, FL-68, 57.6 mm. 6, Protoconch, UF 329861, FL-04, scale bar = 1 mm.

Table 2. Measurements of type and other specimens of *Caviturritella alumensis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
C. alumensis	USNM 370319	lectotype	114.3	26.1	10.7°	-
C. alumensis	USNM 370321	paralectotype	68.5	12.3	10.1°	13.3°
C. alumensis	UF 329858	non-type	57.6	13	13.3°	14.9°
C. alumensis gardnerae	USNM 370325	holotype	50.9	10.6	12°	15.7°
C. alumensis terebriformis	PRI 104759	non-type	46.6	13.8	13°	-

basal keel, after which B cord appears and quickly develops, reaching near equal strength to the C cord. Juvenile whorl profile concave, adult profile subquadrate. Juvenile sculpture controlled by strong A and C cords and a wide concave sulcus between them. C overhangs D; D more pronounced in larger whorls because suture becomes more deeply incised. Threads begin to appear as the individual grows, starting with large threads directly below A and above C. Threads grow more numerous in maturity while major cords recede, creating a less exaggerated sculpture. On the largest whorls, 5 to 10 threads appear between C and D, threads too numerous to count above A. Basal sinus type 3; lateral sinus extremely pronounced on later whorls, a single inflection point on the bottom with an exaggerated apex in the middle. Growth lines prosocline. Aperture shape subquadrate. Hollow newel present.

Remarks.—The name *Turritella terebriformis* has sometimes been associated with *T. alumensis*. Conrad (1863) named but did not describe, illustrate, or give a locality for *Turritella terebriformis*. Dall (1892, p. 311) reported *T. terebriformis* from the “Older Miocene of the Chipola beds…” and the

Table 3. Reports of the presence of embryonic shells within adult turritellid fossils, suggesting that larvae were brooded.

Species	Age	Locality	Formation	Number of embryonic shells	Reference
Turritella alticostata	Miocene–Pliocene?	Hampton, VA	Yorktown	41	Antill (1974)
Caviturritella alumensis	Pliocene	Alum Bluff, FL	Jackson Bluff	48	Sutton (1935)
T. cumberlandia	Miocene	Plum Point, MD	Calvert	>200	Burns (1899)
T. indenta	Miocene	Plum Point, MD	Calvert	"by the hundreds"	Burns (1899)
C. etiwanensis	Pliocene	Kirby, SC	Duplin	4	this paper
T. pilsbryi	Pliocene	Yorktown, VA	Yorktown	104	Palmer (1958)
T. pilsbryi	Pliocene	Yorktown, VA	Yorktown	47	Gardner (1948)
Zeacolpus taranakiensis	Miocene	Wellington, New Zealand	?	40–100	Marwick (1971a, b)

"Chesapeake Miocene of Yorktown, VA" (he later corrected the latter locality to "Greenboro, Maryland" [1903, p. 1653]). Dall mentioned that Gilbert Harris had found what he thought was Conrad's type specimen for *terebriformis* in the collection of the Academy of Natural Sciences, and that this specimen "enabled us to identify the Chipola fossil with his [Conrad's] manuscript name." (The "Chipola beds" in this case very likely refer to the Jackson Bluff Fm. at Alum Bluff, which is the type locality of *C. alumensis*.) Neither Harris nor Dall, however, recorded any other information about this specimen, and neither Moore (1962) nor Richards (1968) list *T. terebriformis* among the types at ANSP. Harris's student Carlotta Maury (1902, p. 59) included *T. terebriformis* in a list of species from the "Chipola marls at Alum Bluff," crediting Harris with the identification. Smith and Aldrich (1902) also reported *T. terebriformis* from the "Alum Bluff horizon" in a core taken at Mobile, Alabama. There are three specimens in the USNM collection (USNM 13478, USNM 113480, and USNM 113481) labeled (by Dall?) as *Turritella terebriformis* from the Chipola Fm. These (and one in the UF collection [UF 35985] labeled as Chipola) are all very likely from the Jackson Bluff Fm. The same may also be true for the record for *T. alumensis* from the Choctawhatchee Fm. from locality FL-08 reported by Mansfield (1930). Gardner (1948, p. 199) was the first to figure specimens referred to *T. terebriformis* (the basis of her identification was not stated), but her two specimens (USNM 113479) are from the Miocene Choptank Fm. of Maryland. Ward (1992, p. 118) designated one of Gardner's specimens (1948, pl. 27, fig. 27), which he said was likely a topotype, as the neotype of *T. terebriformis*.

During our own study, we found two specimens in the PRI collection apparently deposited by Harris and labeled as *Turritella terebriformis* "holotype" from Alum Bluff. It is possible that one of these is the specimen Dall previously referred to as found by Harris, who may have removed this specimen from the Academy, but there is no evidence to confirm that this is the case. These have now been numbered PRI 104759 and PRI 104822.

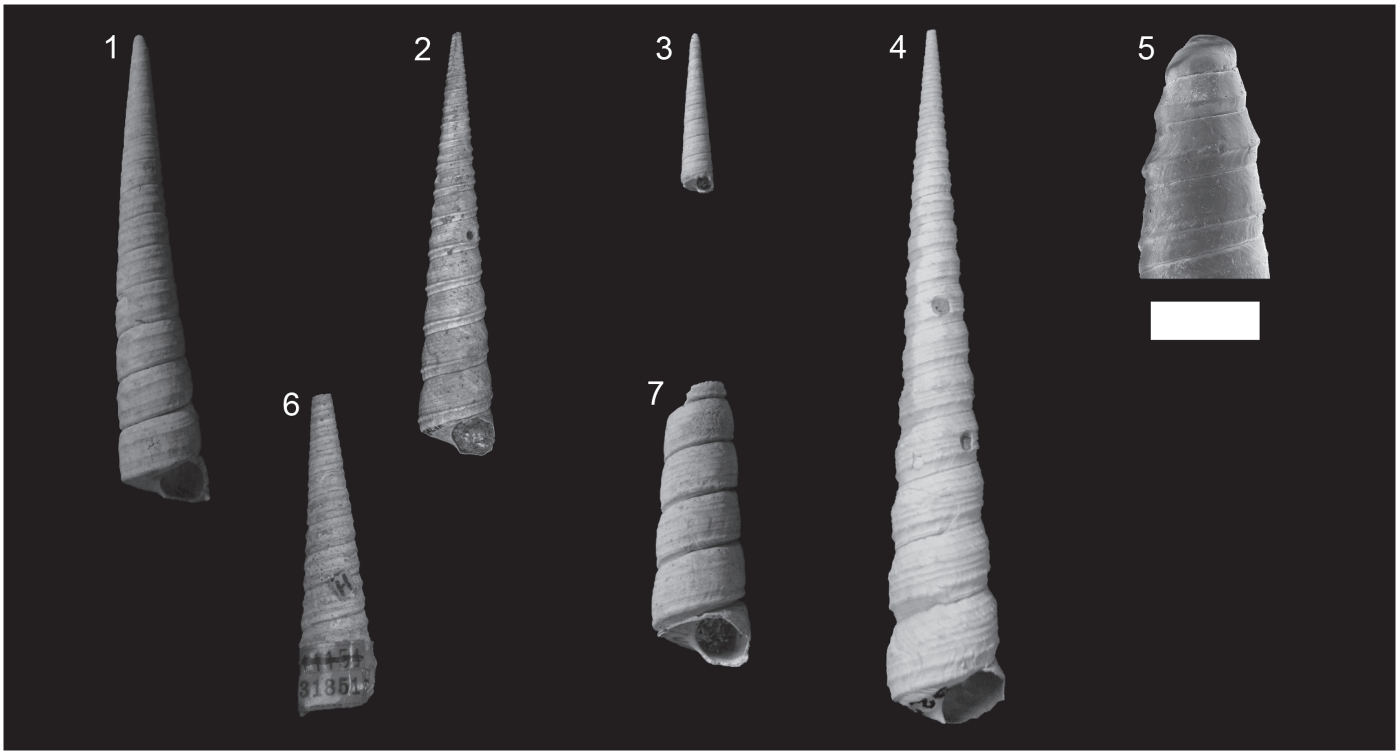
We conclude that the name *T. terebriformis*, if used at all, should be restricted to specimens from the Choptank Fm. and not to the Jackson Bluff Fm. Ward's designation of one of Gardner's specimens as a neotype may provide the basis for a future formal description of the taxon. For now, however, it must be regarded as a *nomen nudum*.

Caviturritella alumensis is a large and distinctive species that is very abundant in the Jackson Bluff Fm. at its type locality of Alum Bluff (see, e.g., Fallon et al., 2014). Sutton (1935) reported finding 48 embryonic shells inside a specimen of *C. alumensis* from what was probably the Jackson Bluff Fm. at Alum Bluff. This is one of at least seven fossil turritellid species known to have brooded their young (Table 3; see further discussion below).

Caviturritella etiwanensis (Tuomey and Holmes, 1856)
Text-figs. 6.2, 15, Table 4

Terebellum etiwanensis Tuomey and Holmes, 1856: p. 122, pl. 26, figs. 9, 10.
Terebellum etiwanensis Tuomey and Holmes. Emmons, 1858: p. 270.
Turritella etiwanensis (Tuomey and Holmes). Dall, 1892: p. 313 (in part).
Turritella etiwanensis (Tuomey and Holmes). Gardner and Aldrich, 1919: p. 18.
Turritella etiwanensis (Tuomey and Holmes). Mansfield, 1930: p. 106, pl. 15, fig. 3.
Turritella etiwanensis (Tuomey and Holmes). Gardner, 1948: pl. 27, fig. 20.
Turritella etiwanensis (Tuomey and Holmes). Petuch, 1994: pl. 13, fig. F.

Type material.—Nine (9) syntypes of *Terebellum etiwanensis* Tuomey and Holmes, 1856, AMNH FI 11154; lectotype of *C. etiwanensis* (Tuomey and Homes, 1856) (herein designated),



Text-fig. 15. *Caviturritella etiwanensis* (Tuomey and Holmes, 1856). 1, PRI 104826, NC-07, 52.5 mm. 2, UF 7683, FL-68, 40.4 mm. 3, PRI 104828, NC-07, 17.3 mm. 4, USNM 370331, FL-19, 103.5 mm. 5, protoconch, PRI 104737, NC-10, scale bar = 1 mm. 6, lectotype, AMNH FI 31851, SC-13. 7, PRI 104827 from NC-07, 37.6 mm.

Table 4. Measurements of type specimens of *Caviturritella etiwanensis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
C. etiwanensis	PRI 104826	non-type	52.5	10	12.5°	-
C. etiwanensis	PRI 104827	non-type	37.6	12.7	7.3°	-
C. etiwanensis	PRI 104828	non-type	17.3	3.6	8.2°	-
C. etiwanensis	UF 7683	plesiotype	134.1	23.8	9.6°	-
C. etiwanensis	USNM 370331	hypotype	103.5	18.1	9.5°	11.2°
C. etiwanensis	AMNH 31851	lectotype	40.0	7.5	9.7°	-

AMNH FI 31851; hypotype of *Turritella etiwanensis* (Tuomey and Holmes, 1856), USNM 370331 (figured by Mansfield, 1930 and Gardner, 1948); three (3) "plesiotypes" (as labeled by G.D. Harris) of *C. etiwanensis* (Tuomey and Holmes, 1856), PRI 104826, PRI 104827, and PRI 104828.

Other material examined.— See Appendix 2.

Measurements.— See Table 4.

Stratigraphic and geographic occurrences.— Virginia: Yorktown Fm., Zone 1 (Pliocene). North Carolina: Duplin Fm. (Pliocene); Chowan River Fm. (Early Pleistocene). South Carolina: Goose Creek Fm., Raysor Fm. (Pliocene); Bear Bluff Fm. (Early Pleistocene). Georgia: Duplin/Raysor Fm. (Pliocene). Florida: Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Peedee, South Carolina (Tuomey and Holmes, 1856).

Other localities.—VA-20, NC-03, NC-07, SC-03, SC-06, SC-09, SC-11, GA-04, FL-01, FL-05, FL-34, FL-52, FL-53, FL-64, and FL-68.

Original description.—"Shell subulate, elongated; with two prominent spiral striæ equidistant from the sutures, and fine intermediate ones on each whorl" (Tuomey and Holmes, 1856, p. 122).

Revised description.—Medium-small shell; pleural angle of 12.4° and an apical angle of 15.7°. Protoconch of one whorl, round and squat. Apical sculpture formula C1A2B2; C begins very strong, creating a campanulate whorl profile by the second whorl. Area above C cord straightens by fourth whorl, rapidly develops to a subquadrate whorl profile. A and C are always the most prominent as the individual grows, with two minor cords between. Numerous fine threads below C. The D cord becomes more prominent in adulthood, very close and immediately below C cord. Growth lines prosocline and beaded. Basal sinus unknown, lateral sinus of single inflection on bottom, with apex in the middle. Aperture shape circular, basement is convex. Basal surface columellar growth margin present.

Remarks.—This species is similar in size to *C. alumensis* but *C. etiwanensis* has a more slender shell and weaker major spiral cords. It is distinct from *"Turritella" pilsbryi* because the spiral cords of *C. etiwanensis* are not closely spaced at the anterior half of the whorls. Additionally, the whorl profile of *T. pilsbryi* is rounded while that of *T. etiwanensis* is subquatrate.

Mansfield (1930, pp. 106, 107) reported *C. etiwanensis* as "abundant" in the Choctawhatchee Fm. in northern Florida (e.g., locality FL-51), but these occurrences are likely to be from the Jackson Bluff Fm.

A specimen of *etiwanensis* from the Duplin Fm. at Kirby's Pond Quarry, Florence County, South Carolina (Loc. SC-11) was found to contain four embryonic shells. This adds another species to the list of fossil turritellids found to contain embryonic shells, implying brooding of crawl-away larvae (Table 3).

Caviturritella magnasulcus (Petuch, 1991)
Text-figs. 6.3, 16, Table 5

Eichwaldiella magnasulcus Petuch, 1991: p. 13, pl. 1, fig. 9.
Eichwaldiella magnasulcus Petuch, 1994: pl. 12, fig. V.
Eichwaldiella magnasulcus Petuch, 2004: p. 175, pl. 56, fig. H.

Type material.—Holotype, CM 35625; paratype, CM 35626.

Other material examined.—See Appendix 2.

Measurements.—See Table 5.

Stratigraphic and geographic occurrences.—Florida: Tamiami Fm., Pinecrest beds and Ochopee Limestone (Pliocene).

Type locality.—Alligator Alley, Monroe County, Florida.

Other localities.—FL-07, FL-17, FL-33, FL-39, FL-41, FL-54 to FL-56.

Description.—Medium-large shell with a pleural angle of 11.8°. Protoconch 1.5 to 2 whorls. Apical sculpture formula C1B2A3. Adult C cord begins on the third whorl, strengthens to produce keeled whorls, followed by appearance of B and A cords respectively. The D cord becomes prominent on the fourth whorl. Nine cords present on the largest whorl, anterior most 3 are the most prominent. Cords border the deeply indented suture, creating an overhang on the sulcus. Suture depth and sulcus width increase in size with growth. Basal sinus type 2; lateral sinus single inflection point on top; apex in lower half. Growth line prosocline. Aperture shape circular; columellar growth margin prominent. Basal surface partially lineated, normal columella.

Remarks.—This species is easily identifiable among other co-occurring turritellines by the incised suture, which makes it appear as if whorls are beginning to separate (not unlike in *Vermicularia*) but never fully detach.

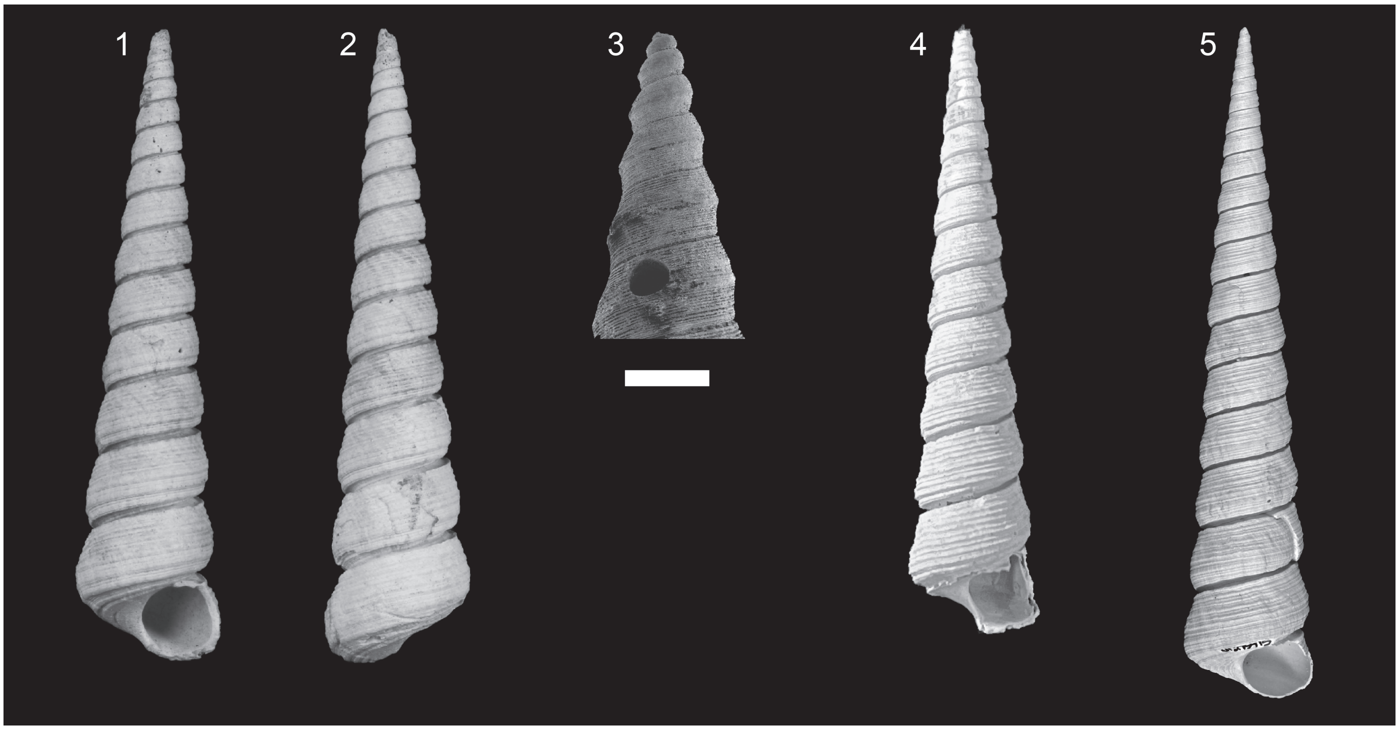
Petuch (1991) erroneously placed this species into *Eichwaldiella* Friedberg, 1933, which is an invalid genus name due to preoccupation by *Eichwaldiella* Whitley, 1930 (Pisces). Note that *Eichwaldiella* Friedberg, 1933 was later considered a junior synonym of *Oligodia* Handmann, 1882 as these share the type species *Turritella bicarinata* Eichwald, 1830 (van Dingenen et al., 2016; Harzhauser and Landau, 2019).

Caviturritella mansfieldi (Olsson, 1967)
Text-figs. 6.4, 17, Table 6

Not *Turritella striata* of Schumacher (1817; *taxon inquirendum*), Sowerby (1825; *nomen nudum*), Woodward (1830; *nomen nudum*), or Anton (1838; *taxon inquirendum*).
Terebellum striatum Tuomey and Holmes, 1856: p. 120, pl. 26, fig. 7.
Terebellum burdenii Tuomey and Holmes, 1856. Emmons, 1858: p. 270, fig. 163.
Turritella striata holmesii Dall, 1892: p. 313.
Turritella aff. *T. cartagensis* Mansfield, 1939: p. 46, pl. 1, figs. 2, 12 (not of Pilsbry and Brown, 1917).
Turritella cf. *T. pontoni* Mansfield, 1931. Mansfield, 1939: p. 47, pl. 1, figs. 3, 8.
Turritella holmesi Dall. Gardner, 1948: p. 198, pl. 27, fig. 23.
Turritella (*Broderiptella*) *mansfieldi* Olsson, 1967: p. 37, pl. 4, fig. 9, pl. 5, fig. 6.
Eichwaldiella mansfieldi (Olsson). Petuch, 1994: pl. 12, fig. U.
Eichwaldiella pontoni (Mansfield). Petuch, 2004: p. 175, pl. 56, fig. J.

Type material.—Holotype, *Turritella mansfieldi*, USNM 645175; paratype, USNM 645883.

Other material examined.—UF 266940, UF 329963, UF 268191. See Appendix 2.



Text-fig. 16. *Caviturritella magnasulcus* (Petuch, 1991). 1, 2, CM 35625, FL-81, 76.0 mm. 3, protoconch, PRI 108269, FL-41, scale bar = 1 mm. 4, paratype, CM 35626, FL-81, 79.4 mm. 5, UF 275915, FL-41, 115.7 mm.

Table 5. Measurements of a specimen of *Caviturritella magnasulcus*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
C. magnasulcus	CM 35625	holotype	76.0	17.2	11.3°	15.7°
C. magnasulcus	CM 35626	paratype	79.4	16.7	9.9°	18.3°
C. magnasulcus	UF 181362	non-type	97	19.8	8.7°	13.9°

Measurements.—See Table 6.

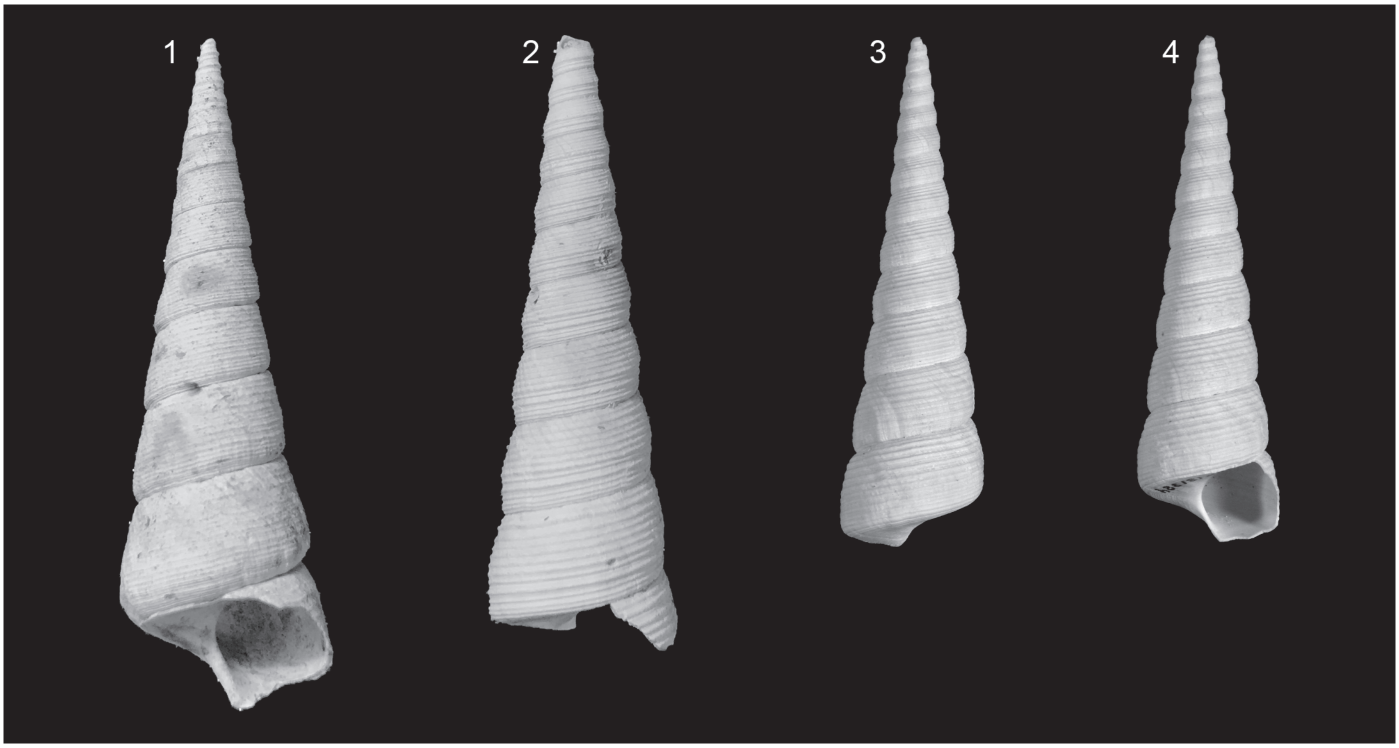
Stratigraphic and geographic occurrences.—North Carolina: Chowan River, Waccamaw Fm. (Early Pleistocene); Duplin Fm. (Pliocene). South Carolina: Duplin Fm. (Pliocene); Raysor Fm. (Pliocene). Georgia: Duplin/Raysor Fm. (Pliocene). Florida: Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Pinecrest, Monroe County, Florida (Olsson, 1967).

Other localities.—NC-03, NC-04, NC-07, SC-03 to SC-06, SC-09 to SC-11, GA-01 to GA-04, FL-03, FL-07, FL-10, FL-14, FL-33, FL-39, FL-77, and FL-78.

Description.—Large shell with a pleural angle of 19.2°, apical angle 21.8°. Protoconch unknown. Whorl profile is subquadrate; 9 to 11 spiral threads of relatively equal strength. Space between anterior threads increases with shell growth. Basal sinus is type 2; lateral sinus in abapical half of whorl with a single inflection point in adapical half of whorl; growth lines prosocline. Aperture shape is subquadrate, basement convex. Columellar growth margin prominent. Basal surface lineated, largest specimens have hollow newels.

Remarks.—The name *T. striatum* was first used by Tuomey and Holmes (1856), but the AMNH type is missing (B. Husseini, pers. comm.). Dall (1892) renamed it *T. striata holmesii* due to *striatum* being preoccupied (by *Turritella striata* of Schumacher (1817), Sowerby (1825), Woodward (1830), and Anton (1838)). We were not able to locate the type of *holmesi* in the WFI collections. We therefore consider *striatum* Tuomey and Homes and *holmesii* Dall to be *nomena nuda*. The genus *Terebellum* Bruguière, 1798 (see Kronenberg and Weneke, 2020) was applied to some species here placed in Turritellidae by Tuomey and Holmes (1856) and Harris (1890), but is now restricted to the family Seraphsidae (WoRMS, 2021).



Text-fig. 17. *Caviturritella mansfieldi* (Olsson, 1967). 1, holotype, USNM 645175, "Kissimmee, FL," Monroe County, Pinecrest beds, 87.4 mm. 2, paratype, USNM 645883, "Kissimmee, FL," Monroe County, Pinecrest beds, 83.4 mm. 3, 4, UF 181384, FL-03, 72.6 mm.

Table 6. Measurements of type and other specimens of *Caviturritella mansfieldi*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
C. mansfieldi	USNM 645175	holotype	87.4	27.3	19.5°	20.3°
C mansfieldi	USNM 645883	paratype	83.4	20.1	15.4°	-
C mansfieldi	UF 181384	non-type	72.6	19.3	15.2°	-

Caviturritella terstriata (Rogers and Rogers, 1837)
Text-figs. 6.5, 18, Table 7

Turritella ter-striata Rogers and Rogers, 1837: p. 331.
Turritella ter-striata Rogers and Rogers, 1839: p. 377, pl. 26, fig. 1.
Turritella ter-striata Rogers, 1884: p. 661.
Turritella variabilis var. A; Martin, 1904: p. 239, pl. 57, figs. 6, 7, 8.
Turritella terstriata Rogers and Rogers. Mansfield, 1937: p. 608, pl. 85, figs. 5, 9.
Turritella terstriata Rogers and Rogers. Gardner, 1948: p. 198, pl. 27, figs. 18, 19.
Turritella terstriata Rogers and Rogers. Campbell, 1993: p. 64, pl. 29, figs. 293, 293a.

Type material.—Holotype, MCZIP 113588; hypotypes (Mansfield, 1937), USNM IP 351756 and USNM MO 496428; hypotypes (two; Gardner, 1948), USNM MO 325456.

Other material examined.—See Appendix 2.

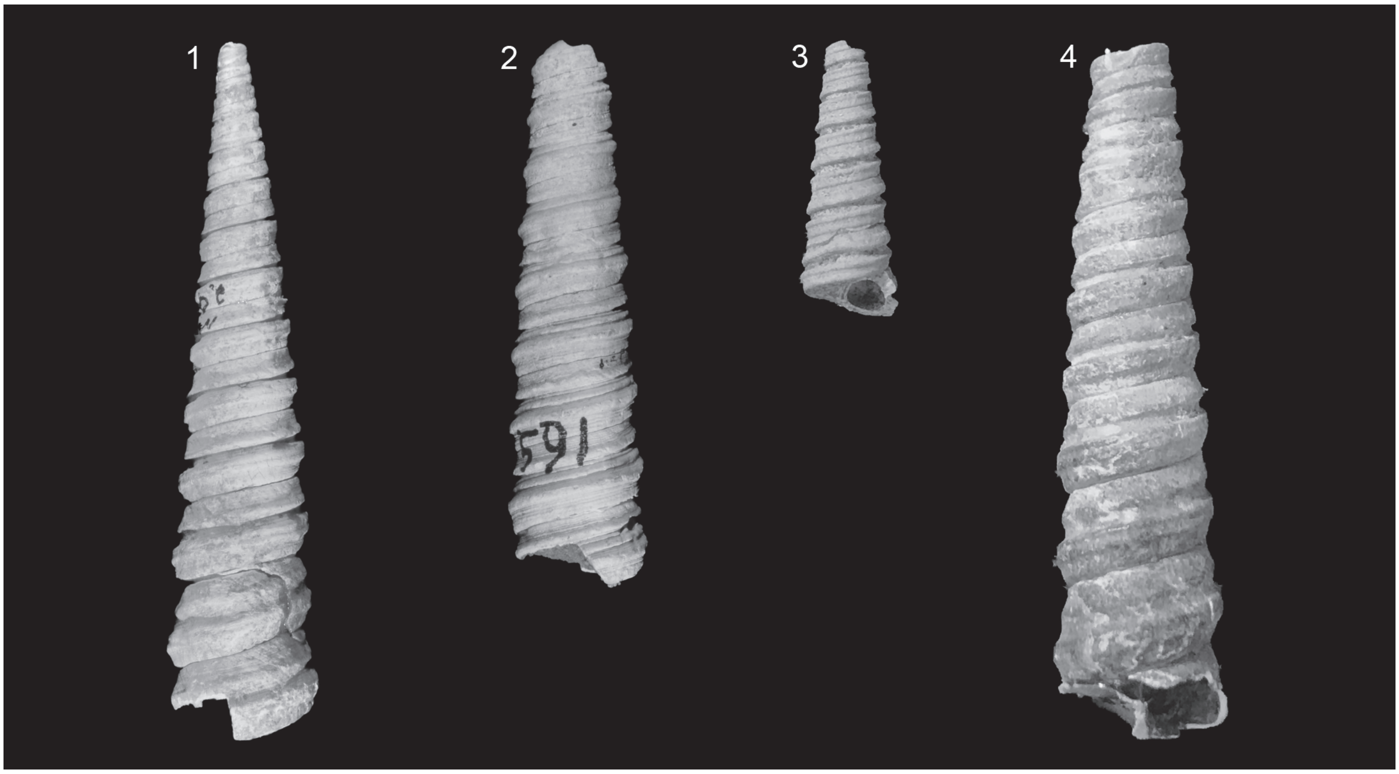
Measurements.—See Table 7.

Stratigraphic and geographic occurrences.—Virginia: Yorktown Fm., Sunken Meadow Member (Pliocene). Florida: Jackson Bluff Fm. (Pliocene).

Type locality.—Williamsburg, VA (Rogers and Rogers, 1837).

Other localities.—VA-10, VA-14 to VA-22, and FL-57.

Description.—Medium shell with pleural angle of 11.5°. Protoconch unknown. Whorl profile is sharply concave, with a groove between cords. Sculpture consists of two major cords. The anterior most cord is the most prominent, appearing bifurcated in later whorls. Between the two major cords is one very deeply incised sulcus (which appears at first glance to be the suture). Wide and sloping shoulders between sutures



Text-fig. 18. *Caviturritella terstriata* (Rogers and Rogers, 1837). 1, holotype, MCZIP 113588, VA-31, 40.5 mm. 2, MCZIP 113591, VA-31, 34.7 mm. 3, *Caviturritella* cf. *terstriata*, USNM 496428, FL-57, 18.3 mm. 4, USNM 351756, VA-14, 43.2 mm.

Table 7. Measurements of type and other specimens of *Caviturritella terstriata*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
C. terstriata	MCZIP 113588	holotype	40.5	8.6	8.6°	15.7°
C. terstriata	MCZIP 113591	non-type	34.7	7.7	7.9°	-
C. terstriata	USNM 496428	non-type	18.3	6.3	10.6°	-
C. terstriata	USNM 351756	non-type	43.2	10.7	8°	-

and the major cords. Basal sinus unknown. Lateral growth lines prosocline with a medially located apex. Aperture shape rounded, columellar growth margin is absent.

Remarks.—This species is easily identifiable due to the deeply incised equatorial sulcus. Without more information on early ontogeny, however, it is difficult to compare it with others. Gardner noted that she thought it was related to *terebriformis*; we compared the holotype to other specimens and they are distinct.

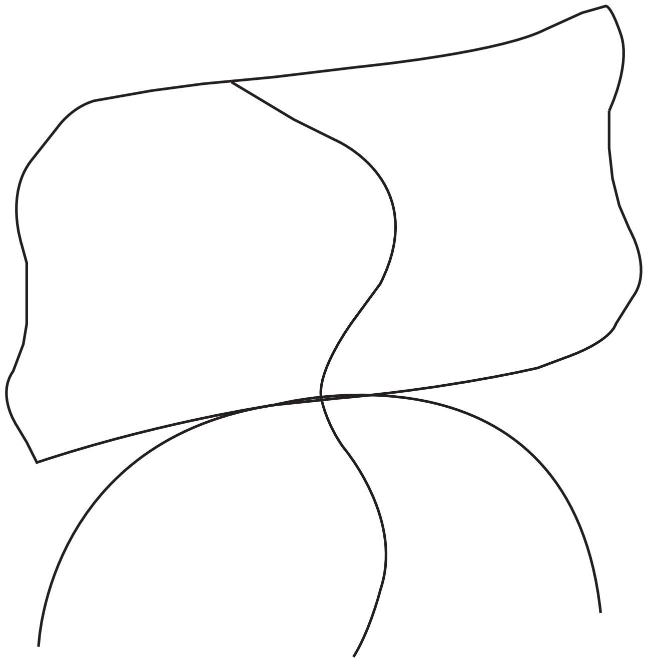
We also examined protoconchs from Chowan River Fm. specimens which may or may not be *T. terstriata.* Further determination requires additional specimens of larger size in order to link protoconch with adult morphology.

Genus ***TORCULA*** Gray, 1847

Type species.—*Turbo exoletus* Linnaeus, 1758. Pleistocene–Recent, western Atlantic Ocean, South Carolina to Brazil.

Original description.—"*Torcula. Haustator*, Gray, 1840; 1844, 60; not Montf. *Turritella* sp. (*biangulata*), Lam. *Turbo exoletus*, Linn." (Gray, 1847, p. 155; mention of "1844" is an error).

Revised description.—Turritellids with strongly concave whorl profiles, distinguished by two prominent cords (A and C) on each whorl separated by a deep sulcus; the C cord being first to develop during ontogeny. Lateral growth line trace prosocline, shallow to moderately deep. Apex of lateral growth line trace located medially.



Text-fig. 19. Lateral and basal growth line sinus shape proposed by Marwick (1957) to characterize the genus *Torcula*, in agreement with our observations of the growth line trace of the type species *Torcula exoleta*.

Genus stratigraphic and geographic occurrences.—Eocene–Recent, subtropical and tropical Americas.

Remarks.—Gray's first use of *Torcula* was not accompanied by a morphological description, leading subsequent authors to attempt the delineation of reliable characters. Marwick (1957) mentioned a turbinate protoconch and cingulate neanic whorls, and he figured the lateral and basal sinus for *Torcula* (Text-fig. 19). Campbell (1993) took a wholly different approach, describing *Torcula* as a subgenus of "straight-sided Turritellas with uneven spiral sculpture." We agree with Petuch and Berschauer's (2020) description of *Torcula* as exhibiting "a sculpture pattern composed of two strong cords on each whorl and a deep central depressed sulcus between the cords" (p. 176).

Torcula apicalis (Heilprin, 1886)
Text-figs. 7.1, 20, Table 8

Turritella apicalis Heilprin, 1886: p. 88, pl. 8, figs. 14, 14a.
Turritella mediosulcata Heilprin, 1886: p. 89, pl. 8, fig. 16.
Terebellum burdenii Tuomey and Holmes, 1856: p. 122, pl. 26, fig. 11.
Turritella burdenii(?) Tuomey and Holmes. Dall, 1892: p. 313
Turritella apicalis Heilprin. Dall, 1892: p. 316–318, pl. 16, figs. 10, 11, 12, 13.
Turritella apicalis var. *mediosulcata* Dall, 1892: p. 317, pl. 16, fig. 12.
Turritella apicalis var. *tensa* Dall, 1892: p. 317, pl. 16, fig. 13.
Not *Turritella apicalis* var. *cingulata* Heilprin. Dall, 1892: p. 317, pl. 16, fig. 11.
Turritella apicalis Heilprin. Mansfield, 1939: p. 48, pl. 1, figs. 9, 10.
Turritella buckinghamensis Mansfield, 1939: pg. 47, pl. 1, fig. 1.
Turritella apicalis (subgenus *Torcula,* section *Apicula*) Heilprin. Olsson and Harbison, 1953: p. 314, pl. 44, figs. 5, 5a.
Turritella (*Torcula*) *mediosulcata* Dall. Olsson and Harbison, 1953: p. 313, pl. 44, figs. 2, 2a, 3, 3a.
Turritella apicalis Heilprin. DuBar, 1958: p. 203, pl. 10, fig. 14.
Apicula apicalis Heilprin. Petuch, 1994: p. 68, pl. 12, fig. A.
?*Apicula mediosulcata* (Dall). Petuch, 1994: pl. 12, fig. K.
Apicula tensa (Dall). Petuch, 1994: pl. 12, fig. D.
Not *Apicula buckinghamensis* (Mansfield). Petuch, 1994: p. 256, pl. 12, fig B.

Type material.—Holotype of *T. apicalis*, WFI 982; hypotypes (six; Olsson and Harbison, 1953), ANSP 18880; hypotypes (two; Mansfield, 1939), USNM 497967; holotype of *Turritella apicalis mediosulcata*, WFI 16933; holotype of *T. apicalis* var. *tensa*, USNM 113461.

Other material examined.—See Appendix 2.

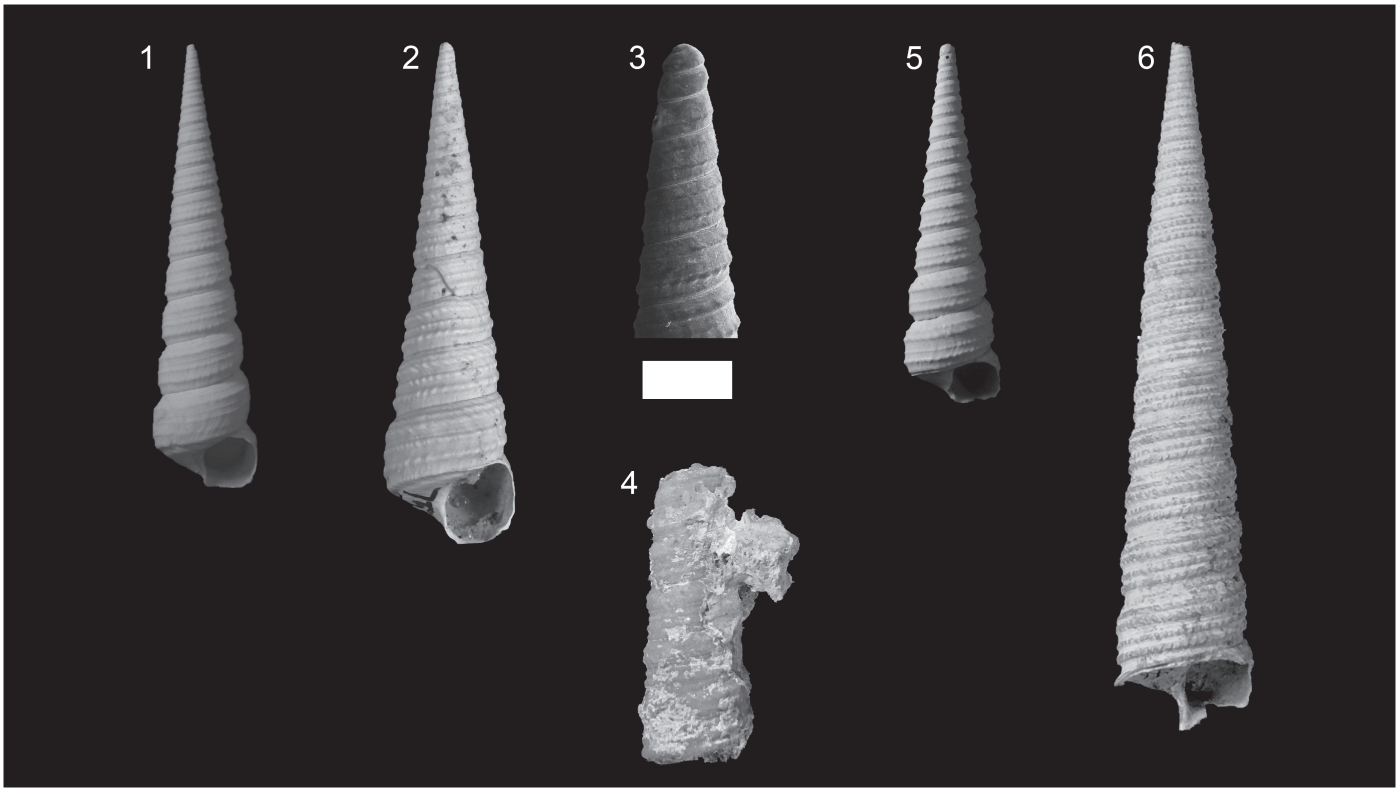
Measurements.—See Table 8.

Stratigraphic and geographic occurrences.—Florida: Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Buckingham Limestone and Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene); Bermont Fm. (Early Pleistocene); Ft. Thompson Fm.? (Late Pleistocene).

Type locality.—Caloosahatchee River, below Fort Thompson (Heilprin, 1886).

Other localities.—FL-17, FL-19 to FL-23, FL-29, FL-38, FL-41, and FL-62.

Description.—Small shell, pleural angle of 15.4°, apical angle 18.8°. Protoconch one smooth whorl. Apical sculpture formula C1A2B3. Order of adult cord prominence C > A > B. Early teleoconch whorls keeled, adult whorls double hypercampanulate (concave with sharply angled cords). A and C cords strong and beaded; a weak and beaded B cord lies directly above the C cord; prominent s-cord beaded; minor r-cord beaded. Suture lightly incised, deepening with age. Basal sinus type 4, lateral sinus deep inflection point on bottom, apex in middle. Growth lines prosocline, aperture shape subquadrate, columellar growth margin prominent.



Text-fig. 20. *Torcula apicalis* (Heilprin, 1886). 1, PRI 108264, FL-85, 48.4 mm. 2, UF 181433, FL-62, 41.0 mm. 3, protoconch, UF 181402, FL-19. Scale bar is 0.5 mm. 4, holotype, *Turritella apicalis buckinghamensis*, USNM 497966, FL-21, 40.4 mm. 5, holotype, *Turritella apicalis*, WFI 982, FL-26, 43.2 mm. 6, holotype, *T. apicalis tensa*, USNM 113461, FL-18, 67.0 mm.

Table 8. Measurements of type and other specimens of *Torcula apicalis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. apicalis	ANSP 18880	hypotype	27.7	7	15.3°	-
T. apicalis	WFI 982	holotype	43.2	10.5	14.9°	24.7°
T. apicalis	PRI 108264	non-type	48.4	10.9	13.0°	11.5°

Remarks.—Coding character states for *T. apicalis* is difficult, partly because of the wide range of variation present. Dall (1892, p. 316) noted that his illustrations "represent only extremes; the gradations between which are extant and may be examined in the collection; but which I could hardly try to figure *in extenso*." He proposed no less than four varieties but insisted that they represented the extremes of a continuous spectrum of morphological characters. Our own observations of *T. apicalis* agree with those of Dall, but we also suggest that some of the variation is explained by progressive dissolution and abrasion of the outer shell layers, flattening the appearance of major cords, effectively decreasing suture depth, and distorting whorl profile.

The largest of the six ANSP hypotypes never displays a B cord. The holotype of *T. apicalis* figured by Olsson and Harbison (1953) clearly shows a beaded B cord, only slightly weaker than the A and C cords, so we find the presence of the B cord is important to the identification of this species.

The holotype of *T. cingulata* (WFI 16932) appears to belong to "*Turritella*" *gladeensis* and the description by Dall (who puts it under *apicalis*) does not match *apicalis* because A is equal to or lesser than the strength of other minor cords. In comparing *T. apicalis* hypotypes with specimens formerly assigned to *T. cingulata and T. apicalis cingulata*, we find the A cord is prominent in *T. apicalis*, but not in *cingulata*.

In describing *T. buckinghamensis,* Mansfield (1939, p. 47) suggested that it is related to *T. apicalis tensa* and *T. burdenii*. The holotype for *T. buckinghamensis* is a very incomplete and recrystallized specimen partially embedded in matrix, and we are unable to match any other supposed subsequent instances of *T. buckinghamensis* to the holotype. There are similarities between the type of *T. buckinghamensis* and *T. apicalis tensa*, including equally strong C and A/B cords. There are, however, differences: the A and B cords of *T. tensa* are clearly defined and separate. In *T. buckinghamensis*, the A and B cords coalesce to form a thick double cord. *Turritella buckinghamensis* was described as beaded (like *T. tensa*) but the holotype specimen does not show clear beading on any of the cords.

There is a single specimen of *Turritella apicalis* in the UF collection (UF 222282) that may be from the Ft. Thompson Fm., but this specimen was not collected in situ, and we consider its age uncertain. Excluding this specimen, the latest known occurrence of the species is Bermont Fm.

Torcula clarksvillensis (Mansfield, 1930)
Text-figs. 7.2, 21.1, 21.2, Table 9

Turritella cookei clarksvillensis Mansfield, 1930: p. 108, pl. 15, fig. 9.

Type material.—Holotype USNM 370355.

Other material.—See Appendix 2.

Measurements.—See Table 9.

Stratigraphic and geographic occurrences.—Florida: Choctawhatchee Fm. (Late Miocene); Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—USGS station 8862, half a mile northeast of Clarksville, Calhoun County, Florida.

Other localities.—FL-06, FL-14, FL-31 to FL-33, FL-41, FL-57, and FL-69.

Description.—Medium shell, pleural angle of 13.9°, apical angle unknown. Protoconch unknown. Whorls have 2 very prominent primary cords (likely A and C) which are heavily beaded. Beads are node-like and shinier than the whorl wall. The posterior primary cord may be doubled, the subsutural one is weaker. Suture medium. Basal sinus type 3, lateral sinus shallow, single inflection point on bottom, apex in middle. Growth lines prosocline. Aperture shape subquadrate

Remarks.—The only specimens we have observed indicate *T. clarksvillensis* is the smallest of all the forms previously considered subspecies of *T. cookei* and it is unclear why it was associated with *T. cookei* to begin with other than that both *cookei* and *clarksvillensis* lack a B cord. In the latter, however, the A and C cords are heavily beaded, almost nodose.

Torcula cookei (Mansfield, 1930)
Text-figs. 7.3, 21.3–21.5, Table 10

Turritella cookei Mansfield, 1930: p. 107, pl. 16, figs. 1, 10.
Turritella cookei harveyensis Mansfield, 1930: p. 107, pl. 16, figs. 2, 4.
Turritella alaquaeënsis Mansfield, 1935: p. 42, pl. 4, figs. 3, 7.
Turritella alaquaënsis vaughanensis Mansfield, 1935: p. 42, pl 4, fig. 8.
Turritella cookei permenteri Mansfield, 1935: p. 43, pl. 4, figs. 4, 6.

Type material.—Holotype, USNM 370345; paratype, USNM 370346; holotype, *T. cookei harveyensis*, USNM 370352; two syntypes, *T. cookei permenteri*, USNM 373154 (Mansfield 1935); two syntypes, *T. alaquaensis* USNM 373152; holotype, *T. alaquaënsis vaughanensis*, USNM 373153.

Other material examined.—See Appendix 2.

Measurements.—See Table 10.

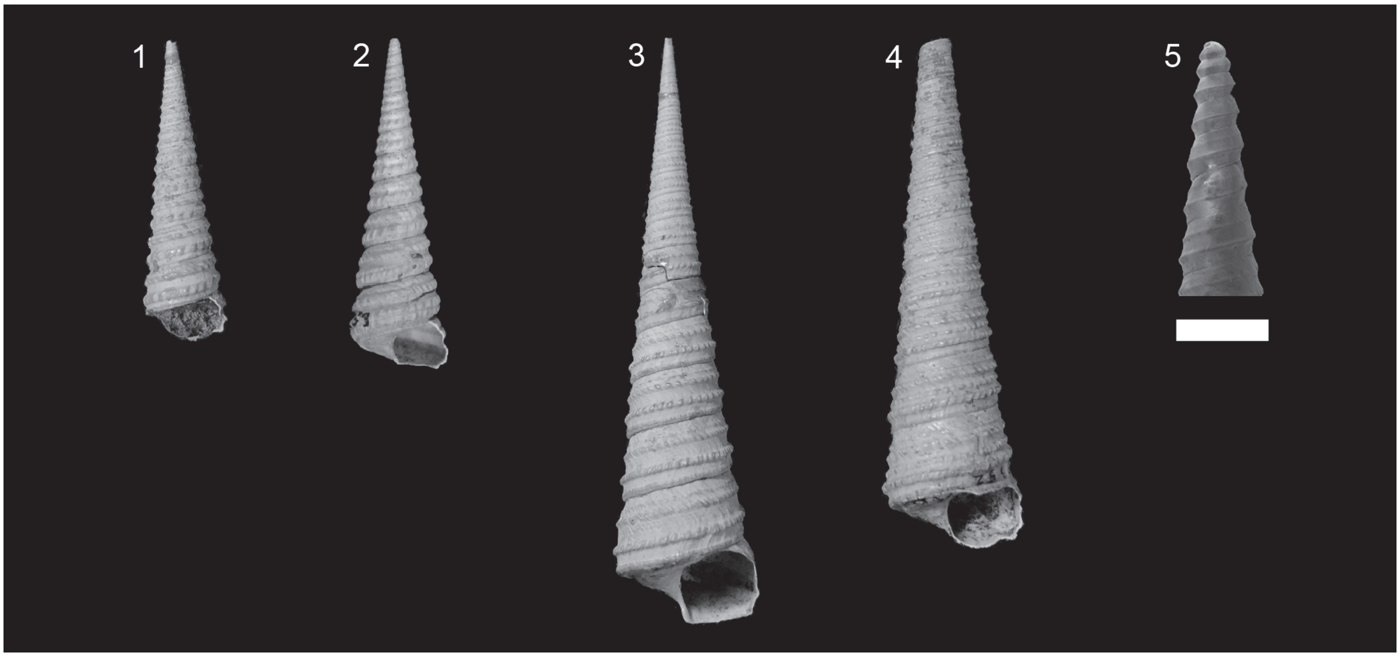
Stratigraphic and geographic occurrences.—Florida: Choctawhatchee Fm. (Late Miocene); Tamiami Fm., Ochopee Limestone (Pliocene); Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene).

Type locality.—USGS station 3421, Harveys Creek, half a mile above abandoned mill, Leon County, Florida. Type locality of *T. cookei harveyensis* is USGS station 10946, Harveys Creek, half a mile above abandoned mill, Leon County, Florida.

Other localities.—FL-14, FL-17, FL-19, FL-34, FL-35, FL-41, FL-50, FL-55, FL-60, and FL-69.

Description.—Medium-sized shell with pleural angle of 15.2°. On protoconch, cord C appears by second whorl to create a keeled shape. Around whorl 4–5, A appears. Apical sculpture formula C1A2. In adult specimen, a wide median sulcus with several spiral threads separate A and C cords, creating a slightly concave whorl profile. Both major cords equally removed from the upper and lower sutures of the whorls. C is slightly more prominent than A. Both cords obliquely beaded. Obscurely beaded, minor cord a appears in fifth whorl from aperture on holotype. Overhanging the suture is a D cord that becomes more prominent with age. Basal sinus type 5; lateral sinus of one inflection point on bottom, lower middle apex; growth line prosocline. Aperture shape subquadrate with flat basement; columellar growth margin prominent.

Remarks.—Mansfield's description of *T. harveyensis* largely matches that of *T. cookei*. But *T. harveyensis* does not match the holotype specimen in that the specimen has five spiral cords (includes A' and D) and Mansfield says it has four spiral



Text-fig. 21. *Torcula clarksvillensis* (Mansfield, 1930) and *Torcula cookei* (Mansfield, 1930). 1, holotype of *Turritella cookei clarksvillensis*, USNM 370355, FL-57, 39.6 mm. 2, *T. clarksvillensis*, UF 221559, FL-69, 42.0 mm. 3, holotype of *Turritella cookei*, USNM 370345, FL-05, 84.0 mm. 4, holotype of *Turritella cookei harveyensis* (Mansfield, 1930), USNM 370352, FL-05, 56.8 mm. 5, protoconch of *T. cookei*, PRI 104744, FL-03, scale bar = 0.5 mm.

Table 9. Measurements of the holotype of *Torcula clarksvillensis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. clarksvillensis	USNM 370355	holotype	39.6	9.9	13.9°	-

Table 10. Measurements of the holotype of *Torcula cookei*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. cookei	USNM 370345	holotype	84.0	18.9	15.9°	11.7°

cords (includes the A' but excludes D). Mansfield's account of the strength of the cords does not match the specimen either. "This subspecies differs from *T. cookei* in having more spirals. In *T. cookei* the medial area has only three to four fine spirals, whereas *T. cookei harveyensis* is centrally ornamented by a rather strong spiral" (Mansfield, 1930, p. 108).

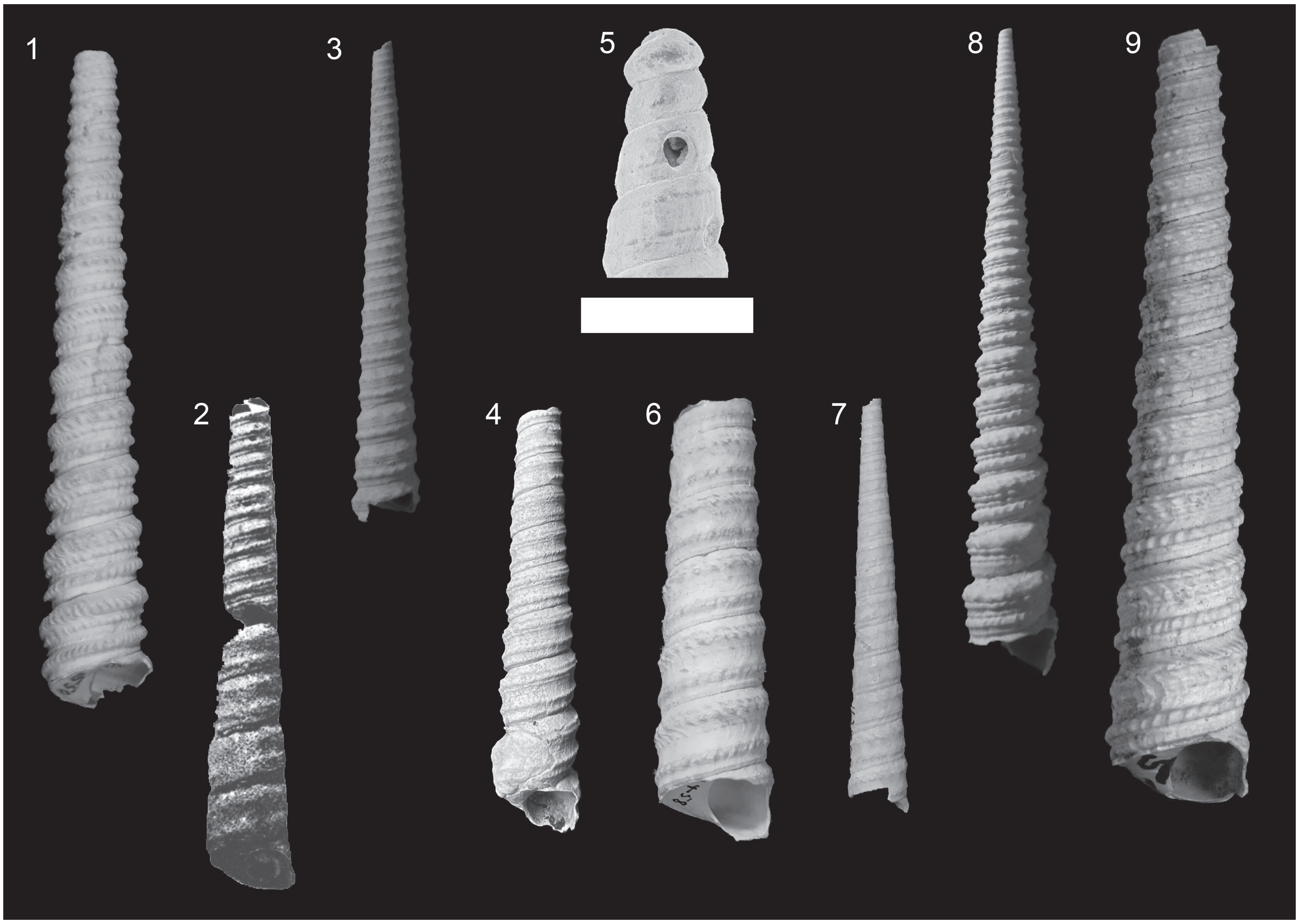
The hypotype of *T. harveyensis* looks more like *T. gladeensis* than *T. cookei* because both *harveyensis* and *gladeensis* have equal number of cords, the same pattern of cord strength, the same whorl profile, and the same aperture shape. We superimposed photos of both, and the apical angle looks similar but whorl expansion rate (Raup, 1966) *w* is higher in *T. gladeensis* than *T. harveyensis*.

Both *T. harveyensis* and *T. cookei's* strongest cords are A and C. However, *T. cookei* does not have B; whorl profile of *T. cookei* is more convex and the sutures are more indented than in *T. harveyensis*.

Comparing *T. permenteri* to *T. cookei*, the latter has a B cord, while no type specimen of the former has this. *Turritella permenteri* also has more strongly raised cords and a more prominent A`. Mansfield (1935) compared *T. permenteri* and *T. harveyensis*, but *T. harveyensis* has five weak cords (compared to four) and a different whorl profile.

Torcula perattenuata (Heilprin, 1886)
Text-figs. 7.4, 22, Table 11

Turritella perattenuata Heilprin, 1886: p. 88, pl. 8, fig. 13.
Turritella perattenuata Heilprin. Dall, 1892: p. 316, pl. 16, figs. 5, 9.
Turritella perattenuata undula. Dall, 1892: p. 316.
Turritella perattenuata obsoleta. Dall, 1892: p. 316.
Protoma (*Bactrospira*) *perattenuata* (Heilprin). Cossmann, 1912: pp. 129, 130, pl. 8, figs. 8, 9.



Text-fig. 22. *Torcula perattenuata* (Heilprin, 1886). 1, hypotype (Olsson and Harbison, 1953), ANSP 550, FL-75, 72.1 mm. 2, holotype as figured by Heilprin (1886), WFI 33612, 43.4 mm. 3, hypotype, USNM 113459, FL-75, 43.5 mm. 4, Heilprin's specimen found at WFI, presumed to be from type locality, 48.0 mm. 5, protoconch from USNM 113459, FL-75, scale bar = 1 mm. 6, holotype of *T. perattenuata undula*, USNM 113458, FL-18, 40.2 mm. 7, holotype of *T. perattenuata obsoleta*, USNM 113455, FL-18, 41.0 mm. 8, PRI 104749, FL-66, 67.8 mm. 9, UF 181701, FL-46, 81.5 mm.

Table 11. Measurements of specimens of *Torcula perattenuata*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. perattenuata	USNM 347417a	non-type	112.3	13.9	6.4°	-
T. perattenuata	USNM 347417b	non-type	38.8	5.1	6.9°	10°
T. perattenuata	USNM 347417c	non-type	49	6.1	7.4°	-
T. perattenuata	USNM 113456	hypotype	85.8	11.5	6.6°	-
T. perattenuata	ANSP 550	hypotype	72.1	7.5	6.1°	-
T. perattenuata	ANSP 550	hypotype	54.3	7.2	7.3°	-
T. perattenuata	UF 332449	non-type	80.8	16	12.3°	14°
T. perattenuata	UF 332446	non-type	68.8	13.9	11.6°	13.6°

Not *Turritella perattenuata praecellens* Heilprin. Pilsbry and Brown, 1917: p. 36, pl. 5, fig. 12.
Turritella perattenuata (subgenus *Torcula,* section *Bactrospira*) Heilprin. Olsson and Harbison, 1953: p. 316, pl. 44, figs. 4, 4a–c.
Turritella (*Bactrospira*) *perattenuata* Heilprin. DuBar, 1958: p. 204, pl. 12, fig. 9.
Bactrospira perattenuata (Heilprin). Petuch, 1994: pl. 12, fig. O.
Bactrospira obsoleta (Heilprin). Petuch, 1994: pl. 12, fig. Q.

Type material.—Neotype (herein designated), WFI 33612; hypotypes (Dall, 1892), USNM 113459; hypotypes (eight; Olsson and Harbison, 1953), ANSP 550; hypotypes (39; Olsson and Harbison, 1953), ANSP 17378; hypotype, USNM MO 113456 (Olsson, 1967); hypotype, USNM MO 371319 (Olsson, 1967); hypotype, USNM 347416, 347417 (Olsson, 1967); holotype, *T. perattenuata obsoleta* USNM 113455; holotype *T. undula*, USNM 113458.

Other material examined.—See Appendix 2.

Measurements.—See Table 11.

Stratigraphic and geographic occurrences.—Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene) and Caloosahatchee Fm. (Early Pleistocene).

Type locality.—Banks of the Caloosahatchee River below Fort Thompson, Hendry County, Florida.

Other localities.—FL-03, FL-07, FL-12, FL-17, FL-20 (*T. perattenuata undula* type locality), FL-25, FL-36 to FL-49, FL-65, FL-67, FL-70 to FL-73.

Description.—Large, slender shell. Pleural angle 8.8°, apical angle 7.5°. Apical sculpture formula C1A2. Protoconch is one whorl before becoming keeled with the appearance of C. By third whorl, cord A appears, gradually growing more prominent, changing the whorl profile to hypercampanulate. No B cord is present. Whorl profile of adult shell is concave. Beading appears on all cords. One or two s cords are inserted between A and C, the top one being more prominent. Some specimens may have a beaded r cord just above A. Sutures deeply incised, appearing more so because of prominent shoulders. Basal sinus type 4, lateral sinus has single inflection point on bottom; apex in upper middle. Growth lines prosocline, particularly visible on largest, most basal whorl. Aperture shape rounded square, columellar growth margin present. Basal surface irregular.

Remarks.—As Heilprin noted, "this shell can at once be distinguished by its extremely elongated or attenuated outline, surpassing in this character all other forms of the genus" (1886, p. 88); the longest non-composite specimen we have seen in museum collections is PRI 45394 (103.5 mm), which has a reconstructed total length (using methods of Johnson et al., 2017) of approximately 147 mm. The degree to which the whorl surface is ornamented by very fine spiral threads is variable. Dall referred to specimens lacking these threads on the middle sulcus as either the "*obsoleta*" or the "*undula*" varieties. The A and C cords of the *obsoleta* variety are faintly beaded, but obliquely beaded in the "*undula*" variety.

We encountered several composite specimens (e.g., PRI 104749) of *T. perattenuata* in museum collections, the longest measuring 20.3 cm with a maximum diameter of only 13.5 mm (WFI 33612). The only specimen of *T. perattenuata* in the WFI collection (WFI 33612) labeled as "Type" does not agree with the specimen figured by Heilprin (1886) (see Text-fig. 22.2, 22.4). Heilprin's figured specimen is a composite of at least two individuals, and is presumed lost. We herein designate WFI 33612 as the neotype. We do not believe these reconstructed specimens accurately reflect the maximum size of this species because the foot of the snail would have been unrealistically large (in order to drag such a long, heavy shell in the sand behind it) for such a restricted aperture.

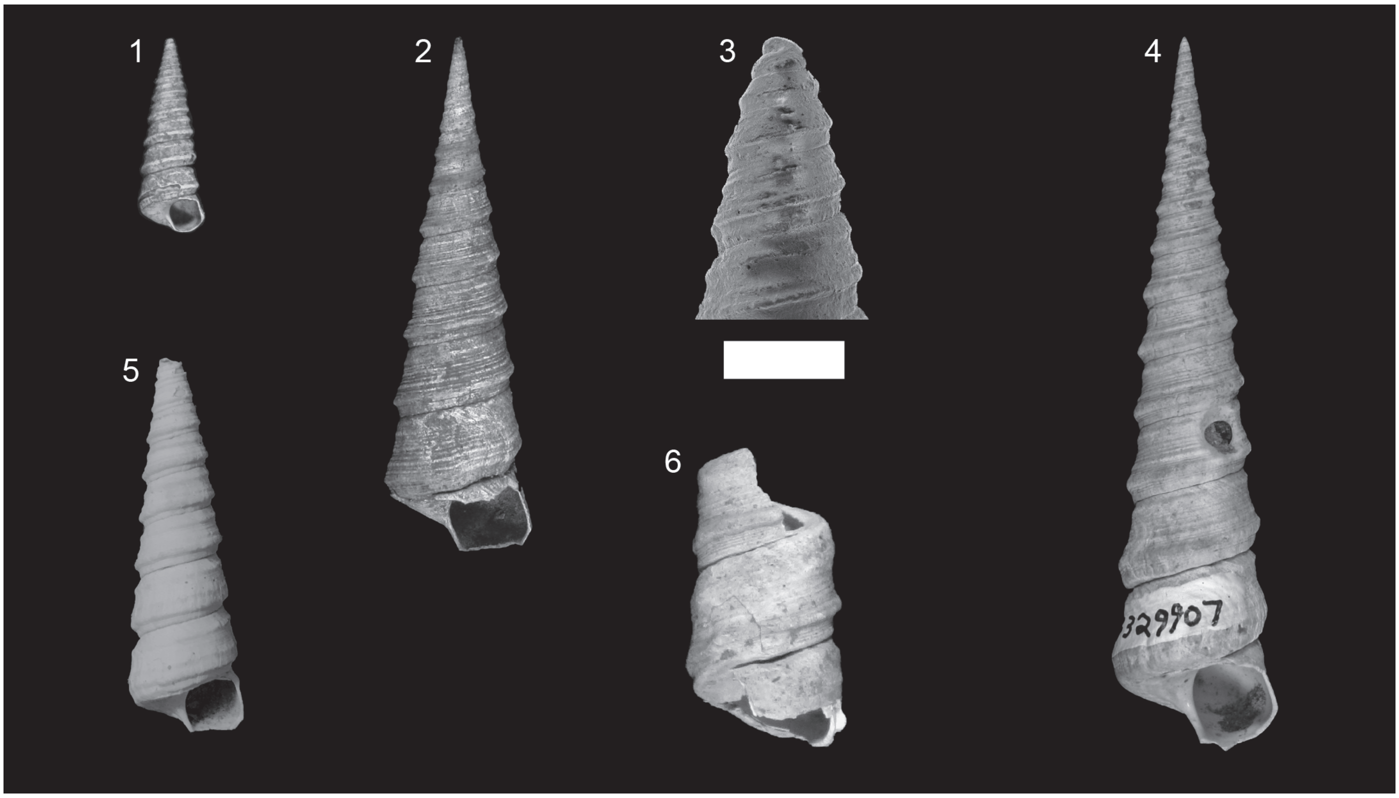
The proportion of shared characters lead us to agree with Dall (1892, p. 316) that *T. perattenuata*'s closest living relative is likely *Torcula exoleta*. *Torcula perattenuata* appears to grade into *T. exoleta* rather than the two overlapping stratigraphically.

Genus "***TURRITELLA***" Lamarck, 1799

Original description.—"Coq. Turriculée; l'ouverture arrondie, entire, mais ayant un sinus au bord droit" (Shell turriculate; aperture round, entire, possessing a sinus at the outer edge) (Lamarck, 1799, p. 74).

Subsequent description.—"The lateral and basal parts of the outer lip combine to form one wide shallow sinus, sweeping back from the adapical suture and crossing the base in a straight line to the columella where it is slightly withdrawn …. The primary spirals appear in the unusual order B-A-C, and a secondary (soon rivaling B) starts between A and B before C begins. On the neanic whorls, the lateral sinus is narrowly rounded, high on the whorl, and has a small growth-line angle... As already noted, this is a primitive kind of sinus widespread in the Cretaceous and early Tertiary" (Marwick, 1957, p. 161).

Remarks.—Where species cannot be confidently assigned to a turritellid genus, we follow the convention of naming them to "*Turritella*" *sensu lato* (e.g., Allmon, 1996; DeVries, 2007; Anderson and Allmon, 2020), in part because we are cautious in assigning species to genera with no synapomorphies, but



Text-fig. 23. "*Turritella*" *alticostata* Conrad, 1834. 1, lectotype, ANSP 81702, VA-09, 19.1 mm. 2, UF 299729, VA-23, 38.3 mm. 3, protoconch, PRI 104731, NC-14, scale bar = 1 mm. 4, UF 329907, VA-06, 55.9 mm. 5, holotype, *Turritella beaufortensis* Ward and Blackwelder, 1987, USNM 204038, NC-01, 29.5 mm. 6, syntype, ANSP 30592, VA-09, 24.7 mm.

Table 12. Measurements of specimens of *"Turritella" alticostata*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. alticostata	UF 299729	non-type	38.3	10.5	15.6°	17.5°
T. beaufortensis	USNM 204038	holotype	29.5	8.6	11.4°	23°

also because we want to emphasize we do not believe these are closely related to *Turritella s.s.* (i.e., *sensu* Marwick, 1957), which is biogeographically implausible for the Americas, being restricted to the tropical Indo-Pacific.

"*Turritella*" *alticostata* Conrad, 1834
Text-figs. 8.1, 23, Table 12

Turritella alticostata Conrad, 1834: p. 144.
Turritella alticostata. Conrad, 1863: p. 567.
Not *Turritella variabilis* var. *alticostata* Martin, 1904: p. 237, pl. 57, fig. 2.
Turritella alticosta [sic] Conrad. Cooke, 1936: p. 125.
Turritella alticostata Conrad. Mansfield, 1943: pp. 9–11.
Turritella alticosta [sic] Conrad. Richards, 1947: p. 29.
Turritella alticostata Conrad. Gardner, 1948: p.196, pl. 27, fig. 17.
Turritella beaufortensis Ward and Blackwelder, 1987: p.167, pl. 35, figs. 1, 2.
Turritella alticostata Conrad. Campbell, 1993: p. 63, pl. 29, figs. 288, 288a.
Turritella beaufortensis Ward and Blackwelder. Campbell, 1993: p. 63.
Torcula alticostata (Conrad). Petuch, 2004: p. 148, pl. 46, fig. K.

Type material.—Lectotype (designated by Campbell, 1993), ANSP 81702; syntypes (4; ANSP 30592); hypotype, *T. alticostata variabilis*, USNM 325455 (Gardner, 1948); holotype, *T. beaufortensis*, USNM 204038 (Ward and Blackwelder, 1987); hypotype, USNM 403441 (Campbell, 1993).

Other material examined.—See Appendix 2.

Measurements.—See Table 12.

Stratigraphic and geographic occurrences.—Virginia: Yorktown Fm. (Pliocene); Chowan River Fm. (Early Pleistocene). North Carolina: Yorktown Fm. (Pliocene); Chowan River Fm. (Early Pleistocene). South Carolina: Waccamaw Fm. (Early Pleistocene). Florida: Tamiami Fm., Pinecrest Beds (Plio-Pleistocene).

Type Locality.—James River, Virginia (VA-09).

Other localities.—VA-01 to VA-03, VA-05 to VA-10, VA-13, VA-15, VA-23 to VA-34, NC-01 to NC-02, NC-08, SC-01, and FL-62.

Original description.—"Shell much elongated, subulate, whorls twelve to fourteen, each profoundly carinated near the base, and with prominent spiral striæ." (Conrad, 1834, p. 144).

Revised description.—Small shell, pleural angle 14.9°, apical angle 21.4°. Round, bulbous protoconch; 2.5 smooth whorls, keeled for 1 whorl before the B cord begins to overhang the anterior half of whorl with A cord arising soon thereafter. Apical sculpture formula B1A2. Early teleoconch whorls concave, adult whorls basally carinate (campanulate). Order of adult cord prominence B>A. Three or four spiral threadlets between A and B. Cords D, C, and B closely grouped on the anterior half of the whorl. D slightly overhangs a shallow suture. Basal sinus type 3; lateral sinus single inflection point on bottom, middle apex. Growth line prosocline, aperture shape is subquadrate. Columellar growth margin is absent.

Remarks.—In naming *T. alticostata*, Conrad reported it from James River, Virginia and Choptank River, Maryland. As noted by Campbell (1993, p. 63), however, Conrad's syntypes were labeled only "Virginia", thus excluding the specimen from the Choptank Fm. (which is not exposed in Virginia) figured by Martin (1904) (which in any case we doubt to be the same species as the remaining syntypes). In choosing a lectotype, Campbell (1993) correctly dismissed the other four syntypes but misidentified them as *T. terstriata*. Campbell's hypotype of *T. beaufortensis* has flat-sided whorls as a juvenile which become subquadrate as an adult. The hypotype is missing a B cord. Sutures are less indented in the hypotype than in the holotype. The largest hypotype appears to be *T. alumensis* with cords tightly spaced at the anterior half of each whorl.

Ward and Blackwelder (1987) named *T. beaufortensis* from the Chowan River Fm. We synonymize it with *T. alticostata* because the holotype of *T. beaufortensis* resembles the lectotype of *T. alticostata* in having deep sutures, subquadrate aperture shape, and a whorl profile dominated by strong A and B cords, B being strongest.

Mansfield (1928; 1943, p. 7, 8) divided the Yorktown Fm. into two biostratigraphic zones: Zone 1, or the *Pecten clintonius* zone, below, and Zone 2, or the *Turritella alticostata* zone, above. Ward and Blackwelder (1980) proposed four member names for the Yorktown Fm. in Virginia that encompass Mansfield's zones: the lowermost Sunken Meadow Member corresponds to Zone 1, and overlying Morgarts Beach, Rushmere, and Moore House members correspond to Zone 2 (*Turritella alticostata* zone) (see Dowsett et al., 2021, and Text-fig. 1). Synonymizing *T. beaufortensis* means *T. alticostata* is no longer restricted to the upper Yorktown Fm.

Antil (1974) reported finding embryonic shells inside a specimen of *T. alticostata* from what was probably the Yorktown Fm. at Rice's Pit in Hampton, Virginia (Table 3).

"Turritella" fluxionalis Rogers and Rogers, 1837
Text-figs. 8.2, 24, Table 13

Turritella fluxionalis Rogers and Rogers, 1837: p. 319, pls. 26, 27.
Turritella duplinensis Gardner and Aldrich, 1919: p. 41, pl. 2, fig. 4.
Turritella duplinensis Gardner and Aldrich. Mansfield, 1930: p. 108, pl. 15, fig. 7.
?*Torculoidella duplinensis* (Gardner and Aldrich). Petuch, 1994: pl. 13, fig. Q.

Type material.—Holotype, *T. duplinensis*, USNM 499110; paratype, *T. duplinensis*, ANSP 60461; hypotype, *T. duplinensis* (Mansfield, 1930), USNM 370359; holotype, *T. fluxionalis* lost (fide Campbell, 1993); hypotype of *T. fluxionalis* (Campbell, 1993), USNM 403443.

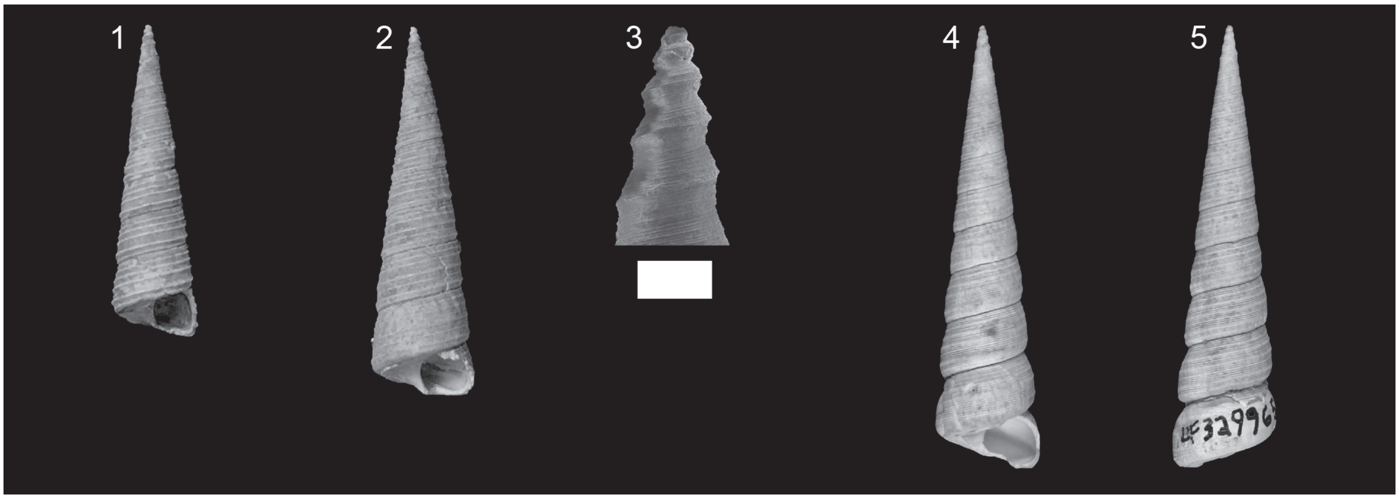
Other material examined.—See Appendix 2.

Measurements.—See Table 13.

Stratigraphic and geographic occurrences.—Virginia: upper (Zone 2) Yorktown Fm. (Pliocene); Duplin Fm. (Pliocene); South Carolina: Raysor Fm. (Pliocene); Duplin Fm. (Pliocene); Bear Bluff Fm. (Early Pleistocene); Waccamaw Fm. (Early Pleistocene); Georgia: Duplin/Raysor Fm. (Pliocene). Florida: Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest Beds (Plio-Pleistocene).

Type locality.—Williamsburg, Virginia (Rogers and Rogers, 1839).

Other localities.—VA-04, VA-08, VA-33, NC-03, NC-10 to NC-11, SC-02, SC-05 to SC-06, SC-09 to SC-10, GA-01 to GA-02, GA-04, FL-01, FL-05, FL-11, and FL-42.



Text-fig. 24. *"Turritella" fluxionalis* Rogers and Rogers, 1837. 1, holotype, *Turritella duplinensis*, USNM 499110, NC-15, 23.5 mm. 2, hypotype (Mansfield, 1930), *Turritella duplinensis*, USNM 370359, FL-05, 27.7 mm. 3, protoconch, PRI 104736, NC-10, scale bar = 0.5 mm. 4, 5, UF 329965, SC-05, 37.6 mm.

Table 13. Measurements of type and other specimens of *"Turritella" fluxionalis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. duplinensis	USNM 370359	hypotype	27.7	7.5	12.7°	27.2°
T. duplinensis	USNM 499110	holotype	23.5	6.2	13.6°	20.1°
T. fluxionalis	UF 329965	non-type	37.6	8.9	10.8°	23.1°
T. fluxionalis	USNM 403443	hypotype	28.4	6.8	14.4°	20.5°

Description.—Small-medium shell, pleural angle of 15°, apical angle 21°. Smooth protoconch for 2.25 whorls. Apical structural formula C1B2A3A'4. Nepionic whorls keeled, adult whorls flat sided. Order of adult cord prominence C > A, A', B. Delicate threads separate the major cords; approximately two spiral threads below C, six between C and B; three between B and A; two to three threads between A and A'; three to four threads above A'. Basal sinus type 3, lateral sinus has no inflection points with the apex on the lower half. Growth lines prosocline. Aperture rounded, basement slightly convex. Basal surface is lineated, normal columella.

Remarks.—Campbell argued that *T. fluxionalis*, thoroughly described by Rogers and Rogers (1837), is synonymous with *T. duplinensis*. We agree, and therefore *T. fluxionalis* takes precedence. *Turritella fluxionalis* has a convex whorl profile, while *T. duplinensis* has a straight-sided whorl profile, but the order, location, distance, of primary cords are identical.

Gardner and Aldrich (1919: p. 41) suggested that *T. duplinensis* was similar to *T. carolinensis*, which as they noted was "vaguely described and badly figured by Conrad in 1875," with no locality given and no existing type specimens. Campbell (1993) likewise suggested it is a synonym of *T. duplinensis.* We consider *T. carolinensis* a *nomen nudum*.

"Turritella" gladeensis Mansfield, 1931
Text-figs. 8.3, 25, Table 14

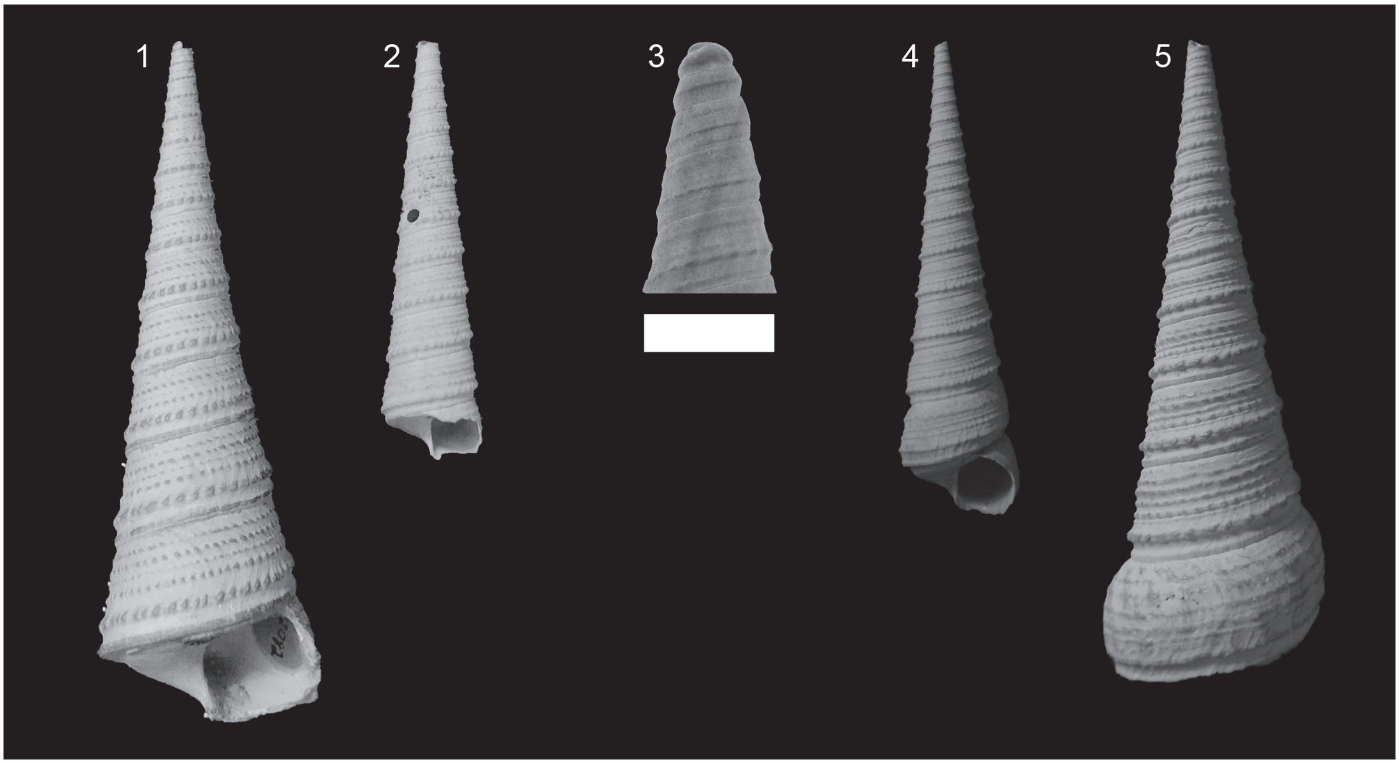
Turritella cingulata Heilprin, 1886: p. 89, pl. 8, fig. 15; not of Sowerby, I (1825), Hisinger (1831), or Hupe (1854).
Turritella apicalis var. *cingulata* Heilprin. Dall, 1892: p.317, pl. 16, fig. 11.
Turritella cookei gladeënsis Mansfield, 1931: p. 7, pl. 2, figs. 1–3.
Turritella gladeënsis (subgenus *Torcula,* section *Apicula*) Mansfield. Olsson and Harbison, 1953: p. 315, pl. 44, figs. 6, 6a, pl. 60, fig. 8.
Apicula gladeënsis (Mansfield). Petuch, 1994: p. 68, pl. 12, fig. H; 2004, p. 175, pl. 56, fig. G.
Turritella gladeënsis Mansfield. Allmon et al., 1995: p. 78, fig. 3.

Type material.—Holotype, USNM 371337; paratypes (two, Mansfield, 1931), USNM 371338; hypotypes (Olsson and Harbison, 1953), ANSP 19312; hypotype, *T. apicalis cingulata*, USNM 113468.

Other material examined.—See Appendix 2.

Measurements.—See Table 14.

Stratigraphic and geographic occurrence.—Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene).



Text-fig. 25. "*Turritella*" *gladeensis* Mansfield, 1931. 1, holotype, *T. cookei gladeensis*, USNM 371337, FL-12, 56.8 mm. 2, hypotype, *T. apicalis cingulata* Dall, 1892, USNM 113468, FL-20, 34.5 mm. 3, protoconch, PRI 104729, FL-33, scale bar = 1 mm. 4, PRI 41862, FL-33, 50.3 mm. 5, paratype, *T. cookei gladeensis*, USNM 371338, FL-12, 56.9 mm.

Table 14. Measurements of type and other specimens of *"Turritella" gladeensis*.

Taxon	**Catalog no.**	**Type status**	**Length (mm)**	**Width (mm)**	**Pleural angle**	**Apical angle**
T. gladeensis	PRI 41862	non-type	50.3	12	14.5°	10.3°
T. gladeensis	USNM 371338	paratype	56.9	20.1	19.2°	13.9°
T. gladeensis	USNM 113468	hypotype	34.5	8	11.3°	13.9°
T. gladeensis	USNM 371337	holotype	56.8	16.1	22°	13.6°

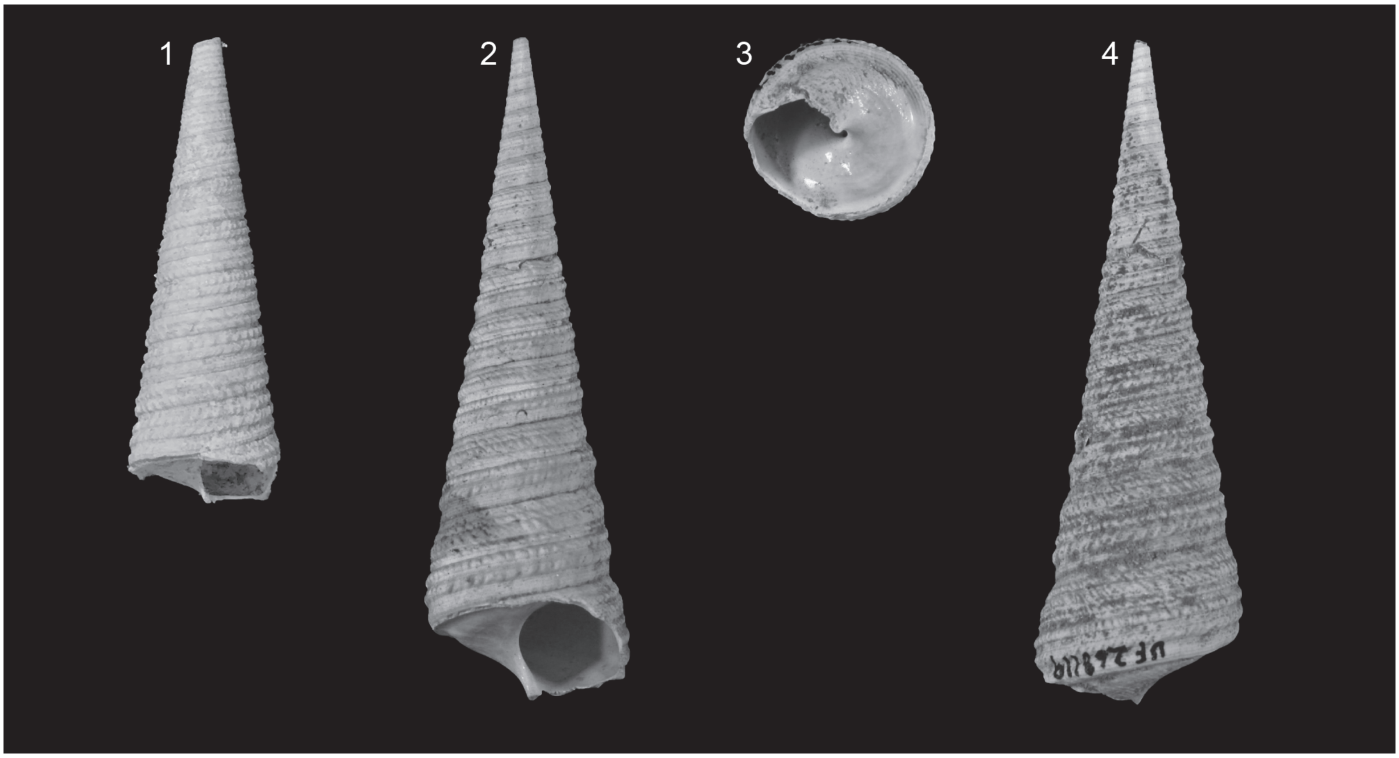
Type locality.—Tamiami Trail, 42 miles west of Miami, Miami-Dade County, FL (Mansfield, 1931).

Other localities.—FL-03, FL-10, FL-12, FL-13, FL-17, FL-29 to FL-30, FL-41, FL-64, FL-65, and FL-67.

Description.—Medium shell with a pleural angle of 19.8° and an apical angle of 17.7°. Protoconch of 2 whorls. Apical sculpture formula C1A2B3. Beading appears early (whorl 5 or 6). At apex, whorl profile is keeled, as individual grows, profile becomes more concave with A, C, and D cords controlling the shape. Posterior whorls become relatively flat-sided. Final whorl displays incongruent allometry. Sculpture of anterior whorls is controlled by a strong C cord. Above are approximately 4 smaller cords of equal strength; below is a slight concave groove leading to D, which is about the strength of the cords above C. All cords strongly beaded. Adult body whorl changes severely, becoming very convex and sometimes uncoiling slightly; all cords become less prominent, with no beading. Basal sinus type 5; lateral sinus has inflection point on bottom with apex in middle; growth line is prosocline. Aperture circular, columellar growth margin acute. Basal surface unlineated, without hollow newel.

Remarks.—The species was first figured by Heilprin (1886) but received an invalid specific name, as *cingulata* was preoccupied. Dall (1892) did not recognize it as unique and erroneously demoted *cingulata* to one of many subspecies of *apicalis*. We confidently place both Heilprin's and Dall's specimens in *T. gladeensis.*

This species is unique in that the adult body whorl differs from the preceding whorls in being inflated and round while the spire is flat-sided (with cords being the only positive relief). It is possible that this feature represents sexual maturity, and



Text-fig. 26. "*Turritella*" *jacula* Gardner, 1947. 1, holotype, USNM 498021, FL-24, Walton County, Florida, 34.7 mm. 2–4, UF 268119, SC-05, 51.9 mm.

Table 15. Measurements of type and other specimens of *"Turritella" jacula*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. jacula	USNM 498021	holotype	34.7	11	16.1°	-
T. jacula	UF 268119	non-type	51.9	15.1	18.8°	-

possibly determinate growth, which is not otherwise known in turritellids.

"Turritella" jacula Gardner, 1947
Text-figs. 8.4, 26, Table 15

Turritella (*Torcula?*) *jacula* Gardner, 1947: p. 596, pl. 57, fig. 6.

Type material.—Holotype, USNM 498021.

Other material examined.—See Appendix 2.

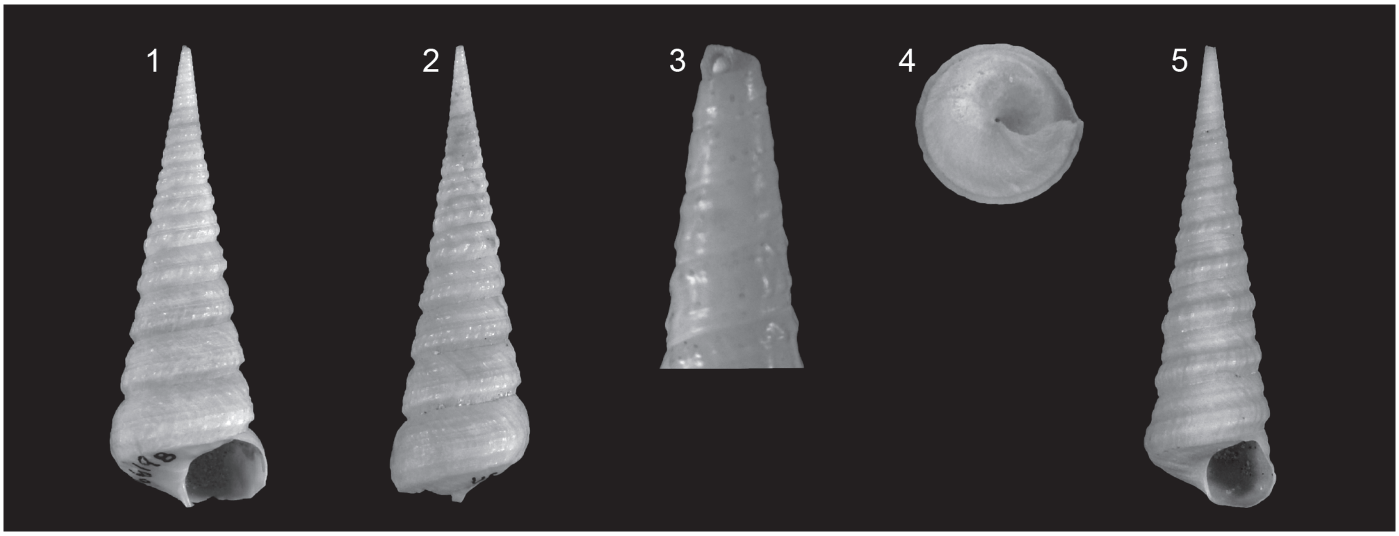
Measurements.—See Table 2.

Stratigraphic and geographic occurrences.—South Carolina: Raysor Fm. (Pliocene); Bear Bluff Fm. (Late Pleistocene). Florida: Shoal River Fm. (Middle Miocene), Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—USGS 10603, "Gully south of the road and east of the bridge over Whites Creek, on road from Eucheeanna to Knox Hill, 6.7 miles south of Argyle, 1.7 miles southeast of Eucheeanna, Walton County, Florida" (Gardner, 1947: p. 596) (=FL-24).

Other localities.—SC-05, SC-09, SC-13, FL-25, and FL-26.

Description.—Shell size medium, with a pleural angle of 16.4°. Protoconch unknown. The earliest whorl of the holotype is trilirate, the anterior most cord close to the suture. The B cord is slightly anterior to whorl midline and lightly beaded A cord within the adapical third of the whorl. Minor cords r and s are inserted later in ontogeny. Adult whorls of the holotype have four beaded primary cords, arranged as two pairs separated by a concave sulcus. The posterior cord of each pair is slightly more prominent. Entire surface of whorl may be finely threaded. Basal sinus type 2; lateral sinus in abapical half of whorl with a single inflection point in adapical half of whorl; growth lines prosocline. Aperture shape is subquadrate. Columellar growth margin prominent. Basal surface lineated.



Text-fig. 27. "*Turritella*" *miamiensis* (Petuch, 1994). 1, 2, holotype, UF 66198, FL-03, 42.9 mm. 3, broken apex of holotype, UF 66198, FL-03. 4, 5, UF 332572, FL-03, 40.8 mm.

Table 16. Measurements of type and other specimens of *"Turritella" miamiensis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. miamiensis	UF 66198	holotype	42.9	12.5	18.4°	15.9°
T. miamiensis	UF 332568	non-type	41.5	11.4	17.2°	15.7°

Remarks.—The range of variation is large; the posterior pair of beaded cords may be less prominent than the anterior pair.

"Turritella" miamiensis (Petuch, 1994)
Text-figs. 8.5, 27, Table 16

Apicula miamiensis Petuch, 1994: p. 255, pl. 12, fig. F.

Type material.—Holotype, UF 66198.

Other material examined.—See Appendix 2.

Measurements.—See Table 16.

Stratigraphic and geographic occurrence.—Florida: Tamiami Fm., Ochopee Limestone (Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Lakes of the Meadows, Bird Road, Miami-Dade County, FL (Petuch, 1994).

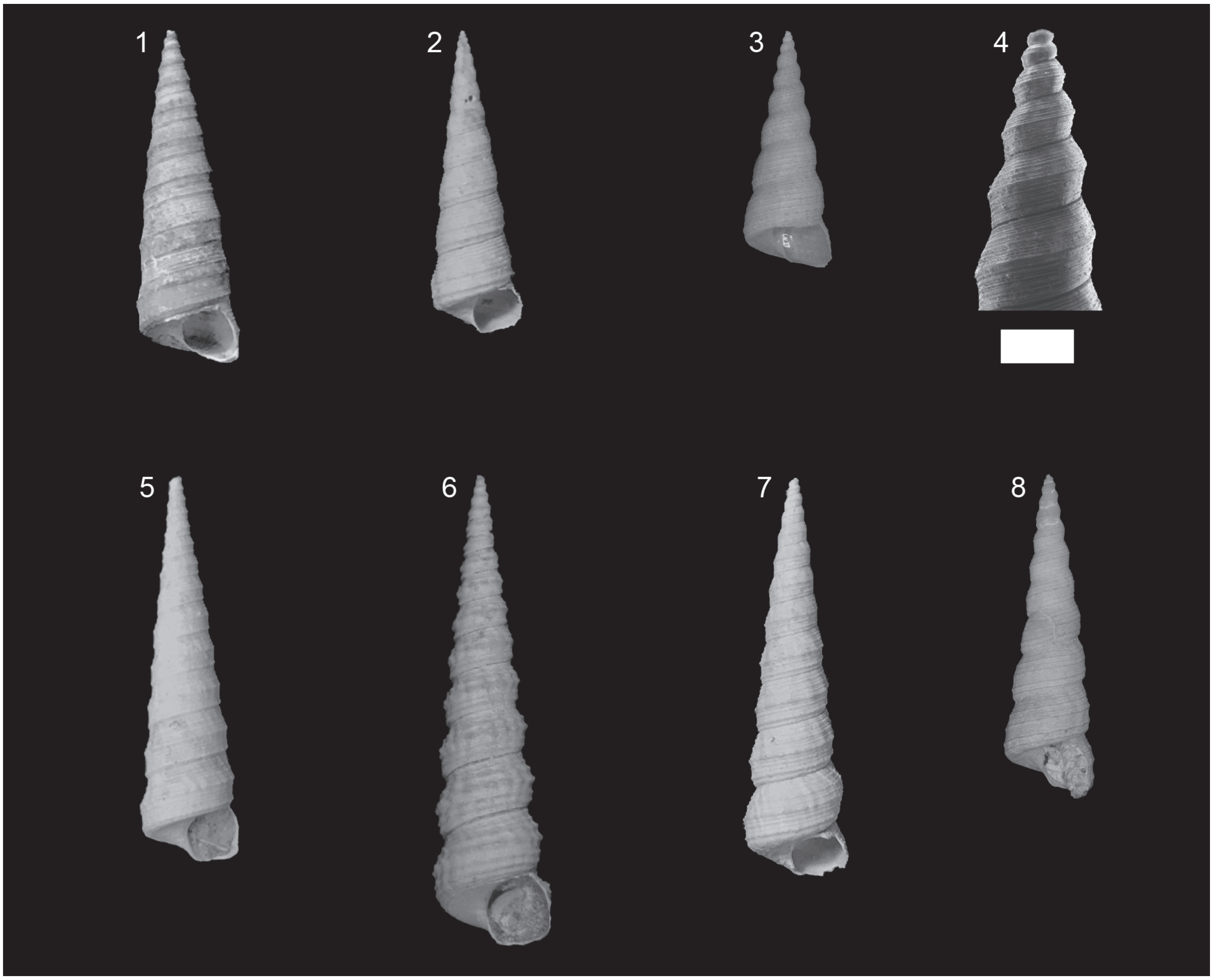
Other localities.—FL-03, FL-16, FL-17.

Original description.—"Shell average size for genus, with rounded, turrited whorls; sutures deeply impressed, producing overhanging whorls; whorls ornamented with 2 wide, rounded spiral cords, spiral cords of early whorls heavily sculptured with large, rounded beads; beaded cords on last 2 whorls break down into 6 thin, nearly obsolete spiral threads, thin spiral thread present between large beaded cord on early whorls; base of shell smooth; aperture circular." (Petuch, 1994, p. 255). Apical structural formula C1A2. Protoconch unknown.

Remarks.—Suture is wider and deeper than most of the other species mentioned here. Numerous specimens other than the holotype of this species have been identified in UF collections (Appendix 2).

"Turritella" perexilis Conrad, 1875
Text-figs. 9.1, 28, Table 17

Turritella perexilis Conrad, 1875: p. 22, pl. 4, fig. 9.
Turritella subannulata Heilprin, 1886: p. 89, pl. 8, fig. 17.
Turritella (*Torcula*) *acropora* Dall, 1889: p. 264.
Turritella subannulata var. *subannulata* Heilprin. Dall, 1892: p. 314, pl. 16, fig. 2.
Turritella subannulata var. *acropora* Dall, 1892: p. 315, pl. 16, fig. 4.
Turritella subannulata var. *intermedia* Dall, 1892: p. 316, pl. 16, fig. 3.
Turritella subannulata var. *perincisa* Dall, 1892: p. 316, pl. 16, fig. 1.
Turritella subannulata var. *Burnsii* Dall, 1892: p. 315.
Torcula acropora Dall. Maury, 1922: pp. 134, 135.



Text-fig. 28. "*Turritella*" *perexilis* Conrad 1875. 1, *T. subannulata acropora*, hypotype, USNM 113444, FL-18, 20.1 mm. 2, hypotype, USNM 204041, NC-05, 19.2 mm. 3, *T. acropora*, syntype, MCZM 7452, FL-27, 16.7 mm. 4, protoconch, PRI 104734, NC-09, scale bar = 1 mm. 5, *T. subannulata acropora*, USNM 113445, FL-37, 25.3 mm. 6, *T. subannulata*, hypotype, ANSP 18263, FL-23, 33.0 mm. 7, *T. subannulata*, holotype, WFI 17281, NC-05, 24.1 mm. 8, *T. acropora*, syntype, MCZM 7453, FL-27, 19.4 mm.

Table 17. Measurements of type and other specimens of *"Turritella" perexilis*.

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. perexilis	USNM 204040	hypotype	23.5	6	12.1°	20.9°
T. perexilis	USNM 204041	hypotype	19.2	5.5	16.9°	20.6°
T. acropora	MCZM 7452	syntype	16.7	6.0	17.3°	25.1°
T. subannulata	WFI 17281	holotype	24.1	6.3	13.2°	22.5°

Turritella subannulata jacksonensis Mansfield, 1930: p. 109, pl. 15, fig. 8.

Turritella subannulata ochlockoneënsis Mansfield, 1930: p. 109, pl. 16, fig. 3.

Turritella subannulata leonensis Mansfield, 1935: p. 43.

Turritella (*Eichwaldiella*) *subannulata* Heilprin. Olsson and Harbison, 1953: p. 312, pl. 44, fig. 8.

Turritella subannulata acropora Dall. Perry and Schwengel, 1955: p. 135, pl. 25, fig. 181.

Turritella (*Eichwaldiella*) *subannulata* Heilprin. DuBar, 1958: p. 203, pl. 12, fig. 13.

Turritella acropora Dall. Abbott, 1974: p. 95, fig. 904.
Turritella perexilis Conrad. Ward and Blackwelder,1987: p. 167, pl. 35, fig. 3, 4.
Torculoidella ochlockoneensis (Mansfield). Petuch, 1994: pl. 13, fig. I.
Torculoidella burnsi [sic] (Dall). Petuch, 1994: pl. 13, fig. J.
Torculoidella subannulata (Dall). Petuch, 1994: pl. 13, fig. L.
Torculoidella perincisa (Dall). Petuch, 1994: pl. 13, fig. M.
Torculoidella acropora (Dall). Petuch, 1994: pl. 13, fig. P.
Torculoidella intermedia (Dall). Petuch, 1994: pl. 13, fig. S.
Turritella acropora Dall. Rosenberg et al., 2009: p. 628.

Type material.—Holotype, *T. perexilis* (Conrad, 1873/1875) unknown; hypotypes of *T. perexilis* (Ward and Blackwelder, 1987), USNM 204040, 204041; syntypes, *T. acropora,* MCZM 7452 (five specimens), 7453 (three specimens), 7454 (one specimen); holotype, *T. subannulata*, WFI 17281; holotype, *T. subannulata acropora*, USNM 112344; hypotype (Dall, 1892), USNM 113444; plesiotypes? (Schuchert et al., 1905), *T. subannulata* USNM 112342; hypotypes, *T. subannulata*, ANSP 18263, 18878 (Olsson and Harbison, 1953); holotype, *T. subannulata leonensis*, USNM 370362 (formerly called *T. subannulata jacksonensis* by Mansfield, 1930); holotype, *T. subannulata* var. b*urnsii*, USNM 113446; holotype, *T. subannulata intermedia*, USNM 113451; holotype, *T. subannulata ochlockoneensis*, USNM 370363; holotype, *T. subannulata perincisa*, USNM 113450; syntypes (12), *T. subannulata burnsi*, USNM 113446 (listed as "cotypes" by Schuchert et al., 1905).

Other material examined.—See Appendix 2.

Measurements.—See Table 17.

Stratigraphic and geographic occurrences.—North Carolina: Chowan River Fm. (Early Pleistocene); Waccamaw Fm. (Early Pleistocene). South Carolina: Goose Creek Fm., Duplin/ Raysor Fm. (Pliocene); Canepatch Fm. (Middle Pleistocene); Chowan River Fm. (Early Pleistocene). Georgia: Duplin/ Raysor (Pliocene). Florida: Tamiami Fm., Ochopee Limestone (Pliocene); Jackson Bluff Fm. (Late Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene); Nashua Fm. (Early Pleistocene); Bermont Fm. (Early Pleistocene).

Type locality of T. acropora.—Recent; Banana River, Fort Denaud, Hendry County, Florida (FL-28).

Type locality of T. perexilis.—Wilmington, North Carolina (Conrad, 1875).

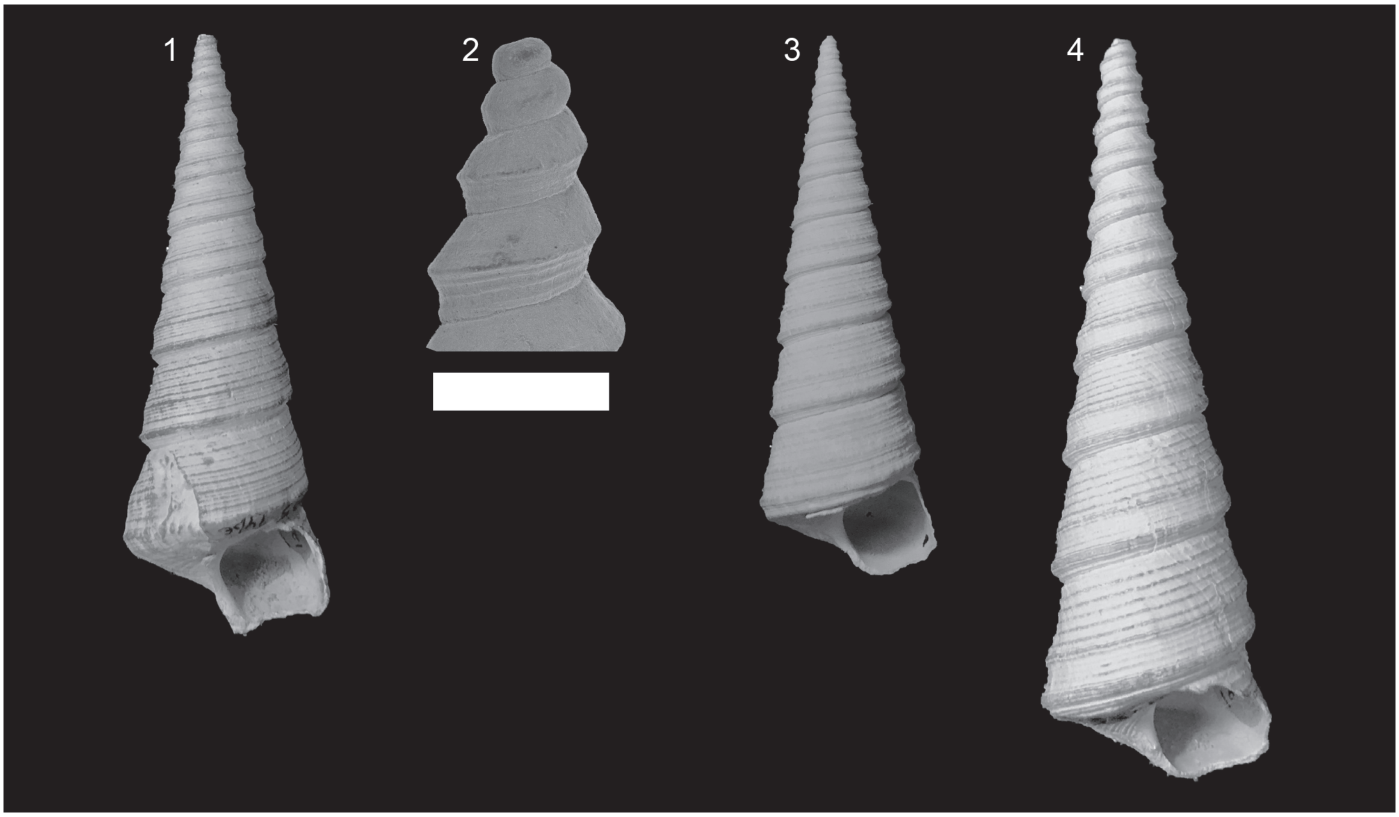
Other localities.—NC-01, NC-03, NC-05, NC-06, NC-09, NC-12, SC-05, SC-06, SC-08, SC-11, SC-12, GA-01, GA-02, GA-04, GA-05, FL-01, FL-03, FL-04, FL-07, FL-17, FL-19, FL-20, FL-25, FL-27 to FL-30, FL-36, FL-38, FL-40, FL-41, FL-43, FL-46, FL-50, FL-55, FL-56, FL-64, FL-70 to FL-73, FL-75, and FL-79. Recent, western Atlantic: North Carolina to Texas; Yucatan to the Antilles.

Original description.—"Shell slender, volutions convex, 3 acute prominent revolving ribs on each, a prominent line below the suture, and fine revolving lines between the ribs; obscure, oblique longitudinal plications which subintercalate the ribs; sutural area deeply impressed" (Conrad, 1875, p. 22).

Revised description.—Small shell with a pleural angle of 14.7° and an apical angle of 25°. Protoconch has 2 smooth whorls followed by the rapid appearance of numerous spirals. Apical sculpture formula B1C2A3. On the first sculptured whorl, A, B, and C are equally strong, surrounded by a number of small threads. Between whorl 3 and whorl 4, intercalated beaded threads appear between the main cords, A′ arises, and A and C recede dramatically. On the 5th whorl, undulation begins. In adulthood, the shape is keeled. Adult cord prominence B > C > A. Below C there are 1–2 spiral threads; there is a canal between C and B with 1–3 spiral threads; between B and A there are 1–2 spiral threads; above A there are 2–3 spiral threads in addition to A′. Undulations/plications are strong and consistent above the midline on all specimens. Basal sinus is type 3; lateral sinus is faint. Suture shallow. Aperture shape subquadrate with flat basement; columellar growth margin prominent. Basal surface lineated, normal columella.

Remarks.—The most conspicuous feature shared by all *T. perexilis* varieties, including some *T. acropora*, are axial undulations (called "longitudinal waves" by Dall (1889, p. 265)).

Dall (1892, pp. 314, 315) placed his modern species *T. acropora* as a variety of Heilprin's fossil species *T. subannulata* and figured Heilprin's hypotype (USNM 113444) for the fossil form. Dall stated: "This is a very remarkable species, which has been collected in such abundance as to throw a flood of light on the variations which may occur in a single species under essentially similar conditions, while the same species exhibits such an inflexibility of constitution as to persist, practically unchanged, for such an immense period as implied by the interval between the deposition of the old Miocene Chipola beds and the present epoch. The figures on Plate 16 represent extremes which no one who did not possess intermediate gradations would for a moment hesitate to regard as 'good species,' …" (1892, p. 314) and "Here we have a form which is not distinguishable by any marked characters from the recent one described by the writer in 1889… as *T.* (*Torcula*) *acropora*."



Text-fig. 29. "*Turritella*" *pontoni* Mansfield, 1931. 1, holotype, USNM 371335, FL-12, 65.7 mm. 2, protoconch, PRI 104729, FL-10, scale bar = 0.5 mm. 3, hypotype (Olsson, 1967), USNM 347411, FL-12, 80.8 mm. 4, paratype, USNM 371336, FL-12, 51.2 mm.

Table 18. Measurements of type and other specimens of *"Turritella" pontoni.*

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. pontoni	USNM 371335	holotype	65.7	20.2	19°	-
T. pontoni	USNM 347411	hypotype	80.8	23.9	18°	28.5°
T. pontoni	USNM 371336	paratype	51.2	17.1	19.7°	-

We agree with Ward and Blackwelder (1987) and synonymize *T. perexilis* and *T. subannulata*. We also agree with Dall and synonymize *acropora* and *perexilis*.

"Turritella" pontoni Mansfield, 1931
Text-figs. 9.3, 29, Table 18

Turritella pontoni Mansfield, 1931: pp. 6, 7, pl. 2, figs. 4, 5, 7.
Turritella cf. *T. pontoni* Mansfield, 1939: p. 47, pl. 1, figs. 3, 8.
?*Turritella* aff. *T. cartagenensis* Mansfield, 1939: p. 46, pl. 1, figs. 2, 12.
Turritella (*Eichwaldiella*) *pontoni* Mansfield. Olsson and Harbison, 1953: p. 311, pl. 30, figs. 9a, b; pl. 44, fig. 7.
Turritella pontoni Mansfield. Olsson, 1967: p. 38, pl. 3, fig. 6.
Eichwaldiella pontoni (Mansfield). Petuch, 1994: pl. 13, figs. A, B.

Type material.—Holotype, USNM MO 371335; paratype USNM MO 371336; hypotypes (three), ANSP 19311 (Olsson and Harbison, 1953); hypotypes, USNM MO 497964 and 497965 (Mansfield, 1939); hypotype, USNM PAL 347411 (Olsson, 1967).

Other material examined.—See Appendix 2.

Measurements.—See Table 18.

Stratigraphic and geographic occurrences.—Florida: Tamiami Fm., Ochopee Limestone (Pliocene); Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Nashua Fm. (Early Pleistocene).

Type locality.—USGS station 12082, Tamiami Trail, 42 miles west of Miami, Monroe County, FL (Mansfield, 1931).

Other localities.—Pinecrest Sand, Tamiami Fm. (Mansfield, 1939; Olsson and Harbison, 1953; Petuch, 1994); "Buckingham marls" (Olsson and Harbison, 1953). FL-07, FL-12, FL-15, FL-17, FL-25, FL-30, FL-39, FL-41, FL-46, FL-48 to FL-50, FL-54, FL-56, FL-58, FL-59, FL-61 to FL-64, and FL-79.

Description.—Large shell; pleural angle 20.1°, apical angle 22.7°. Protoconch of 1.5 smooth, convex whorls. Apical sculpture formula C1B2A3. The C cord defines keeled shape in nepionic whorls; in adult whorls, B recedes while D becomes the most prominent. Adult whorl profile frustate, still retains slight curvature of B cord. Seven cords interspaced with between 14 and 18 threads. Cords relatively smooth, rather than raised. Basal sinus type unknown, lateral sinus has no inflection points; apex in lower half; growth line inclination prosocline. Aperture shape rounded square. Basal surface lineated.

Remarks.—Olsson (1967, p. 38) calls *T. pontoni* "the common *Turritella* at Pinecrest." Mansfield (1931) suggested that the species is related to *T. gatunensis* (Miocene of Panama). *Turritella pontoni* is one of the larger species discussed here (along with *C. mansfieldi*).

"Turritella" pilsbryi Gardner, 1928
Text-figs. 9.2, 30, Table 19

Turritella pilsbryi Gardner, 1928: p. 561, fig 1.
Turritella pilsbryi. Gardner, 1948: p. 196, pl. 27, figs. 11, 25.
Turritella pilsbryi Gardner. Palmer, 1958: pp. 210–213, figs. 1–3.
Not *Torcula pilsbryi* (Gardner). Petuch, 1994: pl. 13, fig. G.

Type material.—Holotype, *T. pilsbryi*, USNM 325457; hypotypes (three; Palmer, 1958), PRI 25176, PRI 25177, PRI 25178.

Other material examined.—PRI 8936, PRI 8937, PRI 25368, PRI 45410. See Appendix 2.

Measurements.—See Table 19.

Stratigraphic and geographic occurrences.—Virginia: Yorktown Fm. (Pliocene). Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Schmidt's Bluff, Zone 1 of Yorktown Fm., 26 to 34 feet above the base of the bluff (Gardner, 1928, p. 562).

Other localities.—VA-11, VA-12, VA-26, VA-35, and FL-65.

Description.—Large shell with pleural angle of 10.6° and apical angle of 23.5°. Apical sculpture formula C1B2A2. Protoconch smooth, first half whorl slightly offset from the normal plane of coiling. C appears on first whorl, immediately begins migrating proportionally downwards as 2 major spiral cords are inserted above it. In the adult form, four major cords are equally prominent; whorl profile convex. The sulcus between D and C is wider than between any other cords (which are evenly spaced) but it decreases as the shell grows; A, B, and C descend proportionally down whorl as the individual grows. Threadlets exist between and on top of major chords in the most basal whorls; occasionally larger threads in between major chords. Space between A and suture increases with growth, obscure threadlets too numerous to count that become more obscure in body whorl. Suture remains slightly incised until body whorl, where it deepens dramatically. Basal sinus is type 4; lateral sinus has single inflection point on bottom with apex in lower middle; growth lines prosocline, sometimes appear so strongly on later whorls as to make cords appear beaded. Aperture shape is rounded; internal lirae possible but rare; columellar growth margin is present.

Remarks.—Internal lirae (Text-fig. 30.5) were observed only in a few specimens, and were not observed in any other Plio-Pleistocene–Recent turritellids from Florida and the Atlantic coastal plain. Harzhauser and Landau (2019) first described lirae in a number of Miocene Paratethyian turritellid species, but—like us—did not find this feature to be of taxonomic value.

Gardner (1948) and Palmer (1958) reported finding numerous embryonic shells inside specimens of *T. pilsbryi* from the Yorktown Fm. in Virginia (Table 3), implying brooding development.

We disagree with Campbell (1993), who identified *T. bipertita* Conrad, 1844 from the Yorktown Fm. at Petersburg, Virginia as being synonymous with *T. alumensis* and *T. pilsbryi*. The holotype of *T. bipertita* is missing (Moore, 1962) but was figured by Conrad (1868). We consider *T. bipertita* a *nomen nudum*.

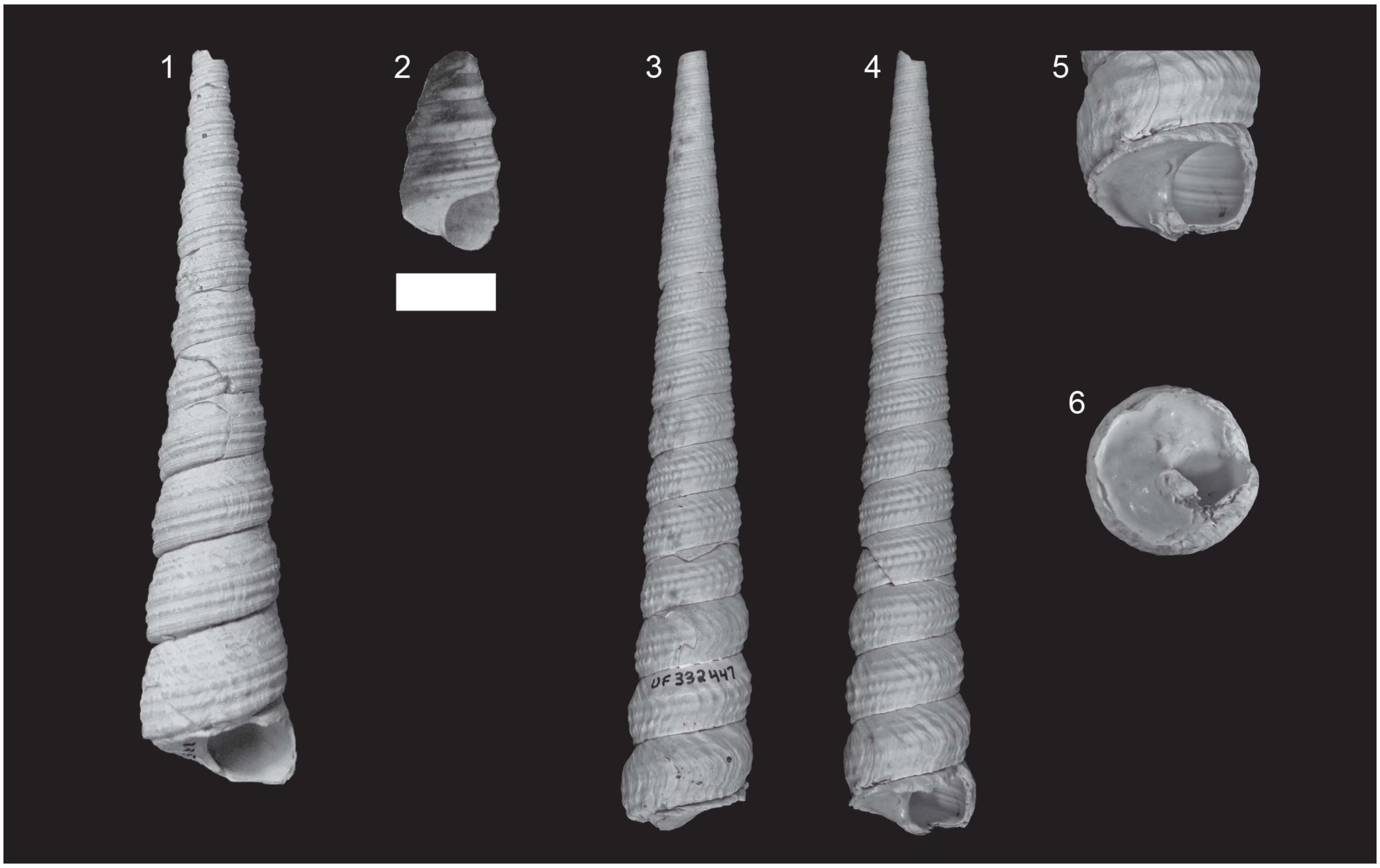
"Turritella" seminole (Petuch, 1994)
Text-figs. 9.4, 31

Apicula seminole Petuch, 1994: pp. 255, 256, pl. 13, fig. c.

Type material.—Holotype, UF 66197.

Other material examined.—See Appendix 2.

Stratigraphic and geographic occurrence.—Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene).



Text-fig. 30. "*Turritella*" *pilsbryi* Gardner, 1928. 1, holotype, USNM 325457, VA-11, 115.5 mm. 2, hypotype (Palmer, 1958), PRI 25177, VA-12, larval shell found within the specimen as described in Palmer (1958), scale bar = 1 mm. 3–6, UF 332447, FL-65, 119.2 mm. 5, view inside aperture. 6, basal view.

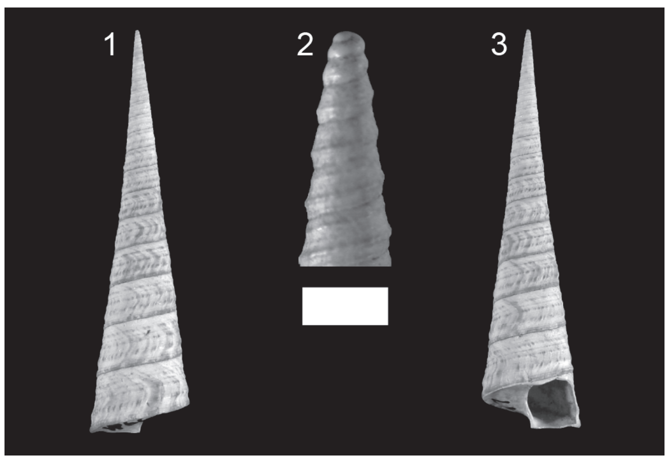
Table 19. Measurements of type and other specimens of *"Turritella" pilsbryi.*

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. pilsbryi	USNM 325457	holotype	115.5	24	9.4°	12.2°
T. pilsbryi	UF 332447	non-type	119.2	19.8	7.8°	-

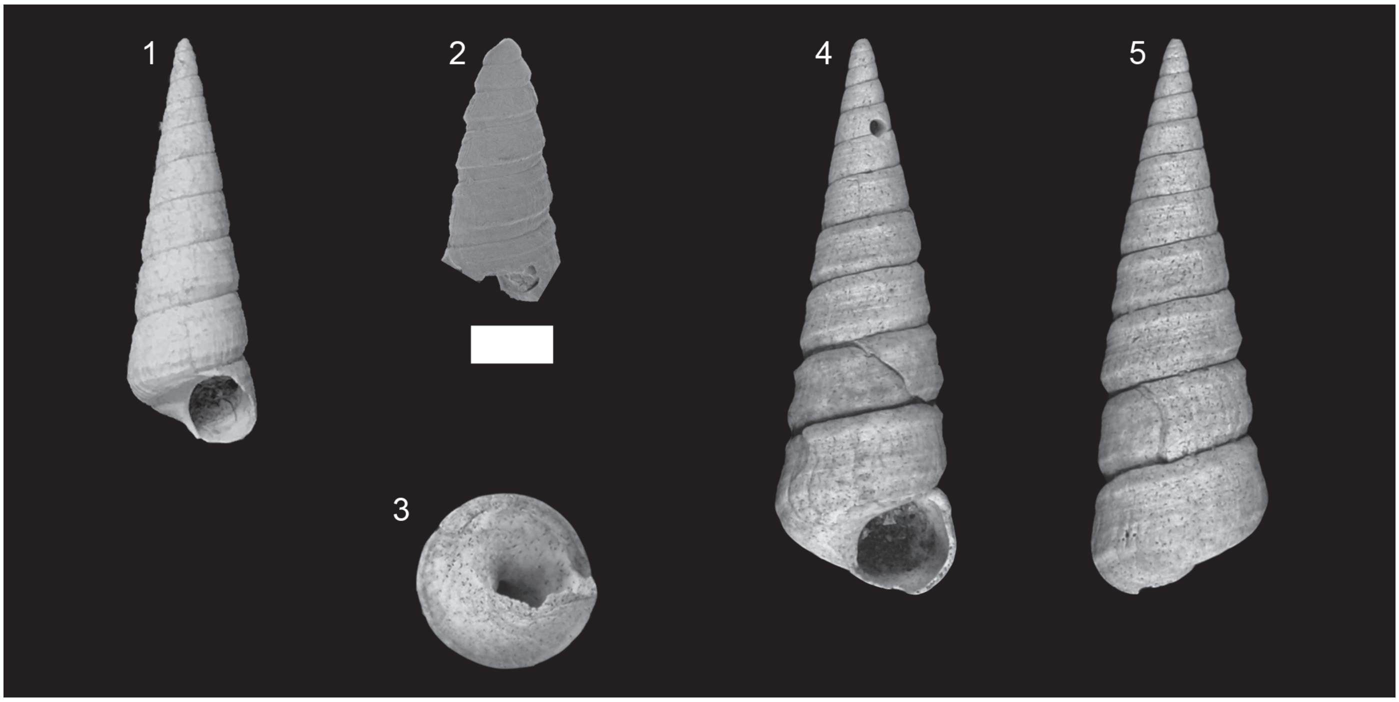
Type locality.—Lakes of the Meadows, 147th and Bird Road, Miami-Dade County, FL (Petuch, 1994).

Other localities.—FL-29, FL-33, FL-82, and FL-83.

Description.—Medium-sized shell with pleural angle of 14.3° and apical angle of 12.7°. Apical sculpture formula C1B3A2. Smooth protoconch of 1.5 whorls immediately followed by appearance of the C cord, followed by the A cord after two additional whorls. A weak B cord appears soon after A. Numerous very fine spiral threads present between spiral cords. Juvenile whorl profile keeled; adult whorl profile flat sided. Suture very shallow. Raised growth lines produce beaded cords. Lateral sinus has no inflection points, apex in middle of whorl; growth lines prosocline. Aperture shape is square; basement is flat; adapical base smooth.



Text-fig. 31. "*Turritella*" *seminole* Petuch 1994. Holotype and its protoconch (scale bar = 1 mm), UF 66197, FL-03, 45.0 mm. Scale bar = 1.0 mm.



Text-fig. 32. "*Turritella*" *virginica* Campbell, 1993. 1, holotype, USNM 403442, VA-01, 18.5 mm. 2, protoconch of PRI 104752, SC-11. 3–5, UF 330229, VA-19, 31.1 mm.

Table 20. Measurements of the holotype of *"Turritella" virginica.*

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. virginica	USNM 403442	holotype	18.5	5.7	16.3°	22.4°

"*Turritella*" *virginica* Campbell, 1993
Text-figs. 9.5, 32, Table 20

Turritella virginica Campbell, 1993: p. 63, pl. 29, fig. 290.
Turritella virginica. Campbell and Campbell, 1995: p. 175.
Not *Archimediella virginica* of Petuch, 1994, p. 66[68], pl. 13, fig. T.

Type material.—Holotype, USNM 403442.

Other material examined.—UF 330228, UF 330229, UF 330230. See Appendix 2.

Measurements.—See Table 20.

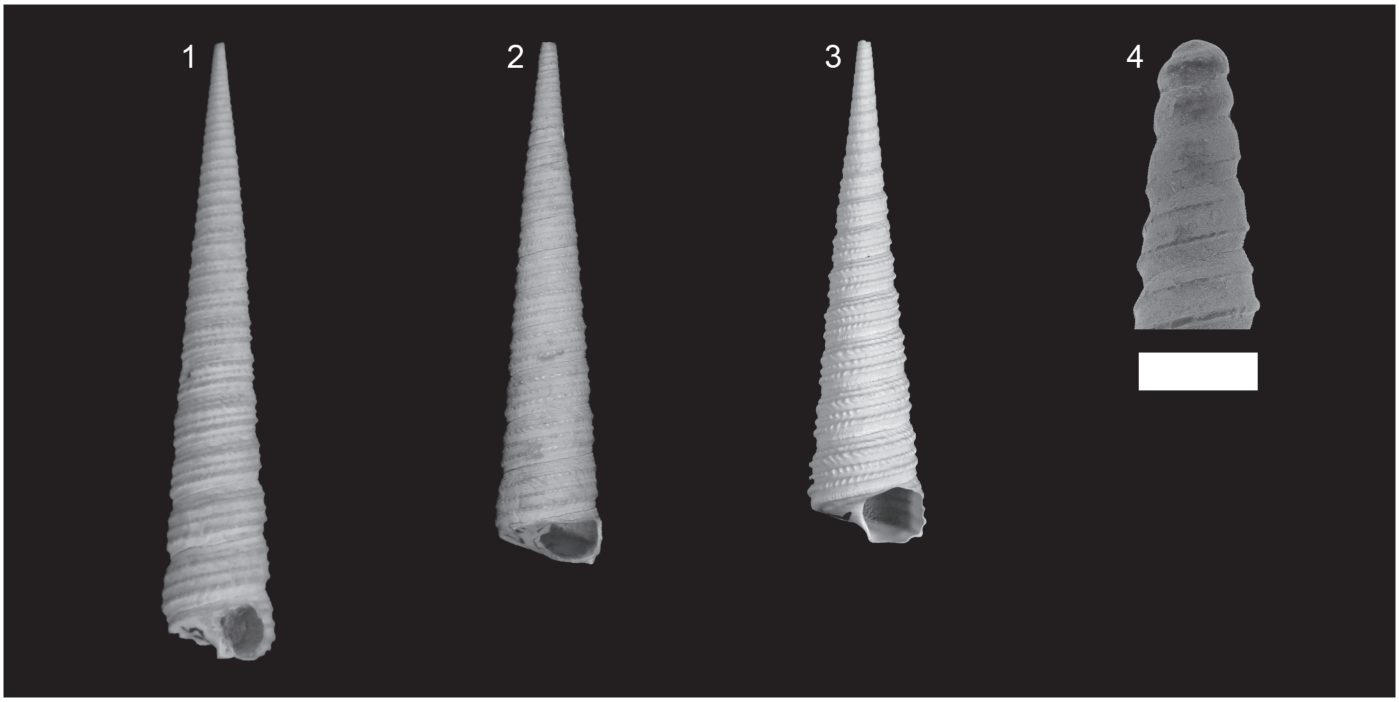
Stratigraphic and geographic occurrences.—Virginia: Yorktown Fm., Chowan River Fm. (Pliocene). North Carolina: Duplin Fm. (Pliocene); Yorktown Fm. (Pliocene). Georgia: Duplin/Raysor Fm. (Pliocene). Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene).

Type locality.—Crane Lake, formerly the Lone Star Cement Company pit, Chuckatuck, City of Suffolk, Virginia (VA-23) (Campbell, 1993).

Other localities.—VA-05, VA-19, NC-02, NC-03, NC-13, GA-01, GA-02, GA-04, GA-05, and FL-03.

Description.—Shell of small to medium size, pleural angle of 15.6°, apical angle 20.9°. Nuclear whorls rounded, smooth; nuclear suture very narrow and shallow. Cord sculpture incipient on volutive fourth whorl. Apical sculpture formula C1B3A2. Sculpture of rather regular, even spiral cords, lower cord somewhat stronger on each whorl. Adult whorl profile subquadrate. Suture broadly indented, forming a very low, even "v"-shaped notch. Basal sinus unknown. Lateral sinus prosocline, simple concave, with apex in middle of whorl. Aperture shape round; basement convex. Basal surface smooth, normal columella.

Remarks.—According to Campbell (1993), exceptional specimens preserve the color pattern of rectangular dots arranged in axial rows. *Turritella virginica* from Chuckatuck consistently showed this same pattern under ultraviolet light, but *T. alticostata* from those same beds showed no fluorescent pattern.



Text-fig. 33. "*Turritella*" *wagneriana* Olsson and Harbison, 1953. 1, holotype, ANSP 556, FL-37, 72.6 mm. 2, paratype, ANSP 79272, FL-37, 55.0 mm. 3, UF 181622, FL-81, 50.4 mm. 4, protoconch, PRI 108263, FL-84, scale bar = 0.5 mm.

Table 21. Measurements of type and other specimens of *"Turritella" wagneriana.*

Taxon	Catalog no.	Type status	Length (mm)	Width (mm)	Pleural angle	Apical angle
T. wagneriana	UF 332447	non-type	122.7	19.6	7.5	-
T. wagneriana	ANSP 79272	paratype	55.0	10.6	10	9.4

"Turritella" wagneriana Olsson and Harbison, 1953
Text-figs. 9.6, 33, Table 21

Turritella (*Torcula*) *wagneriana* Olsson and Harbison, 1953: p. 313, pl. 44, figs. 1, 1a, 1b.
Apicula wagneriana (Olsson and Harbison). Petuch, 1994: pl. 12, fig. N.

Type material.—Holotype, ANSP 566 (Olsson and Harbison 1953); paratype, ANSP 79272.

Other material examined.—See Appendix 2.

Measurements.— See Table 21.

Stratigraphic and geographic occurrences.—Florida: Tamiami Fm., Pinecrest beds (Plio-Pleistocene); Caloosahatchee Fm. (Early Pleistocene).

Type locality.—Shell Creek, Charlotte County, Florida (Olsson and Harbison, 1953).

Other localities.—FL-10, FL-18, FL-40, FL-41, FL-66, FL-71, FL-72, and FL-81.

Description.—Large shell with a pleural angle of 10.5° and apical angle of 13.2°. Smooth protoconch of 1.5 whorls. Apical sculpture formula is C1B3A2. Whorl profile is concave in juveniles and as adults primarily flat sided to subquadrate. A and C are the most prominent cords throughout the individual's life, and the B cord becomes more prominent with growth. In adult individuals, three beaded main cords are equally as strong, separated by concave sulci of similar strength. A beaded 'r' cord sits immediately above the A cord and some specimens show a fine 's' thread between the A and B cords. Medium-shallow suture. Basal sinus is type 4, lateral sinus prosocline, simple concave with an apex midwhorl. Aperture shape is rectangular, basement convex and nonlineated. Columellar growth margin is acute, normal columella.

Remarks.—When naming the new species *Turritella wagneriana*, Olsson and Harbison (1953) noted that many specimens of this form had been previously identified as *Turritella tensa* Dall, 1892, but did not agree with Dall's figure (Olsson and Harbison, 1953, p. 314).

Juvenile specimens of *T. wagneriana* may be confused with *T. apicalis*. Three cords of *T. wagneriana* are more closely spaced and located mid-whorl, whereas major cords A and C of *T. apicalis* are closer to the top and bottom margins of the whorl.

PHYLOGENETIC ANALYSIS

Introduction

Because many morphological features of turritellid shells are known to be highly variable and homoplasious across time and geography (Kotaka, 1978; Allmon, 1992b; Beu, 2010; Anderson, 2018), the uncritical application of morphological cladistic techniques across all species considered together is highly problematic. However, by restricting analyses to groups of species which we already believe are likely to be clades due to unique shared features (be they protoconch morphology, unusual spiral sculpture order of appearance, etc.), the risk of repeated evolution of a character state resulting in incorrect phylogenetic inference is reduced (Anderson, 2018).

Two separate parsimony analyses were run for *Caviturritella* and *Torcula* including Pliocene to Recent members of each clade, identified based on the genus-defining characters described above. We analyzed each independently, as molecular studies have indicated deep divergence between these two clades, with species assigned herein to *Caviturritella* more closely related to the Indian Ocean/tropical western Pacific *Turritella sensu stricto* than *Torcula* (Lieberman et al., 1993; Anderson, 2018; Sang et al., 2019). Further, we anticipated high potential for homoplasy in many teleoconch characters across the family as a whole.

Taxa Analyzed

Plio-Pleistocene to Recent species referred to *Caviturritella* above based on hollow newel morphology and biogeography, but for which protoconch data were not available, were not included in this analysis (*C. broderipiana* and *C. abrupta*). *"Turritella" nodulosa* King, 1832 (year fide Coan et al., 2011) was selected as the outgroup for *Caviturritella* (Text-fig. 34) and "*Turritella" conspersa* Adams and Reeve, 1849, and *Maoricolpus roseus* (Quoy and Gaimard, 1834) were selected as outgroups to *Torcula* (Text-fig. 35). These taxa were chosen based on close relationships with their respective clades found in molecular analyses of Anderson (2018) and Sang et al. (2019). *Vermicularia* was found to be sister to *Torcula* in molecular analyses (Anderson, 2018), but due to its unusual uncoiled morphology *Vermicularia* was not selected as the sole outgroup. Instead, three species representing a range of morphologies found in *Vermicularia* were included in the analysis with *Torcula*.

Characters and Character States

We expanded character and character state descriptions beyond previous analyses via detailed comparative examination of shell features. In total, 33 characters were identified, including a combination of qualitative and quantitative characters (Appendix 3). Quantitative characters were measured for coding using the program ImageJ. A variety of means for coding characters exist, and we have followed the precepts and principles presented by Wiley and Lieberman (2011) for identifying hypotheses of homologies and coding them. No explicit models of character weighting were used, but different morphological systems varied in the number of characters they contained, conferring de facto weighting. Further, some characters may display more homoplasy than others; thus, different characters may provide varying degrees of phylogenetic resolution.

Of the 33 morphological characters coded for the morphological analysis, three refer to the protoconch; three to the apical sculpture; five to the growth line sinus morphology; two to whorl profile; two to angles of growth; seven to cord morphology; two to the suture; four to the aperture/growth margin; two to axial ornaments; one to size; one to the columella; and two respecting uncoilings. Protoconch diameter, order of appearance of spiral ribs A, B, and C, lateral sinus depth, lateral angle, lateral sinus apex location, pleural angle, apical angle, size class, aperture shape, suture depth, and the average whorl number of uncoiling were treated as ordered characters in phylogenetic analysis, all others were unordered. Characters and their states are presented in Appendix 3.

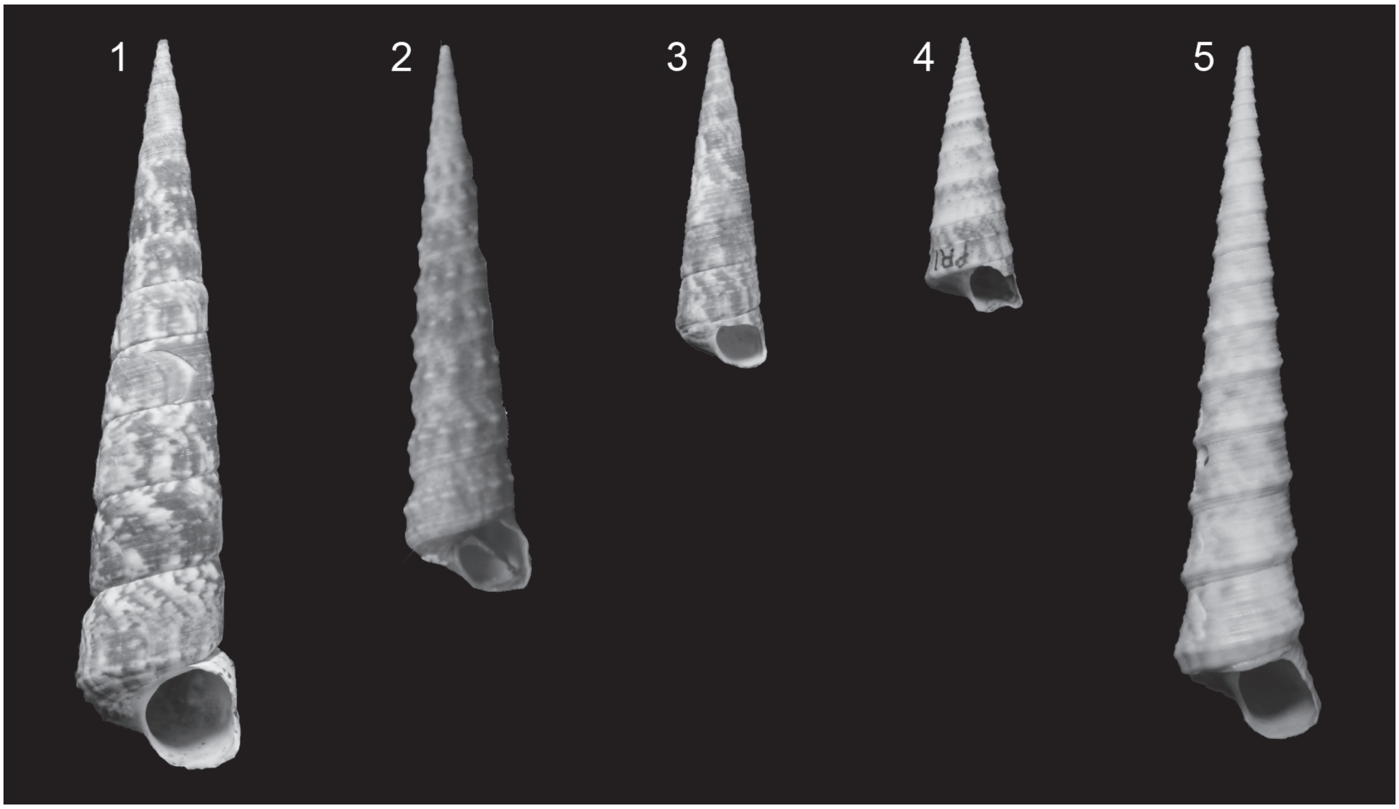
Analyses

A parsimony analysis was implemented using the morphological character matrices in Appendices 4 and 5 in PAUP 4.0 build 168 (Swofford, 2003). Characters were set to equal weighting, with uninformative characters excluded (e.g., the hollow newel character state was uniformly "absent" in the analysis of the *Torcula* tree and was therefore excluded from that analysis). An exhaustive search was performed for each matrix with all other settings left as defaults. Trees were visualized on FigTree v. 1.4.3 (Rambaut, 2016).

Results

Caviturritella

Analysis of the *Caviturritella* matrix resulted in a single most parsimonious tree (length 79; CI 0.620; RI 0.464 ; RC 0.288; Text-fig. 36). The earliest diverging clade consists of *C. terstriata* and *C. etiwanensis* which are united by small



Text-fig. 34. Species included in the phylogeny of *Caviturritella* that are not from the Plio-Pleistocene of Florida or the Atlantic coastal plain. 1, *Caviturritella gonostoma* (Valenciennes, 1832), PRI 104787, tropical eastern Pacific, 116.6 mm. 2, the outgroup species "*Turritella*" *nodulosa* King, 1832, LACM 34-128.13, Bahia Culebra, Costa Rica, 44.2 mm. 3, *Caviturritella variegata* (Linnaeus 1758), PRI 104784, Puerto La Cruz, Venezuela, 77.0 mm. 4, *Caviturritella banksii* (Gray in Reeve, 1849), PRI 104780, Ecuador, 31.0 mm. 5, *Caviturritella leucostoma* (Valenciennes, 1832), PRI 68077, Boca de Soledad, Mexico, 107.8 mm.

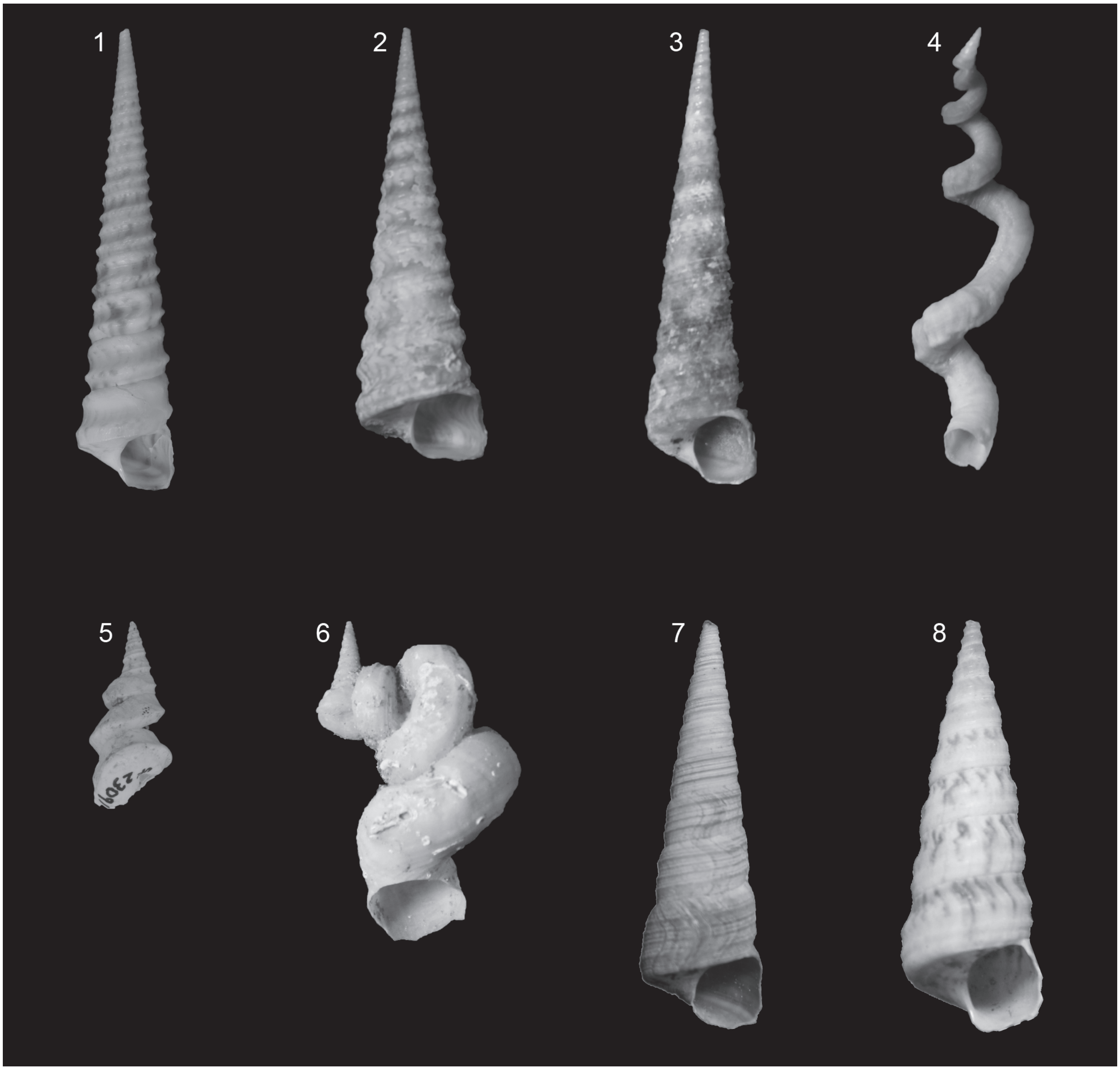
protoconch diameter, circular aperture shape and earlier appearance of primary spiral A after *Caviturritella magnasulcus* branches off from the remaining *Caviturritella* species. The extant eastern Pacific species *C. gonostoma* and *C. leucostoma* form a clade sister to a clade consisting of the extant species *C. variegata* and *C. banksii* along with the extinct species *C. alumensis* and *C. mansfieldi,* with *C. alumensis* as sister to the remaining three species and *C. variegata* + *C. banksii* forming a clade. The sister relationship between *C. variegata* (occurring along the northern coast of South America) and *C. banksii* (occurring in the tropical eastern Pacific, including Panama) is biogeographically plausible but also implies a divergence time for this node no later than the closure of the Central American Seaway (ca. 3.5 Ma) (O'dea et al., 2016). The relationship among extant *banksii*, *gonostoma*, and *leucostoma* is consistent with recent molecular analysis (Anderson, 2018; Sang et al., 2019).

Torcula

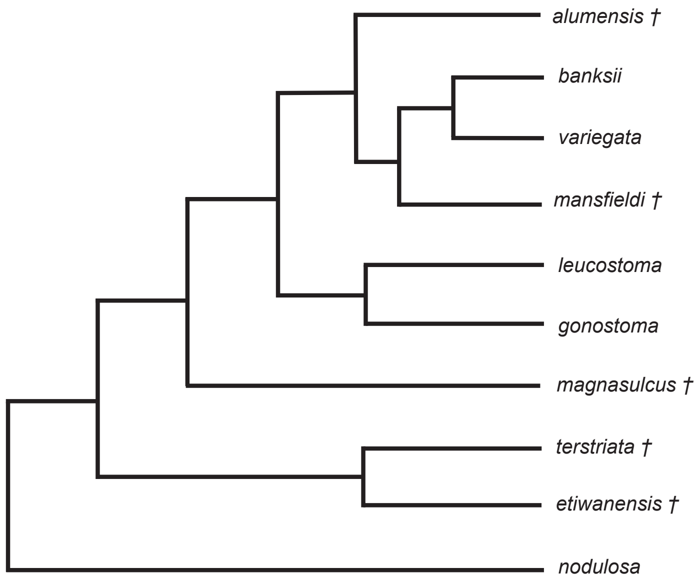
Analysis of the *Torcula* matrix resulted in six equally parsimonious trees (tree length of 89; CI 0.742; RI 0.709, RC 0.526). A strict consensus tree recovers a monophyletic *Vermicularia* sister to a monophyletic *Torcula*, with *Torcula apicalis* sister to all other species. The strict consensus tree also unites three Recent species (*T. exoleta, T. radula*, and *T. clarionensis*) with the Pleistocene species *T. perattenuata*, but does not resolve the relationships among *T. perattenuata*, *T. exoleta*, and the clade of *T. clarionensis* + *T. radula* (Text-fig. 37). As *T. clarionensis* and *T. radula* are both extant tropical eastern Pacific species, it is most biogeographically plausible to presume that *T. perattenuata* and *T. exoleta* are more closely related to one another. The observed range of variation in *T. perattenuata* and lack of stratigraphic overlap suggest that *T. exoleta* may be its direct descendant. The closest relative of this clade is either *T. cookei* or *T. clarksvillensis*, with equal support.

DISCUSSION

Of the 46 previously named Plio-Pleistocene and two Recent species and subspecies from the Atlantic coastal plain and Florida, we find that that 20 fossil and 2 Recent species should be considered valid species (Table 1), a "synonymy rate" (Gaston and Mound, 1993; Solow et al., 1995) of



Text-fig. 35. Species included in the phylogeny of *Torcula* that are not from the Plio-Pleistocene of Florida or the Atlantic coastal plain. 1, *Torcula exoleta* (Linnaeus, 1758), USNM MO 1197262, Trinidad and Tobago (Sarah Klontz, Creative Commons CC0 public domain license, https://creativecommons.org/publicdomain/zero/1.0/), 53.2 mm. 2, *Torcula clarionensis* (Hertlein and Strong, 1951) LACM 34-10.4, Isla Clarion, Mexico, 52.3 mm. 3, *Torcula radula* (Kiener, 1843), LACM 72.55-15, Pacific coastal waters, Costa Rica, 51.8 mm. 4, *Vermicularia lumbricalis* (Linnaeus, 1758) (=*Vermicularia knorrii* Deshayes, 1843), LACM 91751, Lee County, Florida, 52.4 mm. 5, *Vermicularia milleti*† (Deshayes, 1850), UF 230914, Miocene, France, 18.7 mm. 6, *Vermicularia pellucida* (Broderip and Sowerby, 1829), LACM 70-3, Nayarit, Mexico, 33.6 mm. 7, the outgroup species *Maoricolpus roseus* (Quoy and Gaimard, 1834), PRI 104792, Akaroa, New Zealand, 48.4 mm. 8, the outgroup species "*Turritella*" *conspersa* Adams and Reeve, 1849, PRI 104782, Dakar, Senegal, 38.5 mm. This diverse set of outgroup species to *Torcula* was included in our analysis because the closest relatives of *Torcula*, the *Vermicularia*, exhibit highly unusual morphologies for turritellids.



Text-fig. 36. Phylogenetic relationships among fossil (marked with †) and extant *Caviturritella*. "*Turritella*" *nodulosa* is used as an outgroup. This was the single most parsimonious tree generated from a maximum parsimony analysis of morphological characters conducted using PAUP* 4.0 build 168 (Swofford, 2003).

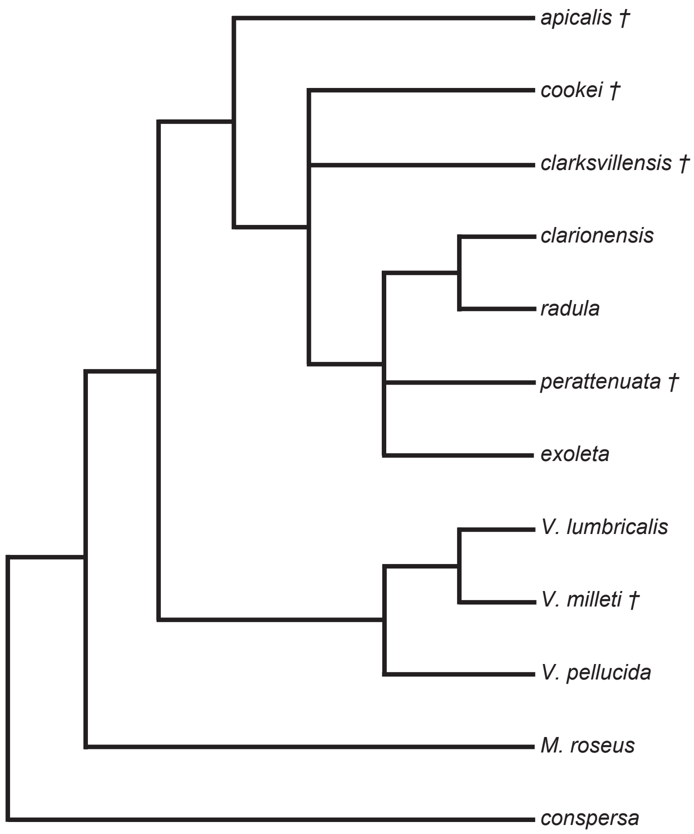
44.7%. This falls between the synonymy rates found in two other recent revisions of fossil turritellid faunas: 35% for the Paleocene and Eocene of the U.S. Gulf and Atlantic coastal plains (Allmon, 1996) and 78% for the Miocene of the European Paratethys (Harzhauser and Landau, 2019).

We recognize five names as *nomena nuda*. The majority of these are the result of a lack of type material for species named by Tuomey and Holmes (1855–1857). Only one of their species was deemed valid, *Caviturritella etiwanensis*, due to its unique morphology. Tuomey and Holmes' species *Terebellum burdenii, Terebellum striatum,* and *Turritella exaltata* are not described sufficiently nor figured clearly enough to provide a stable basis for identification of any lectotypes or neotypes.

This study represents an important addition to our understanding of Atlantic coastal plain Plio-Pleistocene turritellid diversity by including fossils from Georgia. Florida species were previously treated by Conrad (1868, et seq.), Dall (1892, 1903), Gardner (1928), and Mansfield (1930), Olsson and Harbison (1953), and others; Virginia species by Conrad (1834, 1844), Gardner (1948), and Campbell (1993); North Carolina species by Conrad (1875), Gardner (1948), and Ward and Blackwelder (1987); and South Carolina species by Tuomey and Holmes (1856) and Gardner and Aldrich (1919). Specimens from Georgia, however, have never been discussed in the paleontological literature. We can do so here due to the efforts of collector Mr. Chet Kirby, without whose generous donation of samples to the Florida Museum of Natural History, Georgia occurrences would have remained unaddressed. Turritellids identified in sampled material from Georgia include *T. fluxionalis, T. perexilis, C. etiwanensis,* and *T. virginica*, all of which were found in the Pliocene-aged Duplin or Raysor fms.

Most of the species considered valid here occur in the Pinecrest beds, meaning that this unit contains 19 co-occurring turritellid species, which is the highest turritellid species diversity in one formation known in the fossil record (Text-fig. 38). How or why so many species of the group managed to co-occur in this deposit is unclear and should be the topic of future research, but may be related to high primary productivity (Allmon, 1992a, 1993). The subsequent reduction in turritellid diversity throughout the tropical western Atlantic has been linked to a widespread shift to lower nutrient conditions (likely related to both the closure of the Central American Seaway altering circulation/upwelling and changing nutrient delivery via runoff due to modifications to the hydrologic cycle) and the expansion of hardground habitats (Allmon, 1992a, 2001; Collins, 1996; Todd et al., 2002; O'Dea et al. 2016; Anderson et al., 2017; Grossman et al., 2019; Sang et al., 2019; Scholz et al. 2020; Anderson and Allmon, 2020). It is also notable that each of the three extant non-*Vermicularia* turritellid species in the western Atlantic appears to represent a different clade, with *Caviturritella* extirpated from the US Gulf and Atlantic coasts but *C. variegata* remaining in northern South America, principally where upwelling still occurs (Leigh et al., 2014; Lessios, 2008).

There remain a significant number of species assigned to *Turritella s.l.* in our analysis, but this study demonstrates that, at least within a basin or biogeographic province where there are unusual morphological features or derived spiral



Text-fig. 37. Phylogenetic relationships among fossil (marked with †) and extant *Torcula*. Representatives of the *Vermicularia* are included as they were found to be the closest relatives of *Torcula* in recent molecular analyses (Anderson, 2018); however, as these have an extremely unusual morphology for turritelllines, two additional regularly coiled turritelline species were included as outgroup taxa: "*Turritella*" *conspersa* and *Maoricolpus roseus*. This represents the strict consensus of six equally parsimonious trees generated from a maximum parsimony analysis of morphological characters conducted using PAUP* 4.0 build 168 (Swofford, 2003).

ornament ontogenies, it is possible to identify turritellid genera. The historically identified clade *Torcula* (when applied consistently based on defining shell characters described in this paper) was recoverable in previous molecular analyses (Anderson, 2018; Sang et al., 2019), and—conversely—the extant members of *Caviturritella* were found to belong to a clade prior to the identification of the hollow newel state as a clade morphological apomorphy (Anderson, 2018; Sang et al., 2019).

Within clades circumscribed by (*Caviturritella* and *Torcula* + *Vermicularia* herein), it is thus possible to perform intelligible species-level phylogenetic analyses including fossils (Text-figs. 36–38). As turritellids are among the most abundant marine macrofossils of the Cenozoic, this suggests that careful analysis of the fossil species found in additional regions and time periods may provide substantial future opportunities for phylogenetically-informed macroevolutionary and paleoecological analyses.

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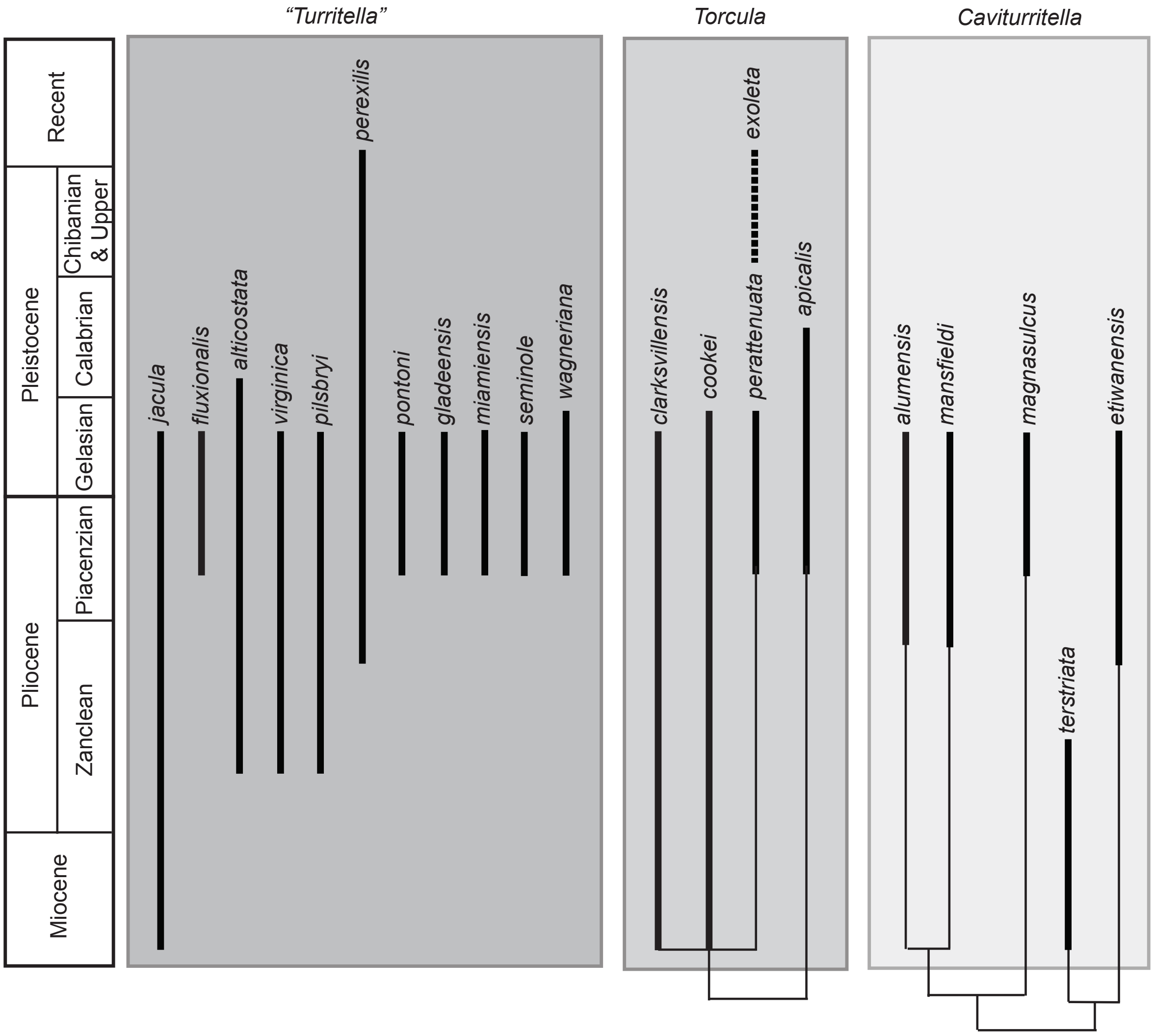

Text-fig. 38. Stratigraphic ranges of species of "*Turritella*," *Torcula*, and *Caviturritella* from the Plio–Pleistocene of Florida and the Atlantic coastal plain. Bold vertical lines represent stratigraphic ranges known from the fossil record. The latter two genera are shown in their phylogenetic context as reconstructed in our analyses. *Torcula perattenuata* and *T. exoleta* were coded as separate species and our analysis assessed the two as closely related (see Text-fig. 37). We consider the extant *T. exoleta* as likely to have descended anagenetically from *T. perattenuata* and present them as a single lineage here. Note that "*Turritella*" *perexilis* Conrad, 1875 is the valid name for the extant "*Turritella*" *acropora* Dall, 1889.

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APPENDIX 1

Alpha-numeric codes for localities referenced in text, along with their U.S. state counties, geologic formations, epochs, and other locality codes corresponding to each. Other locality code abbreviations: FLMNH = Florida Museum of Natural History; TU = Tulane University; USGS = United States Geological Survey.

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
Florida						
FL-01	Jackson Bluff (General)	Leon	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality LN004; USGS 3422; USGS 3423
FL-02	Alum Bluff	Liberty	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality LI002; USGS 2211; PRI Sta. 9681
FL-03	Bird Road	Miami-Dade	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality DA001; PRI Sta. 6926
FL-04	Arvida Pits	Miami-Dade	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality DA015; TU 1493
FL-05	Harvey's Creek	Leon	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality LN003; USGS 3421; USGS 10964
FL-06	Dripping Springs 01	Calhoun	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality CA070; TU 0073
FL-07	Richardson Road Shell Pit 01B	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality SO013; TU 1524
FL-08	Watsons Landing	Liberty	Choctawhatchee? (probably Jackson Bluff)		Miocene, Late	FLMNH-IP Locality 5716; USGS 10962
FL-09	Darlings Slide 01	Calhoun	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality CA071; USGS 10960
FL-10	unnamed	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	PRI Sta. 9708
FL-11	Double Branch 01	Leon	Choctawhatchee? (probably Jackson Bluff)		Miocene, Late	FLMNH-IP Locality LN015; USGS 10966
FL-12	Tamiami Trail	Monroe	Tamiami	Pinecrest beds	Plio-Pleistocene	
FL-13	unnamed	Pinellas	Tamiami	Pinecrest beds	Plio-Pleistocene	
FL-14	unnamed	Leon	Choctawhatchee? (probably Jackson Bluff)		Miocene, Late	
FL-15	Kissimmee Canal 01	Okeechobee	Tamiami		Pliocene	
FL-16	Ochopee 03	Collier	Tamiami	Ochopee Ls	Pliocene	FLMNH-IP Locality CR008
FL-17	Alligator Alley 01	Collier	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CR007; TU 0797
FL-18	Caloosahtchee River 16	Hendry	Caloosahatchee/ Ft. Thompson		Pleistocene	FLMNH-IP Locality HN051
FL-19	Jackson Bluff 01	Leon	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality LN001
FL-20	Shell Creek, Myakka River	Charlotte	Caloosahatchee		Pleistocene, Early	USNM 113451
FL-21	Olga	Lee	Tamiami	Buckingham Ls	Pliocene, Late	USGS 14194; USGS 14190

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
FL-22	Belle Glade	Palm Beach	Ft. Thompson/ Bermont		Pleistocene, Late	
FL-23	St. Petersburg	Pinellas	Caloosahatchee		Pleistocene, Early	
FL-24	White's Creek	Walton	Shoal River		Miocene, Middle	FLMNH-IP Locality WL003; USGS 10603c, USGS 10608c
FL-25	Orangetree 01	Collier	Tamiami		Pliocene	FLMNH-IP Locality CR028; TU 1174
FL-26	unnamed	Broward	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality 5422
FL-27	Sombrero Light	Monroe	-		Recent	PRI 68078
FL-28	Banana Branch, Fort Denaud	Hendry	Caloosahatchee		Pleistocene, Early	
FL-29	Cochran Shell Pit	Hendry	Caloosahatchee		Pleistocene, Early	FLMNH-IP Locality HN004; PRI Sta. 3735
FL-30	Fort Denaud Rock Pit	Hendry	Caloosahatchee		Pleistocene, Early	FLMNH-IP Locality HN023
FL-31	Red Head Still	Washington	Jackson Bluff		Pliocene, Late	USGS 10951
FL-32	Bailey Post Office	Calhoun	Choctawhatchee? (probably Jackson Bluff)		Miocene, Late	USGS 3418
FL-33	APAC Shell Pit	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	PRI Sta. 6053
FL-34	Hamlin Pond	Washington	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality WG015; USGS 10422
FL-35	Gully Pond/Sink	Washington	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality WG014; USGS 1955
FL-36	Miami Canal	Miami Dade	Tamiami	Pinecrest beds	Plio-Pleistocene	USNM 347417
FL-37	Shell Creek	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	USNM 113456
FL-38	Como Waterway 02	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CH043; TU 0532
FL-39	Quality Aggregates Phase 7	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality SO022; Lyons EJXX488
FL-40	Mule Pen	Collier	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CR004; TU 1177
FL-41	MacAsphalt/Warren Brothers/APAC Pit	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality SO017; TU 1000
FL-42	Brighton Canal	Highlands	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality HG002; TU 0520
FL-43	Snell Isle	Pinellas	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality PI009
FL-44	Estero 02	Lee	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality LE008
FL-45	Fort Lee	Hendry	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality HN031
FL-46	Harney Pond Canal 01	Glades	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality GL013; TU 0523
FL-47	Moore Haven 01	Glades	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality GL036; TU 0206
FL-48	Port Charlotte	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
FL-49	Fortymile Bend 01	Miami-Dade	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality DA004
FL-50	Fort Basinger	Okeechobee	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality OB001; TU 0729
FL-51	Econfina Bridge	Bay	Choctawhatchee? (probably Jackson Bluff)		Miocene, Late	USGS 10953
FL-52	Hosford	Liberty	Jackson Bluff	*Cancellaria* zone	Pliocene, Late	USGS 3671, 3672
FL-53	Polk Creek	Leon	Jackson Bluff		Pliocene, Late	
FL-54	Lomax-King Pit	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CH028
FL-55	Florida Shell and Fill	Charlotte	Tamiami	Ochopee Ls	Pliocene	FLMNH-IP Locality CH076
FL-56	Acline Borrow Pits	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CH051; TU 0200
FL-57	Clarksville	Calhoun	Jackson Bluff	*Ecphora* zone	Pliocene, Late	USGS 8862
FL-58	Sunniland	Collier	Tamiami	Ochopee Ls	Pliocene	FLMNH-IP Locality CR009
FL-59	Tamiami Canal, Levee 29	Miami-Dade	Tamiami		Pliocene	FLMNH-IP Locality DA003
FL-60	Interceptor Canal	Hendry	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality HN027
FL-61	Coral Springs	Broward	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality BD009; TU 0742
FL-62	Elkcam Waterway	Charlotte	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CH045; TU 0756
FL-63	Big Cypress	Broward	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality BD003
FL-64	University Parkway Shell Pit	Manatee	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality MA017
FL-65	Proctor Road-Metal Pit	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality SO032
FL-66	La Belle Picnic	Hendry	Caloosahatchee		Pleistocene, Early	PRI Sta. 9707
FL-67	Bermont Excavating	Charlotte	Caloosahatchee		Pleistocene, Early	FLMNH-IP Locality CH117
FL-68	Jackson Bluff 02	Leon	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality LN002
FL-69	Hayes Waterfall 01	Calhoun	Jackson Bluff		Pliocene, Late	FLMNH-IP Locality CA068
FL-70	South Bay 04	Palm Beach	Bermont		Pleistocene, Early	FLMNH-IP Locality PB007
FL-71	SMR Aggregates Phase 10A	Sarasota	Tamiami	Lower	Pliocene	FLMNH-IP Locality SO054
FL-72	Sommers Pit 01	Sarasota	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality SO041
FL-73	Kissimmee River	Okeechobee	Tamiami (Pinecrest beds)/ Caloosahatchee		Plio-Pleistocene	
FL-74	Arcadia	De Soto	Caloosahatchee		Pleistocene, Early	

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
FL-75	Caloosahatchee River 01	Hendry	Caloosahatchee		Pleistocene, Early	FLMNH-IP Locality HN002
FL-76	Alum Bluff 01B	Liberty	Chipola		Miocene, Early	FLMNH-IP Locality LI003
FL-77	Kissimme Canal 02	Highlands	Tamiami	Pinecrest beds	Plio-Pleistocene	
FL-78	unnamed	Polk/Osceola	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality 2665
FL-79	Cracker Swamp Ranch 01	Putnam	Nashua	Upper	Pleistocene, Early	FLMNH-IP Locality PU004
FL-80	Quality Aggregates Phase 6	Sarasota	Tamiami (Pinecrest beds)/ Caloosahatchee		Plio-Pleistocene	FLMNH-IP Locality SO033
FL-81	Alligator Alley 06	Collier	Tamiami	Pinecrest beds	Plio-Pleistocene	FLMNH-IP Locality CR023
FL-82	APAC pit	Sarasota	Caloosahatchee		Pleistocene, Early	PRI Sta. 7400
FL-83	Star Pit	Palm Beach	Caloosahatchee		Pleistocene, Early	PRI Sta. 7856
FL-84	Sarasota unspecified	Sarasota	Caloosahatchee		Pleistocene, Early	PRI Sta. 7400
FL-85	Clewiston	Hendry	Tamiami	Pinecrest beds	Plio-Pleistocene	PRI Sta. 6049
Georgia						
GA-01	Andrews Island	Glynn	Duplin/Raysor		Pliocene	FLMNH-IP Locality ZG047
GA-02	Turtle River 01	Glynn	Duplin/Raysor		Pliocene	FLMNH-IP Locality ZG043
GA-03	Porters Landing, Savannah River	Effingham	Duplin		Pliocene	
GA-04	Fancy Bluff Creek 01	Glynn	Duplin/Raysor		Pliocene	FLMNH-IP Locality ZG038
GA-05	Lanier Bridge 01	Glynn	Raysor		Pliocene	FLMNH-IP Locality ZG046
South Carolina						
SC-01	Crescent Beach 01	Horry	Waccamaw		Pleistocene, Early	FLMNH-IP Locality ZS015
SC-02	Mayesville	Sumter	Bear Bluff		Pleistocene	
SC-03	Muldrow Place	Sumter	Duplin		Pliocene	
SC-04	unnamed	Darlington	Duplin		Pliocene	
SC-05	Stokes Sand and Gravel Eagle Point Pit	Darlington	Raysor		Pliocene	FLMNH-IP Locality ZS022
SC-06	unnamed	Berkeley	Goose Creek		Pliocene	
SC-07	Ned Moore Farm 01	Florence	Duplin		Pliocene	FLMNH-IP Locality ZS056
SC-08	unnamed	Darlington	Raysor		Pliocene	
SC-09	Lockheed Martin Berkeley Quarry 01	Berkeley	Raysor		Pliocene	FLMNH-IP Locality ZS013
SC-10	Tearcoat Branch 01	Sumter	Duplin		Pliocene	FLMNH-IP Locality ZS005

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
SC-11	Kirby's Pond 01	Florence	Duplin		Pliocene	FLMNH-IP Locality ZS031; PRI Sta. 7799
SC-12	unnamed	Horry	Canepatch		Pleistocene, Middle	
North Carolina						
NC-01	Lee Creek Mine	Beaufort	Chowan River/ James River		Pleistocene, Early	USGS 25370
NC-02	Murfreesboro	Hertford	Yorktown		Pliocene	
NC-03	Natural Well	Duplin	Duplin		Pliocene	FLMNH-IP Locality ZN003
NC-04	Neils Eddy Landing 01	Columbus	Waccamaw		Pleistocene, Early	FLMNH-IP Locality ZN077
NC-05	Wilmington	New Hanover	Waccamaw		Pleistocene, Early	
NC-06	Bertie	Bertie	Chowan River		Pleistocene, Early	
NC-07	Chocowinity	Beaufort	Chowan River		Pleistocene, Early	PRI Sta. 2140
NC-08	Tar River 01	Pitt	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZN035; TU 0862
NC-09	Williamson's Pit	Columbus	Waccamaw		Pleistocene, Early	PRI Sta. 9699
NC-10	Lumber River 03	Robeson	Raysor		Pliocene	FLMNH-IP Locality ZN049; PRI Sta. 9698
NC-11	Old Dock 01	Columbus	Waccamaw		Pleistocene, Early	FLMNH-IP Locality ZN022
NC-12	Robeson Farm 01	Bladen	Duplin		Pliocene	FLMNH-IP Locality ZN052
NC-13	Tarboro 01	Edgecombe	Yorktown		Pliocene	FLMNH-IP Locality ZN043
NC-14	Colerain Beach	Bertie	Yorktown	Moorehouse	Pliocene	PRI Sta. 9697
Virginia						
VA-01	unnamed	Isle of Wight	Yorktown		Pliocene	PRI Loc. 1611
VA-02	unnamed	Glouster	Yorktown	Rushmere	Pliocene	USGS 2250
VA-03	unnamed	York	Yorktown	Moore House	Pliocene	USGS 2247a
VA-04	unnamed	Hampton	Yorktown		Pliocene	
VA-05	unnamed	Chesapeake	Chowan River		Pleistocene	
VA-06	Rices Pit	Hampton	Yorktown		Pliocene	FLMNH-IP Locality ZV004
VA-07	James City	James City	Yorktown		Pliocene	
VA-08	Yates Cut 01	York	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV066
VA-09	James River	Surry	Yorktown	Zone 1	Pliocene	
VA-10	Kingsmill 01	James City	Yorktown	Zone 1	Pliocene	FLMNH-IP Locality ZV006
VA-11	Schmidt's Bluff	Surry	Yorktown		Pliocene	
VA-12	York River	Glouster	Yorktown		Pliocene	PRI Sta. 1388
VA-13	Chestnut Bluffs	Surry	Yorktown		Pliocene	FLMNH-IP Locality ZV031; TU 0858

Locality code	Alias	County	Formation	Member	Epoch	Other locality codes
VA-14	Watkins Mill	King and Queen	Yorktown	Zone 1	Pliocene	USGS 11783
VA-15	James River 01	Isle of Wight	Yorktown	Zone 1	Pliocene	FLMNH-IP Locality ZV036; TU 0077
VA-16	Walkerton	King and Queen	Yorktown		Pliocene	
VA-17	Piankitank River 02	Middlesex	Yorktown	Sunken Meadow	Pliocene, Early	FLMNH-IP Locality ZV096
VA-18	Carter's Grove 01	James City	Yorktown	Zone 1	Pliocene	FLMNH-IP Locality ZV008
VA-19	Chesapeake Development Company Pit 01	Chesapeake	Yorktown		Pliocene	FLMNH-IP Locality ZV007
VA-20	Tutter's Neck Dam 01	James City	Yorktown	Zone 1	Pliocene	FLMNH-IP Locality ZV009
VA-21	Chippokes Plantation 01	Surry	Yorktown	Zone 1	Pliocene	FLMNH-IP Locality ZV046
VA-22	Haynes Mill 01	Gloucester	Yorktown	*Leptopecten* bed	Pliocene	FLMNH-IP Locality ZV099
VA-23	Lone Star Marl Pit	Suffolk	Yorktown		Pliocene	FLMNH-IP Locality ZV003
VA-24	A.B. Southall Pit	York	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV074
VA-25	Days Point 02	Isle of Wight	Yorktown		Pliocene	FLMNH-IP Locality ZV055
VA-26	Burwells Bay 02	Isle of Wight	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV097; TU 0856
VA-27	Fort Boykins 01	Isle of Wight	Yorktown		Pliocene	FLMNH-IP Locality ZV037; TU 0855
VA-28	Chesapeake Development Company Pit 02A	Chesapeake	Yorktown		Pliocene	FLMNH-IP Locality ZV048
VA-29	Chuckatuck 04	Isle of Wight	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV064
VA-30	Craney Island 02	Portsmouth	Yorktown		Pliocene	FLMNH-IP Locality ZV054
VA-31	Williamsburg 01	Williamsburg	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV057
VA-32	Mogarts Beach 01	Isle of Wight	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV060
VA-33	Poquoson Lone Star Industries Pit 01	Poquoson	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV059
VA-34	Turners Landing 01	Isle of Wight	Yorktown	Zone 2	Pliocene	FLMNH-IP Locality ZV076
VA-35	Evergreen	Appomattox	Yorktown		Pliocene	PRI Sta. 4793

APPENDIX 2

Additional fossil material positively identified by D. Friend.

Taxon	Catalog No.	Locality	Stratigraphy
Caviturritella alumensis	USNM 113480	Calhoun Co., FL	Jackson Bluff
C. alumensis	USNM 113478	Calhoun Co., FL	Jackson Bluff
C. alumensis	USNM 113481	Calhoun Co., FL	Jackson Bluff
C. alumensis	PRI 104743	Miami-Dade Co., FL	Tamiami
C. alumensis	PRI 104757	Liberty Co., FL	Jackson Bluff
C. alumensis	PRI 104758	Liberty Co., FL	Jackson Bluff
C. alumensis	PRI 104759	Liberty Co., FL	Jackson Bluff
C. alumensis	PRI 104760	Liberty Co., FL	Jackson Bluff
C. alumensis	PRI 104743	Miami-Dade Co., FL	Caloosahatchee
C. alumensis	PRI 70273	Sarasota Co., FL	Pinecrest Beds
C. alumensis	UF 329859	Leon Co., FL	Jackson Bluff
C. alumensis	UF 332412	Liberty Co., FL	Jackson Bluff
C. alumensis	UF 329858	Leon Co., FL	Jackson Bluff
C. alumensis	UF 329861	Miami-Dade Co., FL	Pinecrest Beds
C. alumensis	UF 138690	Leon Co., FL	Jackson Bluff
C. alumensis	UF 160724	Sarasota Co., FL	Pinecrest Beds
Caviturritella etiwanensis	PRI 104827	Chocowinity, NC	Duplin
C. etiwanensis	PRI 45410	Okeechobee Co., FL	Tamiami
C. etiwanensis	PRI 104751	Florence Co., SC	Duplin/Rayson
C. etiwanensis	PRI 104755	Florence Co., SC	Duplin/Rayson
C. etiwanensis	PRI 104735	Robeson Co., NC	Duplin/Rayson
C. etiwanensis	PRI 104738	Robeson Co., NC	Duplin/Rayson
C. etiwanensis	PRI 104737	Robeson Co., NC	Duplin/Rayson
C. etiwanensis	UF 7683	Leon Co., FL	Jackson Bluff
C. etiwanensis	UF 332664	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 332662	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 332661	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 332665	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 216619	Horry Co., SC	Bear Bluff
C. etiwanensis	UF 216620	Horry Co., SC	Bear Bluff
C. etiwanensis	UF 332666	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 332667	Glynn Co., GA	Duplin/Rayson
C. etiwanensis	UF 332663	Glynn Co., GA	Duplin/Rayson
Caviturritella magnasulcus	PRI 104745	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	PRI 41862	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	PRI 41856	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	PRI 45385	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	PRI 70077	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	PRI 40389	Sarasota Co., FL	Pinecrest Beds

Taxon	Catalog No.	Locality	Stratigraphy
C. magnasulcus	PRI 40387	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	UF 332471	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 275915	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	UF 332473	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332474	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332472	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332475	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332469	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332470	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 332468	Collier Co., FL	Pinecrest Beds
C. magnasulcus	UF 160658	Charlotte Co., FL	Ochopee
C. magnasulcus	UF 160723	Sarasota Co., FL	Pinecrest Beds
C. magnasulcus	UF 185998	Charlotte Co., FL	Pinecrest Beds
Caviturritella terstriata	UF 329971	Piankitank River, VA	Yorktown
C. terstriata	UF 329972	Piankitank River, VA	Yorktown
C. terstriata	UF 329973	Piankitank River, VA	Yorktown
C. terstriata	UF 332659	Middlesex Co., VA	Yorktown, Sunken Meadow
C. terstriata	UF 332660	Middlesex Co., VA	Yorktown, Sunken Meadow
C. terstriata	UF 332658	Middlesex Co., VA	Yorktown, Sunken Meadow
C. terstriata	UF 280911	James City, VA	Yorktown, Sunken Meadow
Torcula apicalis	PRI 45371	Hendry Co., FL	Pinecrest Beds
T. apicalis	PRI 40410	De Soto Co., FL	Caloosahatchee
T. apicalis	PRI 70274	Sarasota Co., FL	Pinecrest Beds
T. apicalis	UF 332363	Sarasota Co., FL	Pinecrest Beds
T. apicalis	UF 332489	Miami-Dade Co., FL	Pinecrest Beds
T. apicalis	UF 332534	Collier Co., FL	Pinecrest Beds
T. apicalis	USNM 113463	Hendry Co., FL	Caloosahatchee
Torcula clarksvillensis	UF 221559	Calhoun Co., FL	Jackson Bluff
T. clarksvillensis	UF 332690	Calhoun Co., FL	Jackson Bluff
T. clarksvillensis	UF 78857	Leon Co., FL	Jackson Bluff
T. clarksvillensis	UF 168330	Sarasota Co., FL	Pinecrest Beds
T. clarksvillensis	UF 180425	Sarasota Co., FL	Pinecrest Beds
T. clarksvillensis	UF 332497	Sarasota Co., FL	Pinecrest Beds
Torcula cookei	PRI 104744	Miami-Dade Co., FL	Pinecrest Beds
T. cookei	PRI 45361	Sarasota Co., FL	Pinecrest Beds
T. cookei	UF 329911	Hendry Co., FL	Pinecrest Beds
T. cookei	UF 132838	Leon Co., FL	Jackson Bluff

Taxon	Catalog No.	Locality	Stratigraphy
Torcula perattenuata	PRI 104749	Hendry Co., FL	Caloosahatchee
T. perattenuata	PRI 104750	Hendry Co., FL	Caloosahatchee
T. perattenuata	PRI 40392	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	PRI 45378	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	PRI 40409	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	PRI 40410	De Soto Co., FL	Caloosahatchee
T. perattenuata	PRI 41074	Hendry Co., FL	Caloosahatchee
T. perattenuata	PRI 45378	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	PRI 40406	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	PRI 40396	De Soto Co., FL	Caloosahatchee
T. perattenuata	UF 210596	Charlotte Co., FL	Caloosahatchee
T. perattenuata	UF 67832	Hendry Co., FL	Caloosahatchee
T. perattenuata	UF 181701	Glades Co., FL	Pinecrest Beds
T. perattenuata	UF 332459	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332460	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332461	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332462	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332463	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332464	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332465	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332466	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332467	Collier Co., FL	Pinecrest Beds
T. perattenuata	UF 332656	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	UF 329968	Hendry Co., FL	Caloosahatchee
T. perattenuata	UF 329969	Collier Co., FL	Caloosahatchee
T. perattenuata	UF 329970	Sarasota Co., FL	Pinecrest Beds
T. perattenuata	UF 181354	Hendry Co., FL	Caloosahatchee
T. perattenuata	UF 181359	Collier Co., FL	Caloosahatchee
T. perattenuata	UF 275909	Sarasota Co., FL	Pinecrest Beds
"Turritella" alticostata	PRI 104731	Bertie Co., NC	Yorktown, Moorehouse
T. alticostata	PRI 104730	Bertie Co., NC	Yorktown, Moorehouse
T. alticostata	USNM 325455	Hartford Co., NC	Yorktown
T. alticostata	USNM 204039	Beaufort Co., NC	Chowan River
T. alticostata	UF 181432	Charlotte Co., FL	Pinecrest Beds
T. alticostata	UF 329908	Isle of Wight, VA	Yorktown
T. alticostata	UF 329907	Hampton Co., VA	Yorktown
T. alticostata	UF 191081	Hampton Co., VA	Yorktown
T. alticostata	UF 181435	Isle of Wight, VA	Yorktown
"Turritella" fluxionalis	PRI 104736	Robeson Co., NC	Raysor
T. fluxionalis	PRI 2740	Hampton, VA	Yorktown
T. fluxionalis	UF 268147	Darlington Co., SC	Raysor

Taxon	Catalog No.	Locality	Stratigraphy
T. fluxionalis	UF 329965	Darlington Co., SC	Raysor
T. fluxionalis	UF 329966	Glenn Co., GA	Duplin/Raysor
T. fluxionalis	UF 329967	Glenn Co., GA	Duplin/Raysor
T. fluxionalis	UF 332652	Highlands Co., FL	Pinecrest Beds
"Turritella" gladeensis	PRI 108267	Miami-Dade Co., FL	Pinecrest Beds
T. gladeensis	PRI 40782	Miami-Dade Co., FL	Pinecrest Beds
T. gladeensis	PRI 40403	Sarasota Co., FL	Pinecrest Beds
T. gladeensis	UF 181869	Miami-Dade Co., FL	Pinecrest Beds
T. gladeensis	UF 181870	Miami-Dade Co., FL	Pinecrest Beds
T. gladeensis	UF 209500	Charlotte Co., FL	Pinecrest Beds/Caloosahatchee
T. gladeensis	UF 314753	Charlotte Co., FL	Caloosahatchee
"Turritella" jacula	PRI 45382	Collier Co., FL	Pinecrest Beds
T. jacula	PRI 45383	Broward Co., FL	Pinecrest Beds
T. jacula	UF 171622	Collier Co., FL	Tamiami
T. jacula	UF 171623	Collier Co., FL	Tamiami
T. jacula	UF 172307	Hendry Co., FL	Pinecrest Beds
T. jacula	UF 268119	Darlington Co., SC	Raysor
"Turritella" mansfieldi	PRI 41859	Sarasota Co., FL	Pinecrest Beds
T. mansfieldi	PRI T.0224	Sarasota Co., FL	Pinecrest Beds
T. mansfieldi	PRI 21434	Okeechobee Co., FL	Caloosahatchee
T. mansfieldi	PRI 41859	Sarasota Co., FL	Duplin
T. mansfieldi	PRI 104754	Florence Co., SC	Duplin
T. mansfieldi	PRI 104786	Hendry Co., FL	Caloosahatchee
T. mansfieldi	PRI 104790	Highlands Co., FL	Pinecrest Beds
T. mansfieldi	PRI 104791	Highlands Co., FL	Pinecrest Beds
T. mansfieldi	UF 181385	Miami-Dade Co., FL	Pinecrest Beds
T. mansfieldi	UF 219472	Polk/Osceola Co., FL	Pinecrest Beds
T. mansfieldi	UF 162594	Glynn Co., GA	Duplin/Raysor
T. mansfieldi	UF 332680	Sumter Co., SC	Duplin
T. mansfieldi	UF 332692	Darlington Co., SC	Raysor
"Turritella" miamiensis	PRI T.0110	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	PRI T.0112	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	PRI 45379	Sarasota Co., FL	Pinecrest Beds
T. miamiensis	PRI 104741	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332567	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332564	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332563	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332573	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332575	Miami-Dade Co., FL	Pinecrest Beds

Taxon	Catalog No.	Locality	Stratigraphy
T. miamiensis	UF 332634	Collier Co., FL	Ochopee
T. miamiensis	UF 332561	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332560	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332568	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332574	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332566	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332569	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332571	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332562	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 66198	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332576	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332458	Collier Co., FL	Pinecrest Beds
T. miamiensis	UF 332565	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332572	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332594	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332570	Miami-Dade Co., FL	Pinecrest Beds
T. miamiensis	UF 332537	Collier Co., FL	Pinecrest Beds
"Turritella" perexilis	PRI 41018	Hendry Co., FL	Pinecrest Beds
T. perexilis	PRI 45401	Hendry Co., FL	Pinecrest Beds
T. perexilis	PRI 45403	Hendry Co., FL	Pinecrest Beds
T. perexilis	PRI 104742	Miami-Dade Co., FL	Caloosahatchee
T. perexilis	UF 179622	Sarasota Co., FL	Pinecrest Beds
T. perexilis	UF 332577	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332578	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332579	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332580	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332581	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332582	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332583	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332584	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332585	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332586	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332587	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332588	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332589	Miami-Dade Co., FL	Pinecrest Beds
T. perexilis	UF 332590	Miami-Dade Co., FL	Pinecrest Beds
"Turritella" pilsbryi	PRI 108265	Appomattox, VA	Yorktown
T. pilsbryi	UF 329909	Isle of Wight Co., VA	Yorktown
T. pilsbryi	UF 332447	Sarasota Co., FL	Pinecrest Beds
T. pilsbryi	UF 225231	Sarasota Co., FL	Pinecrest Beds
T. pilsbryi	UF 332443	Sarasota Co., FL	Pinecrest Beds

Taxon	Catalog No.	Locality	Stratigraphy
"*Turritella*" *pontoni*	PRI 45396	Okeechobee Co., FL	Tamiami
T. pontoni	PRI 45397	Okeechobee Co., FL	Tamiami
T. pontoni	PRI 41859	Sarasota Co., FL	Tamiami/Caloosahatchee
T. pontoni	PRI 48902	Collier Co., FL	Pinecrest Beds
T. pontoni	UF 332525	Manatee Co., FL	Pinecrest Beds
T. pontoni	UF 181727	Miami-Dade Co., FL	Pinecrest Beds
T. pontoni	UF 332640	Miami-Dade Co., FL	Pinecrest Beds
T. pontoni	UF 332530	Collier Co., FL	Pinecrest Beds
T. pontoni	UF 252668	Collier Co., FL	Ochopee Ls
T. pontoni	UF 12303	Miami-Dade Co., FL	Tamiami
T. pontoni	UF 36108	Hendry Co., FL	Pinecrest Beds
T. pontoni	UF 159858	Broward Co., FL	Pinecrest Beds
T. pontoni	UF 181431	Charlotte Co., FL	Pinecrest Beds
T. pontoni	UF 248732	Broward Co., FL	Pinecrest Beds
T. pontoni	UF 181376	Sarasota Co., FL	Tamiami/Caloosahatchee
"*Turritella*" *seminole*	PRI 40393	Sarasota Co., FL	Pinecrest Beds
T. seminole	PRI 50131	Sarasota Co., FL	Pinecrest Beds
T. seminole	PRI 108266	Hendry Co. FL	Pinecrest Beds
T. seminole	PRI 50131	Sarasota Co., FL	Pinecrest Beds
"*Turritella*" *virginica*	UF 329967	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 332687	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 329966	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 164189	Glynn Co., GA	Raysor
T. virginica	UF 164195	Glynn Co., GA	Raysor
T. virginica	UF 164308	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 164310	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 165279	Glynn Co., GA	Duplin/Raysor
T. virginica	UF 166712	Glynn Co., GA	Raysor
T. virginica	UF 171920	Glynn Co., GA	Raysor
T. virginica	UF 332693	Glynn Co., GA	Raysor
T. virginica	UF 332668	Glynn Co., GA	Duplin/Raysor
"*Turritella*" *wagneriana*	PRI 40397	De Soto Co., FL	Calosahatchee
T. wagneriana	UF 9742	Sarasota Co., FL	Pinecrest Beds
T. wagneriana	UF 181622	Miami-Dade Co., FL	Pinecrest Beds
T. wagneriana	UF 332629	Collier Co., FL	Pinecrest Beds

APPENDIX 3

Character coding for phylogenetic analyses.

Protoconch characters (1–3)

Character 1. Protoconch, diameter.
- 0 = small (<250μm) (see Text-fig. 5)
- 1 = medium (250–350 μm)
- 2 = large (>350 μm)

Character 2. Protoconch, number of whorls.
- 0 = one
- 1 = two
- 2 = more than 2

Character 3. Protoconch, type.
- 0 = submerged
- 1 = normal
- 2 = nucleus raised/pointed
- 3 = *Gazameda* type
- 4 = conical
- 5 = many spiral

Apical sculpture characters (4–6)

Note: Cords that appear simultaneously share codes. For example, if cord A and C co-appear following cord B, the apical sculpture formula will be B1A2B2.

Character 4. Apical sculpture formula, order of appearance for cord A.
- 0 = first
- 1 = second
- 2 = third
- ? = never

Character 5. Apical sculpture formula, order of appearance for cord B.
- 0 = first
- 1 = second
- 2 = third
- ? = never

Character 6. Apical sculpture formula, order of appearance for cord C.
- 0 = first
- 1 = second
- 2 = third
- ? = never

Sinus characters (7–11)

Character 7. Sinus, basal sinus shape (see Text-fig. 10).
- 0 = type one
- 1 = type two
- 2 = type three
- 3 = type four
- 4 = type five
- 5 = type six

Character 8. Sinus, lateral sinus depth.
- 0 = shallow
- 1 = medium
- 2 = deep

Character 9. Sinus, lateral angle.
- 0 = prosocline
- 1 = straight
- 2 = opisthocline

Character 10. Sinus, lateral type (inflection points).
- 0 = single on bottom
- 1 = double
- 2 = single on top
- 3 = none

Character 11. Sinus, lateral sinus apex location.
- 0 = upper
- 1 = middle
- 2 = lower

Angle characters (12, 13) (see Text-fig. 3)

Character 12. Angle, pleural.
- 0 = >10 degrees
- 1 = 10–15 degrees
- 2 = <15 degrees

Character 13. Angle, apical.
- 0 = >10 degrees
- 1= 10–15 degrees
- 2 = 15–20 degrees
- 3 = >20 degrees

Whorl profile characters (14, 15) (see Text-fig. 4):

Character 14. Whorl profile, juvenile.
- 0 = convex
- 1 = subquadrate
- 2 = flat-sided
- 3 = frustate
- 4 = imbricate
- 5 = concave
- 6 = keeled
- 7 = telescoped
- 8 = campanulate
- 9 = hypercampanulate
- 10 = straight-sided
- 11 = telescoped acute

Character 15. Whorl profile, adult.
- 0 = convex
- 1 = subquadrate
- 2 = flat-sided
- 3 = frustate
- 4 = imbricate
- 5 = concave
- 6 = keeled
- 7 = telescoped
- 8 = campanulate
- 9 = hypercampanulate
- 10 = straight-sided
- 11 = telescoped acute

Aperture characters (16, 17)

Character 16. Aperture, shape.
- 0 = square
- 1 = rounded square (subquadrate)
- 2 = circle
- 3 = teardrop

Character 17. Aperture, internal lirae. Note that the presence of lirae was found to be autapomorphic in our dataset and was not included in analyses.
- 0 = absent
- 1 = present

Suture characters (18, 19)

Character 18. Suture, depth.
- 0 = shallow
- 1 = medium
- 2 = deep or incised

Character 19. Suture, depth change.
- 0 = none
- 1 = depth increases with length

Juvenile chord morphology characters (20–22)

Character 20. Juvenile cord morphology, most prominent.
- 0 = absent/multiway tie
- 1 = A
- 2 = B
- 3 = C
- 4 = D

Character 21. Juvenile cord morphology, number of primary cords.
- 0 = one
- 1 = two
- 2 = three
- 3 = four

Character 22. Juvenile cord morphology, presence of minor cords.
- 0 = absent
- 1 = present

Adult chord morphology characters (23–25)

Character 23. Adult cord morphology, most prominent.
- 0 = absent/multiway tie
- 1 = A
- 2 = B
- 3 = C
- 4 = D

Character 24. Adult cord morphology, number of primary cords.
- 0 = one
- 1 = two
- 2 = three
- 3 = four

Character 25. Adult cord morphology, presence of minor cords.
0 = zero
1 = one
2 = two
3 = three
4 = many

Axial ornament characters (26–28)

Character 26. Axial ornaments, beading.
0 = absent
1 = present

Character 27. Axial ornaments, longitudinal flammules. Unlike other axial ornaments, longitudinal flammules are not the result of exaggerated growth lines and are sometimes vertically aligned from one whorl to the next.
0 = absent
1 = present

Character 28. Axial ornaments, raised growth lines. This character is coded using adult (relatively large) specimens only as this is almost always a gerontic condition in turritellids.
0 = absent
1 = present

Hollow newel (see Text-fig. 11)

Character 29. Hollow newel. First described by Friend et al. (2023), a hollow newel is the opening in the basal end of the columellar region. Like a true umbilicus, this opening can be accessed from outside the shell. It is not, however, a true umbilicus because its opening is *inside* the aperture (and thus a part of the aperture), rather than next to the aperture. A comparison to spiral staircases serves to clarify our observations and nomenclature. In architectural terminology, a *newel* is the central support post or pillar of spiral staircases. A *hollow newel* is "an opening in the center of a winding staircase in place of a newel post, the stairs being supported each step by those below, and all held in place by the wall" (https://www.merriam-webster.com/dictionary/hollow%20newel). In gastropods, the presence of a hollow newel is the result of an absence of complete inner shell wall deposition that would otherwise form the columella, or in cases where D>0, the wall bounding the umbilicus. Hollow newel construction is rare in high spired gastropods, including turritellids. We find it to be most parsimonious to consider these species a clade as this feature is generally rare but occurs in a number of fossil and extant species which share similar biogeography, as well as only in extant species which were found to be closely related in recent molecular analyses (Sang et al. 2019; Anderson 2018). Hollow newel construction also has the advantage of being readily identifiable, even by non-specialists. Some hollow newel species outside of the Western Atlantic may belong in *Protoma*. This genus includes the largest known turritellid, *Caviturritella abrupta* (See Anderson and Allmon 2020). For additional comments on the genus, see Friend et al. (2023).
0 = absent
1 = present

Character 30. Shell size, class.
0 = < 40mm
1 = 40–60mm
2 = > 60mm

Basal surface

Character 31. Basal surface, texture. The rough state is always convex in our species and lineated basal surfaces characterize those specimens with flat basal surfaces.
0 = unlineated
1 = lineated

Uncoiling

Character 32. Uncoiling, typical of ontogeny
0 = does not uncoil
1 = later whorls uncoil

Character 33. Uncoiling, average number of whorls. The number of whorls at the time of uncoiling varies infraspecifically, therefore average values were used with divisions reflecting the most consistent species differences observed.
0 = never
1 = >10 whorls
2 = 7–9 whorls
3 = 6 or fewer whorls

APPENDIX 4

Character matrix used in phylogenetic analysis of *Caviturritella*. The outgroup taxon is indicated by (OG).

Character	*alumensis*	*banksii*	*leucostoma*	*gonostoma*	*magnasulcus*	*mansfieldi*	*variegata*	*terstriata*	*etiwanensis*	*nodulosa* (OG)
1. Protoconch, diameter	1	2	1	2	1	?	1	0	0	0
2. Protoconch, number of whorls	0	0	1	0	1	?	2	0	0	1
3. Protoconch, type	1	1	1	1	1	?	1	1	1	1
4. Apical sculptural formula, order of appearance for cord A	2	1	2	2	2	?	2	1	1	2
5. Apical sculptural formula, order of appearance for cord B	1	1	1	1	1	?	1	2	1	1
6. Apical sculptural formula, order of appearance for cord C	0	0	0	0	0	?	0	0	0	0
7. Sinus, basal sinus shape	2	5	0	0	1	1	1	?	1	2
8. Sinus, lateral sinus depth	2	0	0	1	0	0	2	1	1	0
9. Sinus, lateral angle	0	0	0	0	0	0	0	0	0	0
10. Sinus, lateral type (inflection points)	0	3	2	2	2	2	3	?	0	3
11. Sinus, lateral sinus apex location	2	2	2	2	2	2	2	1	1	1
12. Angle, pleural	1	2	1	1	0	2	2	0	1	1
13. Angle, apical	2	3	1	2	1	3	3	?	?	3
14. Whorl profile, juvenile	5	6	6	2	6	0	6	3	6	6
15. Whorl profile, adult	1	4	3	1	0	1	2	3	1	7
16. Aperture, shape	1	0	1	1	1	1	1	2	2	1
17. Aperture, internal lirae	0	0	0	0	0	0	0	0	1	0
18. Suture, depth	1	0	0	0	2	1	0	0	1	1
19. Suture, depth change	0	0	0	1	0	0	0	0	0	0
20. Juvenile cord morphology, most prominent	3	2	3	2	2	3	2	3	0	3
21. Juvenile cord morphology, number of primary spiral cords	1	1	2	2	1	2	3	1	3	2
22. Juvenile cord morphology, presence of minor spiral cords	0	0	1	1	1	1	1	0	1	1
23. Adult cord morphology, most prominent	0	2	3	2	2	0	0	0	3	3
24. Adult cord morphology, number of primary cords	2	1	2	2	2	3	3	1	1	2
25. Adult cord morphology, number of minor cords	4	4	2	4	4	4	4	4	4	4
26. Axial ornaments, beading	0	1	0	0	0	0	0	0	0	1
27. Axial ornaments, longitudinal flammules	0	0	0	0	0	0	0	0	0	0
28. Axial ornaments, raised growth lines	0	0	0	0	0	0	0	0	0	0
29. Hollow newel	1	1	1	1	1	1	1	1	1	0
30. Shell size, class	3	3	3	3	1	3	2	1	1	0
31. Basal surface, texture lineated	1	1	1	1	1	1	1	?	0	1

APPENDIX 5

Character matrix used in phylogenetic analysis of *Torcula*. The outgroup taxon is indicated by (OG).

Character	*apicalis*	*cookei*	*clarksvillensis*	*clarionensis*	*radula*	*perattenuata*	*exoleta*	*conspersa*	*lumbricalis*	*milleti*	*pellucida*	*M. roseus* (OG)
1. Protoconch, diameter	1	1	?	?	?	1	1	?	2	2	1	2
2. Protoconch, number of whorls	0	?	?	?	?	0	0	?	1	?	1	2
3. Protoconch, type	1	1	?	?	?	1	1	?	1	1	1	2
4. Apical sculptural formula, order of appearance for cord A	1	1	?	?	?	1	1	?	1	1	1	2
5. Apical sculptural formula, order of appearance for cord B	?	2	?	?	?	2	2	0	0	0	0	0
6. Apical sculptural formula, order of appearance for cord C	0	0	?	?	?	0	0	1	?	?	?	1
7. Sinus, basal sinus shape	3	3	3	3	3	3	4	1	0	0	0	2
8. Sinus, lateral sinus depth	1	1	1	3	2	2	2	0	2	0	1	1
9. Sinus, lateral angle	0	0	0	0	0	0	0	0	2	2	1	0
10. Sinus, lateral type (inflection points)	0	0	0	0	3	0	0	3	3	2	0	3
11. Sinus, lateral sinus apex location	1	1	1	1	1	1	1	1	1	0	1	2
12. Angle, pleural	1	2	1	?	0	0	1	2	1	2	0	2
13. Angle, apical	?	0	?	?	?	0	2	3	1	0	0	3
14. Whorl profile, juvenile	6	6	6	5	5	6	6	6	8	8	8	3
15. Whorl profile, adult	5	5	5	5	5	5	5	0	?	?	?	3
16. Aperture, shape	1	1	1	1	1	1	1	3	1	1	1	1
17. Aperture, internal lirae	0	0	?	?	0	0	0	0	0	0	0	0
18. Suture, depth	1	1	1	0	0	1	1	1	0	0	0	1
19. Suture, depth change	1	0	0	0	0	0	0	0	?	?	?	0
20. Juvenile cord morphology, most prominent	1	3	3	1	0	3	3	2	3	4	3	0
21. Juvenile cord morphology, number of primary spiral cords	2	1	1	1	1	1	1	0	2	3	3	2
22. Juvenile cord morphology, presence of minor spiral cords	0	0	0	?	0	1	1	1	0	0	4	1
23. Adult cord morphology, most prominent	3	0	0	0	0	0	0	2	4	4	3	3
24. Adult cord morphology, number of primary cords	2	1	1	1	1	1	1	2	1	1	3	2
25. Adult cord morphology, number of minor cords	2	1	1	3	4	3	3	4	0	0	4	4
26. Axial ornaments, beading	1	1	1	1	1	1	1	0	0	0	0	0
27. Axial ornaments, longitudinal flammules	0	0	0	0	0	0	0	1	0	0	0	1
28. Axial ornaments, raised growth lines	1	1	1	1	1	1	1	0	0	0	0	0
29. Hollow newel	0	0	0	0	0	0	0	0	0	0	0	0
30. Shell size, class	0	3	1	1	2	3	2	1	0	0	1	1
31. Basal surface, texture lineated	0	0	0	?	0	0	0	1	0	0	1	1
32. Uncoiling, typical of ontogeny	0	0	0	0	0	0	0	0	1	1	1	0
33. Uncoiling, average number of whorls	0	0	0	0	0	0	0	0	3	2	2	0

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PREPARATION OF MANUSCRIPTS

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