A Review of the Living *Cinctura* Banded Tulip Shells (Gastropoda: Fasciolariidae), with the Descriptions of Four New Subspecies and a New Subgenus

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ABSTRACT The fasciolariid genus *Cinctura* Hollister, 1957, which is endemic to the Carolinian Molluscan Province, is now known to contain five distinct species: *C. hunteria* (Perry, 1811), *C. keatonorum* Petuch, 2014, *C. lilium* (Fischer von Waldheim, 1807), *C. tortugana* (Hollister, 1957), and *C. branhamae* (Rehder and Abbott, 1951). Four new geographical subspecies are described, *C. hunteria apalachee* Petuch and Berschauer, n. subsp. (Florida Panhandle to Mobile Bay), and three subspecies from deep water along the eastern edge of the Campeche Escarpment in the Yucatan Channel: *C. lilium connori* Petuch and Berschauer, n. subsp., *C. tortugana traciae* n. subsp., and *C. branhamae morganae* Petuch and Berschauer, n. subsp. The new subgenus *Hollisteria* Petuch and Berschauer, n. subgen. is proposed for the elongated, fragile deep water species of the *Cinctura branhamae* Complex.

KEY WORDS Cinctura, C. hunteria apalachee, C. lilium connori, C. tortugana traciae, C. branhamae morganae, Hollisteria, Fasciolariidae, Carolinian Molluscan Province, Gulf of Mexico

INTRODUCTION

The genus Cinctura (Hollister, 1957), the iconic "Banded Tulip Shells" of the southeastern United States and eastern Mexico, contains five known species and four subspecies and is entirely confined to the Carolinian Molluscan Province (Figure 1). Although the genus ranges from Cape Hatteras, North Carolina to Isla Contoy, Yucatan Peninsula, Mexico, majority of the known taxa are restricted to the Gulf of Mexico. Of these, only two, Cinctura hunteria and its subspecies C. hunteria apalachee (described in the next section), are found in shallow water intertidal depths. All the other taxa live in deeper water, offshore areas (in 20-400 m depths), and are primarily collected by the dredging operations of

commercial shrimp and scallop fishermen or from deep water lobster and crab traps. The taxonomy and systematics of this iconic and characteristic Carolinian Province genus are still in flux, with a plethora of misinformation and incorrect range data existing in the current literature. These erroneous data have led to a large amount of confusion concerning species identities and their biogeographical and bathymetric ranges within the Carolinian Province. These errors will be discussed and corrected, individually, in the sections dealing with each species or subspecies. The holotypes of the four new subspecies are deposited in the collection of the Department type Malacology, Los Angeles County Museum of Natural History, Los Angeles, California and bear LACM catalog numbers.

SYSTEMATICS

Class Gastropoda
Subclass Sorbeoconcha
Order Prosobranchia
Infraorder Neogastropoda
Superfamily Buccinoidea
Family Fasciolariidae
Subfamily Fasciolariinae
Genus *Cinctura* Hollister, 1957

Diagnosis of Cinctura. Originally described as a subgenus of Fasciolaria but here elevated to full genus status. (From Hollister, 1957: 76) "Type species: Pyrula hunteria G. Perry, 1811. Recent from Cape Hatteras southward to Florida and westward to Mobile Bay. Shell of medium size, fusiform, the whorls convex, the spire extended. Suture simple. A prominent spiral ridge emerges from the aperture in front of the suture and extends across the parietal wall to the margin of the callus. This subgenus differs from Fasciolaria s.s. in that the latter has no presutural rib on the parietal wall." Hollister created the name "Cinctura" in reference to the cord (cinctus) being present along the posterior (anal) end of the aperture (urus). The original descriptions of C. hunteria and C. lilium, along with the synonymy of C. distans with C. hunteria, were also given by Hollister, 1957 and will not duplicated here.

Of all the diagnostic features that are used to differentiate the various living and fossil *Cinctura* species, the form of the sculpture on the early postnuclear whorls is the most important. Based on the shape and strength of this early whorl sculpture, we here recognize two species groups within the genus *Cinctura* (sensu stricto); the *Cinctura hunteria* Complex, with smooth, unsculptured early whorls (containing the living *C. hunteria* and *C. hunteria apalachee*), and the *Cinctura lilium* Complex, with heavily-sculptured, knobby early whorls (containing the living *C. lilium*, *C.*

lilium connori, C. keatonorum, C. tortugana, and T. tortugana tracieae). A third species group, the Cinctura branhamae Complex, typified by C. branhamae and its subspecies C. branhamae morganae, is here recognized as constituting a new subgenus, Cinctura (Hollisteria), which exhibits early whorl sculpture made up of strong, closely-packed vertical ribs. This new subgenus is described later in this paper. All species within the genus, both Cinctura s.s. and Cinctura (Hollisteria), exhibit conspicuous thin, dark brown or black bands, varying in number depending on the species. Some have as few as 5 on the body whorl while others can have as many as 14 on both the body whorl and the siphonal canal.

Cinctura (sensu stricto) the Cinctura hunteria Complex

This shallow water and intertidal group contains only two living taxa; the wide-ranging C. hunteria and its northwestern subspecies C. hunteria apalachee. All members of this species group, both fossil and living, are characterized as having smooth, rounded protoconchs and smooth unsculptured early whorls, lacking the small sharply-angled knobs seen on the early whorls of members of the C. lilium species group. An overview of the fossil record (given at the end of this paper) demonstrates that the Cinctura hunteria Complex is a geologicallyyoung group of Cinctura species, first appearing in the Early Pleistocene (Gelasian Age) as C. rucksorum (Petuch, 1994). This Gelasian ancestral species gave rise to C. holeylandica (Petuch, 1994) during the Calabrian Age, an undescribed C. holeylandica subspecies during the Ionian Age, and later an undescribed subspecies of C. hunteria during the Tarantian Age of the Late Pleistocene.

Cinctura hunteria (Perry, 1811) (Figure 2A, B, C, D, I; Figure 5F, G)

Shell Shape and Proportions. The shell is of average size for the genus, with inflated, pyriform body whorl and convex sides. The spire is proportionally low or only moderately elevated, subpyramidal in shape, with indented sutures.

Color and Color Pattern. The base color is typically cream-white or bluish-white overlaid with numerous closely-packed longitudinal stripes of bluish-brown or dark khaki-green. Some specimens have scattered bright orange bands and patches, especially along the subsutural area of the shoulders and on the parietal area of the aperture. In some populations, such as those found at Sanibel Island, Florida, the shells are lighter in color, often being a pale tan-brown or light khakibrown. The number of dark bands on the body whorl varies from 5 to 6, with most specimens having 5 lines (as in the specimens shown here on Figure 2). Occasionally, specimens will have a few finer lines intercalated between the larger bands.

Siphonal Canal Structure. Proportionally very short, truncated, and broad, the smallest and least developed siphonal canal of the entire genus; the canal is heavily ornamented with 8-10 large, prominent cords, with secondary smaller cords being present between the large primary cords at the anterior end, often resulting in as many as 12-14 cords of varying sizes being present.

Early Whorls. The early postnuclear whorls are smooth and unornamented, as seen here on Figure 2I. The protoconch is proportionally large, smooth, rounded, and dome-like.

Range. As seen on Figure 1, *C. hunteria* is the widest-ranging species in the genus, extending from Cape Hatteras, North Carolina south to the Florida Keys and then northward to St. George Island and Apalachicola Bay, Franklin County,

Florida. The extensive fresh water effluent from the Apalachicola River, which empties into Apalachicola Bay, acts as an ecological barrier between *C. hunteria* and its western subspecies *C. hunteria apalachee. Cinctura hunteria hunteria* is also the only member of its genus that is distributed over three subprovinces of the Carolinian Province; the Georgian, Floridian, and Suwannean Subprovinces (Petuch, 2013).

Ecology. Cinctura hunteria, the type of the genus (Hollister, 1957: 76), prefers intertidal sand flats in quiet lagoonal water conditions, and is often associated with beds of sea grasses such as *Halodule* and *Thalassia* (Petuch and Myers, 2014: 63). In the Ten Thousand Islands of southwestern Florida, *C. hunteria* is frequently collected in tide pools on the extensive barrier reef systems built by the worm gastropod *Petaloconchus*, where it feeds on the cerithiid gastropod *Batillaria minima* (Petuch and Myers, 2014: 163).

Discussion. Hollister (1957: 79) demonstrated that the taxon "Fasciolaria distans Lamarck, 1822" is a synonym of Cinctura hunteria and is not referable to C. lilium, as suggested by biogeographical previous workers. The distribution of C. hunteria has also been in a confused state, often with completely erroneous data being published by some recent workers. An example of this incorrect information is seen in the recent book by Mallard and Robin (2017: 170), where they show the range of C. hunteria as extending to both sides of the Yucatan Peninsula and even to the coast of Belize and both coasts of Cuba (which are within the boundaries of the Caribbean Province). They also show the species being absent from the northeastern Gulf and from the North Carolina coast. The true range of C. hunteria is shown here in Figure 1.

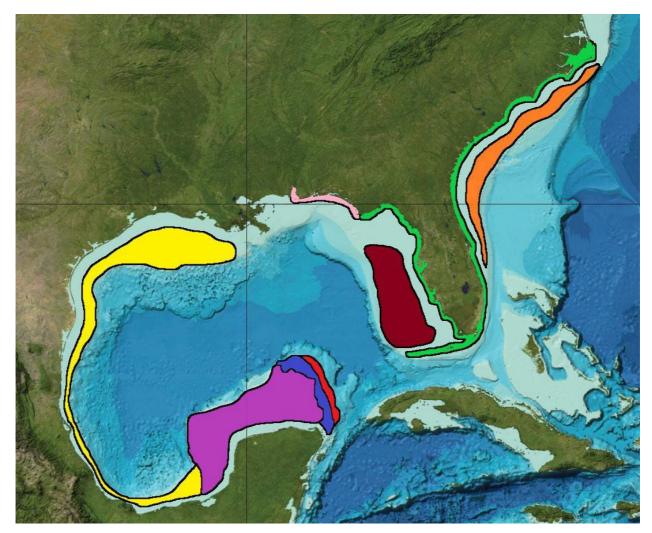


Figure 1. Map of the Gulf of Mexico and southeastern United States, showing the ranges of *Cinctura* (s.s.) and *Cinctura* (Hollisteria) species and subspecies. Green = Cinctura hunteria; Pink = Cinctura hunteria apalachee; Orange = Cinctura keatonorum; Burgundy = Cinctura tortugana; Yellow = Cinctura lilium; Purple = Cinctura (Hollisteria) branhamae; Blue = Cinctura lilium connori; Red = Cinctura tortugana tracieae and Cinctura (Hollisteria) branhamae morganae.

Cinctura hunteria apalachee Petuch and Berschauer, new subspecies (Figure 2E, F, G, H, J)

Description. Shell of average size for genus and same size as nominate subspecies, stocky, with pyriform shape and very inflated body whorl; spire proportionally low, subpyramidal, with indented sutures and slightly convex sides; siphonal canal proportionally short, truncated, and broad, ornamented with 6 to 10 large, prominent cords, with few smaller secondary

cords being present on some individuals; base color pale salmon-orange or cream-white, overlaid with numerous irregular, narrow, longitudinal dark orange-tan or salmon-orange elongated flammules which are best developed along subsutural area and around mid-body; base color pattern overlaid with 6 to 9 thin, prominent, regularly-spaced dark brown lines; smaller secondary lines often present between primary lines, producing pattern consisting of 9 to 14 lines on body whorl; aperture proportionally large, open, oval shaped; anterior

end of columella with 2 large rib-like folds, with the posteriomost fold being largest in size; postnuclear and early whorls smooth and unsculptured; protoconch smooth, rounded, domelike.

Type Material. HOLOTYPE - Length 67.4 mm, width 33.1 mm, from Panama City, Florida, LACM 3803; OTHER MATERIAL EXAMINED - 3 specimens, lengths 64 mm, 67 mm, and 79 mm, from the same locality as the holotype, in the research collection of the senior author; 3 specimens, lengths 71.6 mm, 69.2 mm, and 54.2 mm, from the same locality as the holotype, in the research collection of the junior author.

Type Locality. St. Andrew Bay, Panama City, Bay County, Florida.

Range. The subspecies ranges from St. Joseph Bay and Port St. Joe, Gulf County, Florida westward to Mobile Bay, Alabama.

Ecology. The holotype and type lot were collected in shallow pools at low tide, on sand flats in a protected bay. The new subspecies prefers intertidal sand flats and sea grass beds, where it was observed feeding on small tellinid and mactrid bivalves.

Etymology. The taxon honors the Apalachee Indian Tribe of the Florida Panhandle. Once a large and powerful tribal group, only a few members survived the diseases brought by the first Spanish settlers. Their descendants now live in Louisiana.

Discussion. This previously-unrecognized subspecies of *C. hunteria* primarily differs from the nominate subspecies in having a narrower, more slender spire with distinctly less-inflated early whorls (easily seen in a comparison of Figures 1I and 1J). *Cinctura hunteria apalachee* also differs from the nominate subspecies in consistently having a much lighter shell color, being dominated by shades of salmon-orange, reddish-tan, or pale orange-tan, and lacking the dark khaki-green color seen on typical *C. hunteria hunteria*. The banding pattern is also

different on the two subspecies, with the nominate subspecies typically having 5 or 6 dark bands on the body whorl and with *C. hunteria apalachee* typically having 6 to 8 dark bands, and sometimes with as many as 14.

Cinctura (sensu stricto) - the Cinctura lilium Complex

The members of this species group, the most species-rich of the entire genus, differ from members of the C. hunteria Complex in having narrower, more elongated and distinctly fusiform shells with higher spires, and with heavily-sculptured early spire whorls that are ornamented with sharply-angled small knobs. This type of knobbed spire sculpture was best developed on the mid-Pleistocene (Ionian Age) Cinctura evergladesensis (Petuch, 1991), from the Belle Glade Member of the Bermont Formation of southern Florida (Figure 5D). During the warm Ionian time, the southern half of the Florida Peninsula was under water, allowing C. evergladesensis to extend its range into the Gulf of Mexico and northward to at least North Carolina. The many populations of this heavily-knobbed species became isolated from each other during the low sea levels that occurred between the Ionian and Tarantian Ages Pleistocene (the Middle Pleistocene-Late geographically-isolated boundary). These populations evolved into the species and subspecies of the C. lilium Complex; with the Gulf housing four distinct taxa, C. lilium, C. lilium connori, C. tortugana, and C. tortugana traciae and with the relictual C. keatonorum being isolated along the Atlantic coast from North Carolina to central Florida. The presence of two distinct subspecies along the eastern edge of the Yucatan Peninsula (Yucatan Straits) demonstrates that the group is presently undergoing rapid speciation.

Cinctura lilium (Fischer von Waldheim, 1807) (Figure 4A, B, G; Figure 5E)

Shell Shape and Proportions. The shell is large for the genus, elongated and fusiform, with rounded spire whorls. The body whorl is moderately inflated, with rounded, convex sides. The spire is elevated and protracted, almost the same length as the body whorl. The anterior end of the columella is ornamented with two large, prominent rib-like folds, with the posteriormost fold being the largest.

Color and Color Pattern. The base color of the shell is a pale grayish-white or salmon-gray overlaid with numerous irregular, narrow, longitudinal dark gray or dark orange-tan elongated flammules. The flammules are best developed along the subsutural area and around the mid-body. This base color pattern is overlaid with 8-10 thin, prominent, regularly-spaced thin dark brown bands, with 2 or 3 bands extending onto the siphonal canal. In some specimens, thin, less-developed secondary lines are sometimes present between the primary lines. The parietal area characteristically has a white glaze.

Siphonal Canal Structure. The siphonal canal is proportionally very long and narrow, being wider at the juncture with the body whorl and tapering to the anterior tip. The canal is ornamented with 7 or 8 large low cords with 2-3 very fine threads being present between each pair of large cords. The anteriormost siphonal cords are generally smaller and less developed than the posterior cords.

Early Whorls. The postnuclear whorls are ornamented with 7 to 9 large rounded knobs, with the larger knobs being distinctly angled. The sloping subsutural area that is posterior to the postnuclear knobs are ornamented with 3 large cords.

Range. As seen on Figure 1, *Cinctura lilium* has the second-largest biogeographical range of the genus, ranging from the western side of the Mississippi River Delta south to off the coast of

Tabasco State, Mexico. This species is confined to the Texan Subprovince of the Carolinian Province (Mississippi River Mouth south to Veracruz, Mexico; see Petuch, 2013), and is considered to be a primary subprovincial index species.

Ecology. Found on muddy sand sea floors in depths ranging from 4 m to 46 m (Tunnell *et al.*, 2010: 220), but most commonly collected in depths of around 25 m.

Discussion. The lectotype of *C. lilium*, designated by Hollister and illustrated in his 1957 paper (plate 6, figure 1), was collected in the Bay of Campeche (designated type locality), probably off Veracruz, Mexico. The lectotype is an 82 mm specimen, very similar to the shell shown here on Figure 5E and is deposited in the British Museum (Natural History) under the Sloane Catalog number 1481. Hollister's lectotype, however, has a damaged siphonal canal, with the entire anterior end broken off. The complete specimen would have had a proportionally longer siphonal canal, similar to the specimens shown here on our Figures 4 and 5. Cinctura lilium is the only member of its genus to exhibit large variations in the length and development of the siphonal canal, often from within the same population. Juveniles and smaller specimens have proportionally shorter siphonal canals, similar in length to those seen on C. keatonorum and C. tortugana (as in the specimen shown in Figure 5E). Full adult and large specimens will often have proportionally longer siphonal canals (as seen here on Figure 4A, B), approximating the long, narrow canal seen on C. (Hollisteria) branhamae (Figure 4E, F). Indeed, the elongated siphonal canal on older adults has led some workers (Tunnell, et al., 2010: 220) to misidentify specimens of Texas C. lilium as C. (Hollisteria) branhamae, a species now known to be confined to the Campeche Bank and Yucatan Peninsula and not found off Texas (discussed later in this paper). Mallard and Robin (2017: 171, figure 1) show a

classic *C. lilium* but give no detailed locality data for the specimen ("Gulf of Mexico").

Cinctura lilium connori Petuch and Berschauer, new subspecies (Figure 4C, D, H)

Description. Shell of average size for genus, elongated, with rounded whorls and sloping shoulders; spire elevated, protracted, more than two-thirds total body length; siphonal canal proportionally long, well-developed, with only a slight stricture at the body whorl-siphonal canal juncture; shell color pale orange-white or salmon overlaid with numerous irregular, narrow, longitudinal dark orange-tan or orangered flammules; longitudinal flammules best developed along subsutural area and around mid-body; flammule pattern overlaid with 8-12 thin, regularly-spaced dark brown lines; thinner and less-developed secondary lines frequently present between pairs of primary lines; siphonal canal dark orange or orange-tan with 1-4 dark brown thin lines, ornamented with 4-7 raised spiral cords; aperture proportionally small, oval in shape; early post-nuclear whorls of spire heavily sculptured with 14-16 large, sharply angles knobs (Figure 4H).

Type Material. HOLOTYPE - length 72.5 mm, width 31.4 mm, 250 m depth off Cabo Catoche, Mexico, LACM 3804; OTHER MATERIAL EXAMINED - length 91 mm, width 47 mm, from the same depth and locality as the holotype, in the research collection of the senior author.

Type Locality. Trawled by deep water prawn (*Glyphograngon*) fishermen from 250 m depth in the Yucatan Channel, off Cabo Catoche, Quintana Roo, Mexico.

Range. As shown on Figure 1, Cinctura lilium connori is confined to the eastern side of the Campeche Escarpment, along the Yucatan Channel.

Ecology. The new subspecies lives in deep water areas along the upper edge of the bathyal

zone, ranging from 100 to 250 m depths. This deep neritic-upper bathyal bathymetric preference differs dramatically from that of the nominate subspecies, *C. lilium lilium*, which prefers depths of only around 25 to 40 m.

Etymology. Named for Connor Johnson, Wilmington, North Carolina; son of Mark Johnson, who kindly donated the holotype to our research project.

Discussion. This new eastern Yucatan subspecies of the Texan Subprovince C. lilium represents an isolated population of the nominate subspecies that has become cut-off from the main eastern Mexican population, probably during the extreme sea level drop at the end of the Late Pleistocene. Since that time, genetic isolation and genetic drift have allowed this eastern population to evolve distinctive shell characters that readily separate it from C. lilium lilium in the western Gulf of Mexico. As can be seen in Figure 4, the new subspecies has a much more elongated and fusiform shell than does the nominate subspecies, with a more slender and less-inflated body whorl. It is also a much more colorful shell, exhibiting shades of bright red and dark orange. The principal difference between the two subspecies is seen in the structure and development of the knobbed sculpture on the early whorls. In C. lilium lilium, the spire knobs are proportionally smaller and have more sloping and rounded edges (Figure 4G), while the spire knobs of C. lilium connori are proportionally larger, fewer in number, and have sharper and more angled edges (Figure 4H).

> Cinctura keatonorum Petuch, 2014 (Figure 3A, B, H)

Shell Shape and Proportions. The shell is of average size for genus, elongated and fusiform, with rounded whorls and a distinctly sloping shoulder. The body whorl is moderately inflated, with rounded, convex sides. The spire is

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elevated and protracted, almost the same length as the body whorl. The anterior end of the columella is ornamented with two large, prominent rib-like folds, with the posteriormost fold being the largest.

Color and Color Pattern. The base color of the shell is a pale salmon-orange overlaid with numerous irregular, narrow, longitudinal dark orange-tan or salmon-orange elongated flammules. The flammules are best developed along the subsutural area and around the midbody. This base color pattern is overlaid with 6 thin, prominent, regularly-spaced dark brown lines. Thin, less-developed secondary lines are sometimes present between the primary lines, especially along the anterior end of the body whorl (as in the specimen shown here in Figure 3). The parietal area characteristically has a bright orange-tan glaze.

Siphonal Canal Structure. The siphonal is proportionally short, wide, and truncated, with a solid orange-tan color, with 7 large raised cords. The anteriormost siphonal cords are generally smaller than the posterior cords.

Early Whorls. The postnuclear whorls are ornamented with 5-6 deeply incised spiral sulci and 6-8 low, poorly-developed, undulating, riblike knobs, which are often suppressed by the prominent spiral grooves.

Range. As shown in Figure 1, *C. keatonorum* ranges from offshore of Cape Hatteras, North Carolina, southward to near Fort Pierce, St. Lucie County, Florida.

Ecology. Cinctura keatonorum lives in depths of 30-50 m in offshore areas on shell hash and coarse sand, where it is most often associated with the immense shoal-like beds of the large endemic Georgian Subprovince scallop Argopecten gibbus carolinensis. Since this endemic subspecies is the source of a large commercial scallop fishery, C. keatonorum is most often collected as a by-catch of scallop dredging.

Discussion. The senior author originally described this offshore Georgian Subprovince species as a bathymetric subspecies of the shallow water Cinctura hunteria (Petuch, 2013: The deeper water 203-204). Cinctura keatonorum also differs from the shallow water C. hunteria in being a larger and more elongated shell with a proportionally much higher and more protracted spire, in having a distinctive orange-salmon shell color, and in having heavily-sculptured grooved early whorls instead of the smooth postnuclear whorls seen on C. hunteria. Because of these differences, we now consider C. keatonorum to be a full species all to itself and also to be a member of the C. lilium Complex, and not closely-related to C. hunteria. Richards (1962: plate 20, figure 6) illustrates a fossil specimen of C. keatonorum from the Pamlico Formation at Beaufort, North Carolina, but misidentifies it as "Fasciolaria distans Lamarck" (now known to be a synonym of the shallow water C. hunteria). This fossil specimen demonstrates that C. keatonorum was the only Cinctura species living in North Carolina during the cold late Pleistocene time and that the warmer-water C. hunteria moved into that area only when sea temperatures rose during the latest Pleistocene and Holocene. The deeper water C. keatonorum can then be seen to be an isolated Pleistocene relict of the C. lilium Complex that has found a refuge in the East Coast offshore scallop beds.

> Cinctura tortugana (Hollister, 1957) (Figure 3C, D, G)

Shell Shape and Proportions. The shell is of average size for genus, elongated and fusiform, with rounded whorls and a distinctly sloping shoulder. The body whorl is moderately inflated, with rounded, convex sides. The spire is elevated and protracted, almost the same length as the body whorl. The anterior end of the columella is ornamented with two large,

prominent rib-like folds, with the posteriormost fold being the largest.

Color and Color Pattern. The base color of the shell is a pale salmon-orange overlaid with numerous irregular, narrow, longitudinal dark orange-tan or salmon-orange flammules. The flammules are best developed along the subsutural area and around the midbody. This base color pattern is overlaid with 6 thin, prominent, regularly-spaced dark brown lines. Thin, less-developed secondary lines are sometimes present between the primary lines, especially along the anterior end of the body whorl (as in the specimen shown here in Figure 3). The parietal area characteristically has a bright orange-tan glaze.

Siphonal Canal Structure. The siphonal is proportionally short, wide, and truncated, with a solid orange-tan color, with 7 large raised cords. The anteriormost siphonal cords are generally smaller than the posterior cords.

Early Whorls. The postnuclear whorls are ornamented with 5-6 deeply incised spiral sulci and 6-8 low, poorly-developed, undulating, riblike knobs, which are often suppressed by the prominent spiral grooves.

Range. As can be seen on Figure 1, *Cinctura tortugana* is found in deeper, offshore areas along western and southwestern Florida, from north of the Dry Tortugas, Florida Keys (type locality) northward to off Cedar Key, Levy County, Florida. *Cinctura tortugana* is confined to the southern part of the Suwannean Subprovince of the Carolinian Province (Petuch, 2013).

Ecology. Cinctura tortugana lives on carbonate rubble sea floors on the West Florida Shelf and along the edge of the bathyal zone, in depths of 50 to 200 m. In the deeper areas along the edge of the Florida Escarpment, C. tortugana is associated with sea floors that are dominated by the red coralline algae Porolithon and Goniolithon, which form thick and densely-intertwined beds composed of algal nodules

(rhodoliths). Here, it occurs along with other distinctive rhodolith-associated mollusks such as the muricid *Chicoreus rachelcarsonae* Petuch, 1987, the cone shell *Dauciconus aureonimbosus* (Petuch, 1987), the busyconid *Lindafulgur lyonsi* (Petuch, 1987), and the scallop *Lindapecten lindae* Petuch, 1995.

Discussion. This impressive and colorful species was originally described as a subspecies of Cinctura lilium (Hollister, 1857: 79-80), with the type locality being from "Off the Dry Tortugas, to the northwest" (now known as the "Tortugas Shrimping Ground"). Besides being isolated from each other on either side of the Gulf of Mexico, the Suwannean Subprovince C. tortugana differs from the Texan Subprovince C. lilium in being a smaller, more slender species with a much shorter and less developed siphonal canal and also in being a much more colorful shell, ornamented with conspicuous bright orange or orange-red flammules. The early whorl structure of the Texan and eastern Mexico C. lilium also differs from that of the western Florida C. tortugana in having larger, more prominent, and better developed angled knobs on the early postnuclear whorls (seen here in a comparison of Figures 3G and 4G). Because of these differences in shell morphology and biogeography, we consider C. tortugana to be a full species unto itself. Mallard and Robin (2017: 171, figures 2 and 3) show two specimens of the classic C. tortugana but only give their collection localities as "Gulf of Mexico" and "Florida, USA". The actual biogeographical distribution of *C. tortugana* is shown here in Figure 1.

> Cinctura tortugana traciae Petuch and Berschauer, new subspecies (Figure 3E, F, I)

Description. Shell is of average size for genus, thickened and heavy, elongated and fusiform, with rounded whorls and distinctly sloping

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subsutural area; body whorl moderately inflated, with slightly rounded sides; spire elevated and protracted, almost same length as body whorl; The anterior end of columella ornamented with two large, prominent rib-like folds, with posteriormost fold being largest; shell base color pale salmon-orange or cream-white overlaid with numerous irregular, narrow, longitudinal bright blood red flammules which are best developed along subsutural area and around mid-body; often fusing into nearly solid blood red bands; red color pattern overlaid with 7 thin, prominent, regularly-spaced dark brown lines; thin, less-developed secondary lines sometimes present between pairs of primary lines, especially along anterior end of body whorl (as shown here in Figure 3E); siphonal canal proportionally short, narrow, with dark reddish-brown anterior tip, ornamented with 7 large raised cords; anteriormost siphonal cords are generally smaller than posterior cords; postnuclear whorls ornamented with 5-6 deeply incised spiral sulci and 8-10 proportionally large, well-developed, sharply-angled knobs.

Type Material. HOLOTYPE - Length 72.3 mm, width 31.5 mm, off Cabo Catoche, Mexico, LACM 3805; OTHER MATERIAL EXAMINED - length 73 mm, width 31 mm, from the same locality and depth as the holotype, in the research collection of the senior author.

Type Locality. Trawled by deep water prawn (*Glyphograngon*) fishermen from 250 m depth in the Yucatan Channel, off Cabo Catoche, Quintana Roo, Mexico.

Range. As seen in Figure 1, this new subspecies is confined to the eastern side of the Campeche Escarpment, along the Yucatan Channel.

Ecology. The new subspecies lives in deep water areas along the lower neritic and upper bathyal zones, ranging from 200 to 300 m depths. This deep neritic-upper bathyal bathymetric preference differs dramatically from that of the nominate subspecies, *C.*

tortugana tortugana, which prefers shallower depths of 50 to 200 m in the lower neritic zone.

Etymology. Named for Traci Kelley Johnson, Wilmington, North Carolina; wife of Mark Johnson, who kindly donated the holotype to our research project.

Discussion. This new isolated deep water eastern Yucatan subspecies differs from the western Florida nominate subspecies in being a smaller, heavier, and more slender shell with a less inflated body whorl and narrower spire whorls. Cinctura tortugana traciae is also a much more colorful shell, usually exhibiting bright blood-red flammules and wide broken red bands as opposed to the orange and pale reddish-orange flammules seen on C. tortugana tortugana. The primary difference between the two subspecies is seen in the structure of the early whorls. In C. tortugana tortugana, the postnuclear whorls are low and rounded (Figure 3G) while those of C. tortugana traciae are large, prominent, and sharply-angled (Figure 3I). Mallard and Robin (2017: 171, figure 4) show a specimen of C. tortugana traciae from Cabo Catoche, but misidentify it as a "C. lilium".

During the major sea level drop in the Middle Pleistocene (Calabrian-Ionian Age Boundary), which may have been as extreme as 200 m below the present sea level, the eastern edge of the Campeche Escarpment (off the eastern side of the Campeche Bank) and the western edge of the Florida Escarpment (off the western edge of the West Florida Shelf) would have been separated by only 80 km. During this time of extremely low sea levels and much shallower water than is seen today, the ancestor of C. tortugana would have been able to colonize both sides of the area north of the Yucatan Channel. When sea level rose at the end of the Pleistocene, this ancestral species would have been bisected into two geographically-isolated populations, one along the eastern edge of the Campeche Bank and one off southwestern

Florida. During the Tarantian Age of the Late Pleistocene, these two isolated populations evolved into *C. tortugana* in Florida and *C. tortugana traciae* in Mexico.

Cinctura (Hollisteria) - the Cinctura branhamae Complex

Because of the unique shell characters and geographical isolation of this group, we here propose a new subgenus for *C. branhamae* and its new subspecies, *C. branhamae morganae*.

Family Fasciolariidae Subfamily Fasciolariinae Genus *Cinctura* Hollister, 1957 Subgenus *Hollisteria* Petuch and Berschauer, new subgenus

Diagnosis. Shells large for genus, thin and delicate, very elongated and fusiform, with elevated, protracted spires and long, narrow siphonal canals; shoulder rounded and spire whorls convex; body whorl inflated and subglobose; postnuclear and early whorls sculpted with numerous small, thin, closely-packed vertical ribs, which are, in turn, overlaid with 6 strong spiral threads; constriction at body whorl-siphonal canal juncture very deep and abrupt; pre-sutural parietal cord proportionally very small, thin, and poorly-developed.

Type Species. Cinctura branhamae (Rehder and Abbott, 1951) (originally Fasciolaria distans branhamae), from deep water off the Yucatan Peninsula of Mexico.

Species in *Hollisteria.* Only two taxa are presently referable to the new subgenus; *Cinctura (Hollisteria) branhamae* (Rehder and Abbott, 1951) and *Cinctura (Hollisteria) branhamae morganae* Petuch and Berschauer, n. subsp

Range. The subgenus *Hollisteria* is known only from the eastern Bay of Campeche, the

Campeche Bank, and the Yucatan Escarpment of the Yucatan Peninsula of Mexico.

Etymology. The new subgenus is named in honor of Solomon Cady Hollister, renowned structural engineer and university professor and also the Dean of the College of Engineering at Cornell University (1937 to 1959). In his spare time, Professor Hollister also collected and studied living and fossil mollusks, mostly those from southern Florida and the Gulf of Mexico. His research resulted in papers on the living fasciolariids, the living and fossil busyconids, and on Florida fossil vase shells. He was also the author of several new genera, including *Cinctura*.

Discussion. This group of thin, fragile, and very elongated deep water *Cinctura* taxa is restricted to the Yucatan Peninsula of Mexico and shows no relationship to any other group of Banded Tulips found elsewhere in the Carolinian Province, living or fossil. The distinctive early whorl sculpture of this group, consisting of small, sharply-defined vertical ribs, is unique within the genus *Cinctura* and indicates that *Hollisteria* evolved as a local endemic radiation that has always been confined to the Campeche Banks. Unlike the other species groups within the genus *Cinctura*, the pre-sutural cord along the posterior end of the parietal region is greatly reduced, being only a faint, thin, blade-like cord.

Cinctura (Hollisteria) branhamae (Rehder and Abbott, 1951) (Figure 4E, F, I)

Shell Shape and Proportions. The shell is the largest in the genus, and is thin and fragile with a distinctive elongated, slender, and fusiform shape. The body whorl is inflated and the spire is highly elevated, almost equal in length to the body whorl. The constriction at the body whorl-siphonal canal juncture is very well developed. The aperture is proportionally very wide and open, oval in shape.

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Color and Color Pattern: Cinctura (Hollisteria) branhamae is generally a pale salmon-orange color with scattered thin, longitudinal, slightly darker salmon-orange flammules. This base color is overlaid with 10 or 11 evenly-spaced, thin dark brown bands. The siphonal canal is colored a darker orange or orange-tan.

Siphonal Canal Structure. The siphonal canal is proportionally very long and narrow, almost tubular in shape. This Campeche Bank endemic species has the longest and best-developed siphonal canal of the entire genus *Cinctura*.

Early Whorls. The protoconch is proportionally large and rounded. The postnuclear and early whorls are ornamented with numerous small, thin, closely-packed vertical ribs, which are, in turn, overlaid with 6 strong spiral threads.

Range. As can be seen in Figure 1, Cinctura (Hollisteria) branhamae is found all across the wide Campeche Bank off northern Yucatan, from Tabasco State to Quintana Roo State, and northward to the Arcas Cays and Alacran Reefs along the Yucatan Escarpment adjacent to the Mexico Basin.

Ecology. This large and conspicuous Campeche Bank species prefers carbonate mud sea floors in depths ranging from 50 to 150 m. There, it is associated with other classic Yucatan endemic gastropods such as the cone shell Gradiconus sennottorum (Rehder and Abbott, 1951), the volute Scaphella junonia butleri Clench, 1953, the busyconids Lindafulgur candelabrum (Lamarck, 1816) and Busycoarctum coarctatum (Sowerby I. 1825), muricid and the Vokesimurex sallasi (Rehder and Abbott, 1951). Discussion. This large and characteristic Yucatan gastropod was originally described as "Fasciolaria distans branhamae" by Rehder and Abbott (1951), but is here considered to be a full species, distinct from "F. distans" (which is now considered to be a synonym of Cinctura hunteria, as discussed earlier in this paper). In their recent book on the Fasciolariidae, Mallard and Robin (2017: 169) show a typical specimen of *C. (Hollisteria) branhamae* from off Campeche but also illustrate two specimens of *C. tortugana* ("Gulf of Mexico") on the same figure. Although they considered all three shells to be conspecific, the two illustrated *C. tortugana* have noticeably short siphonal canals that are not even close to the length of the siphonal canal of the illustrated *C. (Hollisteria) branhamae*. They also lack the inflated body whorl-siphonal canal juncture that typifies true *C. (Hollisteria) branhamae*.

Cinctura (Hollisteria) branhamae morganae Petuch and Berschauer, new subspecies (Figure 5A, B, C)

Description. Shell large for genus but small for subgenus Hollisteria, thin and fragile, elongated, fusiform. with high protracted spire; constriction at body whorl-siphonal canal juncture very well developed, producing proportionally long, narrow siphonal canal; base shell color dark salmon-orange or pale lavendertan with darker salmon-tan or brownish-purple elongated longitudinal flammules; base color overlaid with 12-15 thin, evenly-spaced, dark brown bands; occasional specimens with thin brown bands extending onto siphonal canal; specimens may also have finer secondary brown bands present between pairs of larger bands; aperture proportionally large, oval in shape; presutural parietal cord poorly developed, thin and blade-like; 2 folds at anterior end of columella equal in size, proportionally large prominent; postnuclear and early whorls sculpted with numerous prominent, thin, closely-packed vertical ribs, which are, in turn, overlaid with 6 strong spiral threads; constriction at body whorl-siphonal canal juncture very deep and abrupt; pre-sutural

parietal cord proportionally very small, thin, and poorly-developed.

Type Material. HOLOTYPE - Length 71.2 mm, width 30.5 mm, off Cabo Catoche, Quintana Roo, Mexico, LACM 3806; OTHER MATERIAL EXAMINED - length 103 mm, width 42 mm, from the same locality and depth as the holotype, in the research collection of the senior author.

Type Locality. Trawled by deep water prawn (*Glyphograngon*) fishermen from 250 m depth in the Yucatan Channel, off Cabo Catoche, Ouintana Roo, Mexico.

Range. As seen in Figure 1, Cinctura (Hollisteria) branhamae morganae is confined to deep water along the eastern side of the Campeche Escarpment, bordering the Yucatan Channel.

Ecology. The new subspecies lives in deep water areas along the lower neritic and upper bathyal zones, preferring depths of 200 to 300 m. There, the new subspecies lives on a carbonate mud and shell hash sea floor and is associated with two other deep water Cinctura subspecies, C. lilium connori and C. tortugana traciae, along with the large volutes Aurinia macginnorum (Garcia and Emerson, 1987) and Caricellopsis contovensis (Emerson, 1979). The neritic-upper bathyal bathymetric preference of C. (Hollisteria) branhamae morganae differs dramatically from that of the subspecies. *C*. (Hollisteria) branhamae branhamae, which prefers depths of 50-150 m in the lower neritic zone of the main Campeche Banks.

Etymology. Named for Morgan Taylor Berschauer, Laguna Hills, California, daughter of the junior author, an inspired natural historian and professional photographer.

Discussion. This new deep water subspecies from the eastern Yucatan Escarpment differs from the shallower water Campeche Bank nominate subspecies in being a smaller, less elongated shell with a noticeably lower and less

protracted spire. Cinctura (Hollisteria) branhamae morganae also differs from C. (Hollisteria) branhamae branhamae in being a more darkly-colored shell, with darker salmontan or brownish-purple flammules, and in having more numerous and proportionally wider dark spiral bands. The nominate subspecies has 10 or 11 dark spiral bands on the body whorl, while the new subspecies generally has between 12 and 15 bands on the body whorl. Some specimens of C. (Hollisteria) branhamae morganae also have fine secondary bands present between pairs of primary bands and also fine bands on the siphonal canal.

Fossil Record and Evolutionary History

The genus Cinctura first appears in the Buckingham Member of the Tamiami Formation of southern Florida, during the early Piacenzian Age of the Pliocene Epoch, around 4.2 million years BP. There, it is represented by a rare, elongated unnamed species that is a member of the C. lilium Complex. The genus began to diversify during the late Piacenzian Pliocene, evolving at least three more species. The peak evolutionary development of the genus took place during the Early and Middle Pleistocene Epoch, when an additional seven species appeared in the fossil record. This last evolutionary radiation was the ancestor of the species complexes seen in the modern Carolinian Province. For illustrations and descriptions of the fossil Cinctura taxa listed here, see Petuch, 1994 and 2004; Richards, 1962; and Ward and Blackwelder, 1987. The known fossil Cinctura species are listed here by geochronology.

Late Pliocene (Piacenzian Age) - 3.6 to 2.58 mya

Tamiami Formation, Buckingham Member (Southern Florida)

Cinctura unnamed species (highly elongated shell and short siphonal canal) (C. lilium Complex)

Tamiami Formation, Pinecrest Member (Southern Florida)

Cinctura rhomboidea (Rogers, 1839) (also the Yorktown Formation of Virginia and North

Carolina, the **Duplin Formation** of North and South Carolina, and the **Jackson Bluff**

Formation of northern Florida and the Florida Panhandle (*Cinctura lilium* Complex)

Tamiami Formation, Fruitville Member (Unit 4) (Southern Florida)

Cinctura sarasotaensis (Petuch, 1994) (C. lilium Complex)

Chowan River Formation (Virginia and North Carolina)

Cinctura beaufortensis (Ward and Blackwelder, 1987) (C. lilium Complex)

Early Pleistocene (Gelasian Age) - 2.58 to 1.8 mya

Caloosahatchee Formation, Fort Denaud Member (Southern Florida)

Cinctura apicina (Dall, 1890) (C. lilium Complex)

Caloosahatchee Formation, Ayers Landing Member (Southern Florida)

Cinctura lindae (Petuch, 1994) (C. lilium Complex)

Nashua Formation, Rucks Pit Member (Southern Florida)

Cinctura rucksorum (Petuch, 1994) (C. hunteria Complex)

Early Middle Pleistocene (Calabrian Age) - 1.8 mya to 780,000 BP

Bermont Formation, Holey Land Member (Southern Florida)

Cinctura capelettii (Petuch, 1994) (C. lilium Complex)

Cinctura holeylandica (Petuch, 1994) (C. hunteria Complex)

Late Middle Pleistocene (Ionian Age) - 780,000 to 126,000 BP

Bermont Formation, Belle Glade Member (Southern Florida)

Cinctura evergladesensis (Petuch, 1991) (Figure 5E; C. lilium Complex)

Cinctura holeylandica subspecies (C. hunteria Complex)

Late Pleistocene (Tarantian Age) - 126,000 to 11,700 BP

Fort Thompson Formation, Coffee Mill Hammock Member (Southern Florida)

Cinctura hunteria subspecies (C. hunteria Complex)

Pamlico Formation (North Carolina)

Cinctura keatonorum Petuch, 2013 (C. lilium Complex; illustrated in Richards, 1962)

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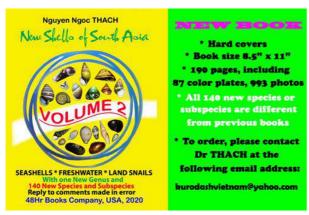
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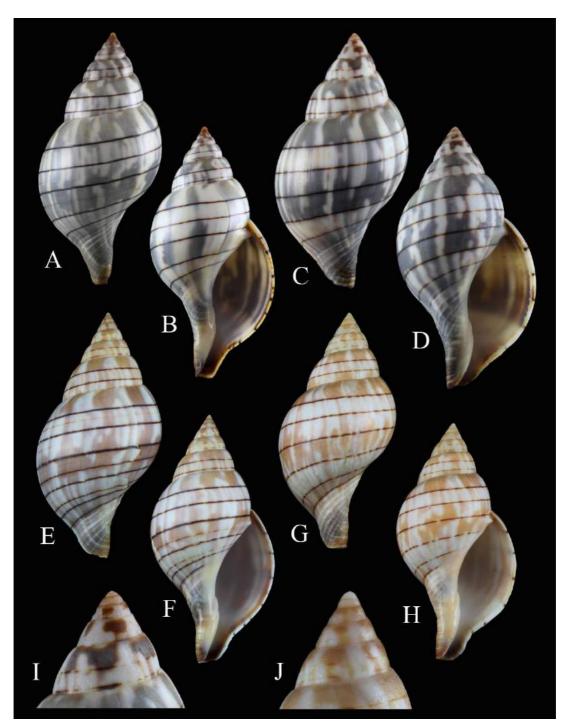


Figure 2. Members of the Cinctura hunteria Species Complex.

A, B= Cinctura hunteria (Perry, 1811), length 78 mm, collected in a tide pool on a vermitid gastropod reef off Turtle Key, Ten Thousand Islands, Collier County, Florida. Petuch collection; C, D= Cinctura hunteria (Perry, 1811), length 62.4 mm, Rabbit Key, Ten Thousand Islands, Collier County, Florida, Berschauer collection; E, F= Cinctura hunteria apalachee Petuch and Berschauer, new subspecies, holotype, length 67.4 mm, LACM 3803, low tide on sand flats, St. Andrew Bay, Panama City, Bay County, Florida; G, H= Cinctura hunteria apalachee Petuch and Berschauer, new subspecies, length 64 mm, low tide on sand flats, St. Andrew Bay, Panama City, Bay County, Florida. Petuch collection; I= Cinctura hunteria, close-up of the protoconch and early whorls; J= Cinctura hunteria apalachee, close-up of the protoconch and early whorls.

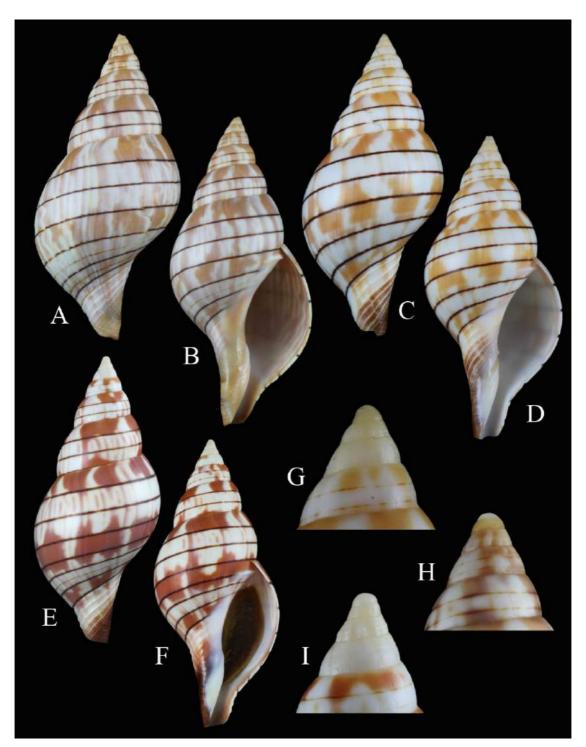


Figure 3. Members of the Cinctura lilium Species Complex.

A, B= Cinctura keatonorum Petuch, 2014, length 92 mm, 50 m depth off Cape Canaveral, Brevard County, Florida, from commercial scallop boats. Petuch collection; C, D= Cinctura tortugana (Hollister, 1957), length 74 mm, 60 m depth north of the Dry Tortugas, Monroe County, Florida, in a deep water lobster trap. Petuch collection; E, F= Cinctura tortugana traciae Petuch and Berschauer, new subspecies, holotype length 72.3 mm, holotype, LACM 3805, trawled from 250 m depth off Cabo Catoche, Quintana Roo State, Mexico; G= Cinctura tortugana, close-up of the protoconch and early whorls; H= Cinctura keatonorum, close-up of the protoconch and early whorls.

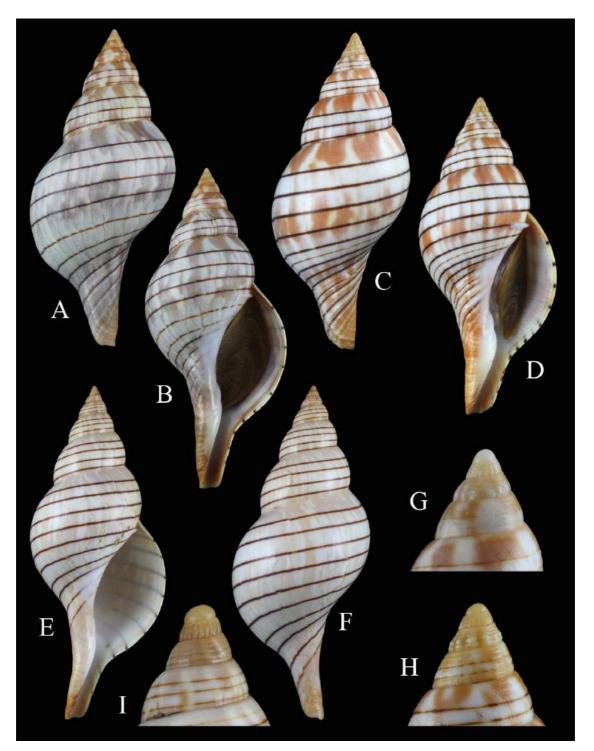


Figure 4. Members of the Cinctura lilium Species Complex.

A, B= Cinctura lilium (Fischer von Waldheim, 1807), length 101 mm, 20 m depth off Mustang Island, Port Aransas, Nueces County, Texas. Petuch collection; C, D= Cinctura lilium connori Petuch and Berschauer, new subspecies, holotype, length 72.5 mm, LACM 3804, trawled from 250 m depth off Cabo Catoche, Quintana Roo State, Mexico; E, F= Cinctura (Hollisteria) branhamae (Rehder and Abbott, 1951), length 131 mm, trawled from 60 m depth north of Progreso, Yucatan State, Mexico. Petuch collection; G= Cinctura lilium, close-up of the protoconch and early whorls; H= Cinctura lilium connori Petuch and Berschauer, new subspecies, close-up of the protoconch and early whorls; I= Cinctura (Hollisteria) branhamae, close-up of the protoconch and early whorls.

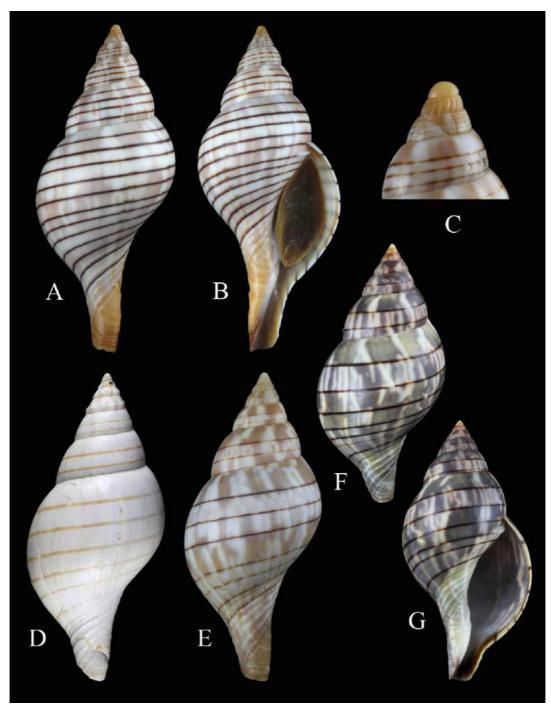


Figure 5. Cinctura species from the Georgian, Floridian, Suwannean, Texan, and Yucatanean Subprovinces of the Carolinian Molluscan Province.

A, B= Cinctura (Hollisteria) branhamae morganae Petuch and Berschauer, new subspecies, holotype length 71.2 mm, LACM 3806, trawled from 250 m depth off Cabo Catoche, Quintana Roo State, Mexico; C= Cinctura (Hollisteria) branhamae morganae holotype, close-up of the protoconch and early whorls; D= Cinctura evergladesensis (Petuch, 1991), length 47 mm, from the Belle Glade Member of the Ionian Formation, Palm Beach County, Florida, late Calabrian Age, Pleistocene. Petuch collection; E= Cinctura lilium (Fischer von Waldheim, 1807), length 59.0 mm, found on the beach, South Padre Island, Texas, (specimen similar to Fischer's holotype; Berschauer collection); F, G= Cinctura hunteria (Perry, 1811), length 64.9 mm, Alligator Point, Franklin County, Florida (collected near the westernmost end of the range for the nominate subspecies; Berschauer collection).