Bulletins of American Paleontology

Published since 1895

Number 401, August 2021

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Lindsey T. Groves and Bernard M. Landau

BULLETINS OF AMERICAN PALEONTOLOGY

Established 1895

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This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Cover image: Cypraeoideans from the Neogene of the Dominican Republic, including (from left to right): *Muracypraea benekeni* (G. B. Sowerby I, 1850) (first and second specimens), *Cyphoma intermedium* (G. B. Sowerby I, 1828), *Jenneria dominicensis* Olsson, 1967, and *Dolichupis islahispaniolae* (Maury, 1917a).

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Lindsey T. Groves* and Bernard M. Landau*

*joint senior authors

DEDICATION

The authors dedicate this volume to Harold and Emily Vokes in recognition of their tremendous contribution to Caribbean paleontology and Emily Vokes's unswerving encouragement and enthusiasm for the Dominican Republic Project in particular.

Harold and Emily Vokes collecting fossils in the Dominican Republic. Left: Harold Vokes at Tulane University (TU) locality 1210, Río Gurabo at Los Quemados, lower Pliocene Gurabo Formation; photograph by Emily Vokes. Right: Emily Vokes at TU locality 1367, roadcut on the road to Los Quemados; photograph by Matthew James.

ISSN 0007-5779

ISBN 978-0-87710-533-6

doi: 10.32857/bap.2021.401.01

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NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC. 25.
THE SUPERFAMILY CYPRAEOIDEA (FAMILIES CYPRAEIDAE, OVULIDAE,
TRIVIIDAE, AND ERATOIDAE) (MOLLUSCA: GASTROPODA)

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ABSTRACT

As part of the ongoing series of taxonomic monographs published by the Paleontological Research Institution covering the Neogene fossils of the Cibao Valley in the northern Dominican Republic, the present study focuses on the marine gastropod superfamily Cypraeoidea. Thirty-one species of cypraeoideans are documented and figured from Miocene and Pliocene strata of the Cibao Valley, Dominican Republic. Taxa include 13 species of Cypraeidae within eight genera, nine species of Ovulidae in four genera, five species of Triviidae in three genera, and four species of Eratoidae in a single genus, for a total of 31 species in 16 genera. Three Cypraeidae are described as new: *Cypraeorbis alisonkayae* n. sp., *Trona colossus* n. sp., and *Zonaria vokesae* n. sp.; two species are left in open taxonomy; and *Cypraea dominicensis* Gabb, 1872, originally described from Dominican Neogene deposits, is here considered a *nomen inquirendum*. One new species of Ovulidae is described as *Cyphoma guraboensis* n. sp., and two species are left in open taxonomy. One species of Triviidae is left in open taxonomy. Two species of Eratoidae are described as new: *Hespererato canae* n. sp. and *Hespererato praeclusa* n. sp.

This diversity is an important increase from the twelve cypraeoidean species previously described from Dominican Republic strata: the cypraeids *Muracypraea henekeni* (G. B. Sowerby I, 1850), *Macrocypraea dominicensis* (Gabb, 1872), *Luria patrespatriae* (Maury, 1917a), *Pseudozonaria raymondrobertsi* (Pilsbry, 1922), and *Zonaria spurcoides* (Gabb, 1872); the ovulids *Neosimnia wisewoodae* (Maury, 1917a), *Jenneria dominicensis* Olsson, 1967, *Jenneria gabbiana* (Guppy, 1876), and *Jenneria pilsbryi* Olsson, 1967; the triviids *Dolichupis islahispaniolae* (Maury, 1917a) and *Niveria sanctidominici* (Maury, 1917a); and the eratoid *Hespererato domingensis* (Maury, 1917a). *Cypraea gurabonis* Ingram, 1939, was also described previously from the Dominican Republic; however, it is based on a poorly preserved specimen and is herein synonymized with *Naria acicularis* (Gmelin, 1791). In addition, there are six extant Caribbean species that are also found in the fossil record: *Naria acicularis* (Gmelin, 1791), *Macrocypraea zebra* (Linnaeus, 1758), and *Luria cinerea* (Gmelin, 1791) in Cypraeidae; *Cyphoma intermedium* (G. B. Sowerby I, 1828), and *Simnialena uniplicata* (G. B. Sowerby I, 1849a) in Ovulidae; and *Pusula pediculus* (Linnaeus, 1758) in Triviidae. Once unreliable historical records are removed or reassessed, 58% of the species are endemic to the Dominican Republic assemblages. Of note is the presence of the ovulid genus *Jenneria*, represented by three species in these Dominican Republic assemblages; this is a paciphile genus today restricted to the Pacific side of its originally wider Neogene distribution on either side of the Isthmus of Panama.

RESUMEN

Este trabajo forma parte de una serie de monografías taxonómicas publicadas por el Paleontological Research Institution sobre los fósiles neógenos del Valle del Cibao en el norte de la República Dominicana. Este presente estudio se centra en la superfamilia de gastrópodos marinos Cypraeoidea. Treintiuna especies de cypraeoideans están documentadas e ilustradas de los estratos Miocenos y Pliocenos del Valle de Cibao, República Dominicana. Estos taxones incluyen 13 especies de Cypraeidae en ocho géneros, nueve especies de Ovulidae en cuatro géneros, cinco especies de Triviidae en tres géneros y cuatro especies de Eratoidae en un solo género; sumando un total de 31 especies en 16 géneros. Tres nuevas especies de Cypraeidae son descritas: *Cypraeorbis alisonkayae* n. sp.,

Trona colossus n. sp. y *Zonaria vokesae* n. sp.; dos especies se dejan en taxonomía abierta; y *Cypraea dominicensis* Gabb, 1872, originalmente descrita del Neogeno de la República Dominicana, es aquí considerado como *nomen inquirendum*. Una nueva especie de Ovulidae es descrita, *Cyphoma guraboensis* n. sp., y dos se dejan en taxonomía abierta. Una especie de Triviidae se dejan en taxonomía abierta. Dos nuevas especies de Eratoidae son descritas: *Hespererato canae* n. sp. and *Hespererato praeclusa* n. sp.

Esto representa un importante incremento en diversidad comparado con las doce especies de cypraeoideans que se conocían hasta ahora en estos yacimientos de la República Dominicana que incluye los cypreidos *Muracypraea henekeni* (G. B. Sowerby I, 1850), *Macrocypraea dominicensis* (Gabb, 1872), *Luria patrespatriae* (Maury, 1917a), *Pseudozonaria raymondrobertsi* (Pilsbry, 1922), y *Zonaria spurcoides* (Gabb, 1872); los ovulidos *Neosimnia wisewoodae* (Maury, 1917a), *Jenneria dominicensis* Olsson, 1967, *Jenneria gabbiana* (Guppy, 1876), y *Jenneria pilsbryi* Olsson, 1967; las trivias *Dolichupis islahispaniolae* (Maury, 1917a) y *Niveria sanctidominici* (Maury, 1917a); y el erato *Hespererato domingensis* (Maury, 1917a). *Cypraea gurabonis* Ingram, 1939, también descrito de la República Dominicana, es basada sobre material en pobre estado de conservación y es aquí considerado como sinonimo de *Naria acicularis* (Gmelin, 1791). Seis de las especies presentes in el Mio-Plioceno de la República Dominicana existen aún en aguas Caribeñas: Cypraeidae: *Naria acicularis* (Gmelin, 1791), *Macrocypraea zebra* (Linnaeus, 1758), *Luria cinerea* (Gmelin, 1791); Ovulidae: *Cyphoma intermedium* (G. B. Sowerby I, 1828), *Simnialena uniplicata* (G. B. Sowerby I, 1849a); and Triviidae: *Pusula pediculus* (Linnaeus, 1758). Una vez reanalizado or rechazado registros históricos poco fiables, 58% de las especies son endémicas al Neogeno de la República Dominicana. Relazamos la presencia del género de ovulido *Jenneria*, representado en la República Dominicana por tres especies, ya que es el único ejemplo en estos yacimientos de un genero pacífico, hoy restringido al lado Pacífico de su más amplia distribución Neógena en ambos lados del Istmo de Panamá.

INTRODUCTION

This study of the marine gastropod superfamily Cypraeoidea is one of a series of taxonomic monographs on Neogene fossils of the Cibao Valley in the northern Dominican Republic (DR). The earliest collections of mollusks from the Dominican Republic were made by Colonel Thomas S. Heneken of the Geological Society of London in the Yaque River section of the island formerly known as Santo Domingo (see Moore, 1850, 1853). In the material was a cowrie specimen appropriately named *Cypraea henekeni* by G. B. Sowerby I in 1850, but misspelled “*henekeri*” in the original publication. Now known as *Muracypraea henekeni*, it has become one of the most well-known species in the Dominican assemblages and is one of eleven cypraeid species in eight genera here recognized in the late Miocene and early Pliocene fossil record of the Cibao Valley. This collection also includes material added later from the Richard Weyl collection (University of Giessen, Germany). This was reported on by Hans D. Plug (1961), who re-described and re-illustrated *C. henekeni*, and selected a lectotype, but no additional cypraeoideans were added. Other cypraeoidean species described from the Dominican Republic include the cypraeids *Macrocypraea dominicensis* (Gabb, 1872), *Luria patrespatriae* (Maury, 1917a), *Pseudozonaria raymondrobertsi* (Pilsbry, 1922), and *Zonaria spurcoides* (Gabb, 1872); the ovulids *Neosimnia wisewoodae* (Maury, 1917a), *Jenneria dominicensis* Olsson, 1967, *Jenneria gabbiana* (Guppy, 1876), and *Jenneria pilsbryi* Olsson, 1967; the triviids *Dolichupis islahispaniolae* (Maury, 1917a) and *Niveria sanctidominici* (Maury, 1917a); and the eratoid *Hespererato domingensis* (Maury, 1917a). Herein, three new species of Cypraeidae, one new species of Ovulidae, and two species of Eratoidae are described.

FOSSIL CYPRAEOIDEANS IN THE DOMINICAN REPUBLIC NEOGENE: HISTORICAL REVIEW

In 1850, George Brettingham Sowerby I described *Cypraea henikeri*, the first fossil cypraeoidean species described from the northern Dominican Republic. The species name was initially misspelled and was later redesignated *C. henekeni* [= *Muracypraea henekeni*] for collector Colonel T. S. Heneken of the Geological Society of London. Extensive geological reconnaissance and surveys of the Dominican Neogene led by William More Gabb from 1869 through 1871 resulted in the descriptions of two cypraeoideans, the new species *Cypraea spurcoides* [= *Zonaria spurcoides*] and *Cypraea dominicensis* [= *Macrocypraea dominicensis*]. R. J. Lechmere Guppy (1876) reidentified one of Gabb's species—misidentified as *Cypraea pustulata* Lightfoot, 1786 by Gabb—and described it as the first ovulid from the DR, *Cypraea gabbiana* [= *Jenneria gabbiana*]. The most comprehensive works on the geology and paleontology of the Dominican Miocene were published by Carlotta Joaquina Maury; these were her monumental 1917a and 1917b papers on the fossils of the Cibao Valley. In them she described *Cypraea patrespatriae* [= *Luria patrespatriae*], *Cypraea noueli* [= juvenile *C. henekeni*], *Ovula wisewoodae* [= *Neosimnia wisewoodae*], *Trivia islahispaniolae* [= *Dolichupis islahispaniolae*], *Trivia sanctidominici* [= *Niveria sanctidominici*], and *Erato domingensis* [= *Hespererato domingensis*]. In a review and revision of the collections made by Gabb, Henry A. Pilsbry (1922) described *Cypraea raymondrobertsi* [= *Pseudozonaria raymondrobertsi*] and *Cypraea campbelliana* [= *Luria cinerea* (Gmelin, 1791)]. F. A. Schilder (1932a) reidentified one of the species figured by Woodring (1928) as *Pusula* (*Niveria*) *suffusa jamaicensis* [= *Niveria jamaicensis* (Schilder, 1932a)]. Hans D. Pflug (1961) illustrated and updated the taxonomy of many of G. B. Sowerby

Text-fig. 1. Locality map for the sections measured and described by Saunders et al. (1986). 1. Río Cana; 2. Río Gurabo; 3. Río Mao; 4. Río Amina; 5. City of Santiago; 6. Arroyo Zalaya; 7. Río Yaque del Norte; 8. Arroyo Puñal; 9. Río Verde (adapted from Jung, 1986, text-fig. 1).

I's species and proposed a lectotype for *Cypraea* (*Muracypraea*) *henekeni*. In a review of the ovulid genus *Jenneria*, Axel A. Olsson (1967) described *Jenneria dominicensis* and *Jenneria pilsbryi* from the Dominican Republic.

The DR Neogene cypraeoidean fauna includes three extant cypraeid species, *Naria acicularis* (Gmelin, 1791), *Macrocypraea zebra* (Linnaeus, 1758), and *Luria cinerea* (Gmelin, 1791); two extant ovulids, *Cyphoma intermedium* (G. B. Sowerby I, 1828) and *Simnia uniplicata* (G. B. Sowerby II, 1849a); and one extant triviid species, *Pusula pediculus* (Linnaeus, 1758). All live in the DR today. New species described herein include three cypraeids (*Cypraeorbis alisonkayae*, *Trona colossus*, and *Zonaria vokesae*), one ovulid (*Cyphoma guraboensis*) and two eratoids (*Hespererato canae* and *Hespererato praeclusa*).

MATERIALS AND METHODS

In the mid-1970's, a team led by Peter Jung (Switzerland), John Saunders (England), and Bernard Biju-Duval (France) began the Dominican Republic Project (DRP) to resample fossil invertebrates in the Cibao Valley (see Saunders et al., 1986; Text-fig. 1). Their goals were to determine the precise ages of the strata, collect more samples using modern sampling methods, and record locality data in great detail. Samples were deposited at the Naturhistorisches Museum in Basel (NMB), Switzerland to await analysis by worldwide

experts. In the late 1980's Dr. E. Alison Kay (University of Hawai'i, Manoa) began gathering information and examining materials collected by the DRP held at NMB to monograph the Cypraeidae of the northern Dominican Republic. Unfortunately, she passed away in 2008 before her manuscript could be completed. In 2010, one of us (LG) was contacted by Regina Kawamoto of the Bernice P. Bishop Museum, Honolulu, Hawai'i and the University of Hawai'i, Manoa, asking if Alison's manuscript could be completed. It wasn't until 2015 that it was determined that the project could indeed be completed. BL examined the cypraeoidean materials deposited previously at NMB and determined that they were insufficient to complete a survey of the DR assemblage. He proceeded to collect specimens in a better state of preservation during his own field work in the Dominican Republic from 1999–2019. That material is described herein and deposited in the Naturhistorisches Museum in Vienna, Austria (NHMW). The Panama Paleontology Project (PPP) collection in NMB and the BL collection in NHMW were further supplemented by examination of the cypraeids collected by Emily and Harold Vokes and now housed at the Paleontological Research Institution (PRI) in Ithaca, New York, USA. Access to this collection was facilitated by Jonathan R. Hendricks, Director of Science Communication, Leslie L. Skibinski, Collections Manager, and Vicky Wang, Collections Assistant, who located the material and provided

Table 1. Distribution of the cypraeid gastropods found in the Dominican Republic assemblages within the Dominican formations, and stratigraphic distribution. (Table 1 continues on next page.)

Species	Dominican Republic Formations			Stratigraphical distribution								
	Baitoa	Cercado	Gurabo	Miocene			Pliocene		Pleistocene		Hol	
				Lower	Middle	Upper	Lower	Upper	Lower	Upper		
CYPRAEIDAE Rafinesque, 1815												
<i>Naria acicularis</i> (Gmelin, 1791)		●	●						■	■		
<i>Cypraeorbis alisonkayae</i> n. sp.		●										
<i>Muracypraea henekeni</i> (G.B. Sowerby I, 1850)		●	●									
<i>Macrocypraea zebra</i> (Linnaeus, 1758)		●	●									
<i>Macrocypraea dominicensis</i> (Gabb, 1872)				nomen inquirendum								
<i>Luria cinerea</i> (Gmelin, 1791)	●	●	●						■	■		
<i>Luria patrespatriae</i> (Maury, 1917a)	●	●	●									
<i>Trona colossus</i> n. sp.	●											
<i>Pseudozonaria raymondrobertsi</i> (Pilsbry 1922)	●	●	●									
<i>Pseudozonaria</i> sp.			●									
<i>Zonaria spurcoides</i> (Gabb, 1872)	●	●	●									
<i>Zonaria</i> cf. <i>pseudotumulus</i> Landau and Groves, 2011	●											
<i>Zonaria vokesae</i> n. sp.	●											
OVULIDAE Fleming, 1822												
<i>Cyphoma guraboensis</i> n. sp.			●									
<i>Cyphoma intermedium</i> (G.B. Sowerby I, 1828)		●	●									
<i>Cyphoma</i> sp.		●	●									
<i>Neosimnia wisewoodae</i> (Maury, 1917a)		●	●									
<i>Neosimnia</i> sp.		●	●									
<i>Simnialena uniplicata</i> (G.B. Sowerby II, 1849a)			●									
<i>Jenneria dominicensis</i> Olsson, 1967	●											
<i>Jenneria gabbiana</i> (Guppy, 1876)			●									
<i>Jenneria pilsbryi</i> Olsson, 1967		●	●									

high-quality images of these shells during these difficult times when travel is restricted due to Coronavirus.

For the sake of coherence, TU (Tulane University, localities for the Vokes collection) and NMB locality numbers have been allocated to the material collected by BL and deposited in the NHMW. Complete locality data can be found in Saunders et al. (1986: appendix 2 and 3, pp. 41–64 for NMB localities; appendix 4, pp. 64–67 for TU localities).

Numerous historical works dealing with tropical American cypraeids consist of records or lists of species without illustrations and with imprecise or outdated stratigraphic data (e.g., F. A. Schilder, 1939a; Ingram, 1947c; M. Schilder and F. A. Schilder, 1971). These have been included in the

distribution for each species in square brackets, [], but excluded from the stratigraphic distribution chart (Table 1), which includes only records that the authors are confident belong to that species and originate from localities that can be dated stratigraphically. The formation ages determined by Landau et al. (2012) are followed throughout.

RESULTS

BIOSTRATIGRAPHY

Based on early observations by Moore (1850, 1853) and G. B. Sowerby I (1850), Maury (1918) noted a resemblance between the Dominican Republic assemblages and those

Table 1, continued. Distribution of the cypraeid gastropods found in the Dominican Republic assemblages within the Dominican formations, and stratigraphic distribution. (Table 1 begins on previous page.)

Species	Dominican Republic Formations			Stratigraphical distribution								
	Baitoa	Cercado	Gurabo	Miocene			Pliocene		Pleistocene		Hol	
				Lower	Middle	Upper	Lower	Upper	Lower	Upper		
TRIVIIDAE Troschel, 1863												
<i>Dolichupis islahispaniolae</i> (Maury, 1917a)		●	●		■			■				
<i>Niveria jamaicensis</i> Schilder, 1932a		●			■			■				
<i>Niveria sanctidominici</i> (Maury, 1917a)		●	●			■		■				
<i>Niveria</i> sp.			●				■		■			
<i>Pusula pediculus</i> (Linnaeus, 1758)		●	●			■						
ERATOIDAE Gill, 1871												
<i>Hespererato canae</i> n. sp.		●	●			■		■				
<i>Hespererato chipolana</i> (Maury, 1910)		●		■		■	■	■				
<i>Hespererato domingensis</i> (Maury, 1917a)		●	●			■		■				
<i>Hespererato praeclusa</i> n. sp.	●			■		■						

of Dax, Nouvelle-Aquitaine, France, and all these authors considered the Dominican assemblages to be of Miocene age. Gabb (1872) agreed with their age determination, but considered all the Yaqui Valley deposits to represent a single formation composed of upper Miocene fossiliferous beds. This is reflected in the imprecise records Gabb kept of his collecting localities, most of which are simply labeled “Miocene, Santo Domingo” (which is now the Dominican Republic).

Maury (1918: p. 225) noted, “Our 1916 expedition was undertaken with the express object of determining the exact stratigraphic sequence.” She concluded that three formations were represented in the Dominican assemblages and named them after their characteristic fossils; from stratigraphically oldest to youngest, they are the *Orthaulax inornatus* horizon ($\approx$ Rupelian of Europe and upper Oligocene *Silex* beds of Florida), the *Aphera islacolonis* horizon ($\approx$ upper Aquitanian of Europe and lower Miocene, Chipola River, Florida), and the *Sconsia laevigata* horizon ($\approx$ Burdigalian of Europe and middle Miocene Alum Bluff beds, Florida). Maury (1919) formally named the Cercado Formation (= the *Aphera islacolonis* horizon) and the Gurabo Formation (= the *Sconsia laevigata* horizon). C. W. Cooke (1920) described the Baitoa Formation for outcrops downstream from Baitoa on the Río Yaque del Norte. Bermudez (1949) described the Mao Formation, which included the Mao Adentro Limestone and Mao (=Valverde) Clay of Cooke (1920).

In their landmark works, Saunders et al. (1982, 1986) published a detailed biostratigraphic framework, measured sections, and macrofossil and microfossil analysis from the study area. According to them, the oldest formation is the

Baitoa Formation, which is recognized only from the type area and dated as late early to early middle Miocene based on ostracod and molluscan evidence; this is followed by the Cercado Formation, dated as late Miocene (NN11 zone) based on calcareous nannofossils, then by the Gurabo Formation, dated as latest Miocene to early Pliocene (zones NN11 to NN13) based on calcareous nannofossils and planktonic foraminifera; lastly, the Mao Formation is dated as late early Pliocene to middle Pliocene (upper part *Globorotalia margaritae* Zone to upper part *Globorotalia miocenica* Zone). These ages were reviewed by McNeill et al. (2012), who provided better resolution for the ages: the Cercado Formation, late Miocene, Messinian (6.6–6.0 Ma); the Gurabo Formation, early Pliocene, early Zanclean (ca. 5.8–4.0 Ma); and the Mao Formation, Pliocene, late Zanclean to early Piacenzian (3.9–3.5 Ma) (see MacNeill et al., 2012: fig. 4). Hendy et al. (2015, tables 3, 5) provided an age of 17.5–14.5 Ma for the Baitoa Formation). These age assignments are followed in this work. For more details, see Saunders et al. (1986). Cypraeoideans included in this work were found in all formations except the Mao Formation.

In the Dominican Republic assemblages, five species—*Trona colossus*, *Zonaria* cf. *pseudotumulus* Landau and Groves, 2011, *Zonaria vokesae*, *Jenneria dominicensis*, and *Hespererato praeclusa*—are restricted to the lower middle Miocene Baitoa Formation, found only at the Río Yaque del Norte. *Cypraeorbis alisonkayae*, *Cyphoma* sp. and *Hespererato domingensis* are found only in the upper Miocene Cercado Formation. *Pseudozonaria* sp., *Jenneria gabbiana*, *Jenneria pilsbryi*, and *Niveria* sp. are found only in the lower Pliocene

Table 2. Cypraeidae described and/or recorded from the Dominican Republic. Numbers of specimens of 13 taxa of cypraeid gastropods collected in the Cibao Valley for this study.

Taxon	Current Genus	No. of Specimens
<i>Cypraea acicularis</i> (Gmelin, 1791)	<i>Naria</i>	200+
<i>Cypraea gurabonis</i> Ingram, 1939b	= <i>Naria acicularis</i>	
<i>Cypraeorbis alisonkayae</i> n. sp.		32
<i>Cypraea henekeni</i> G. B. Sowerby I, 1850	<i>Muracypraea</i>	157
<i>Cypraea henekeni potreronis</i> Ingram, 1939b	= <i>Muracypraea henekeni</i>	
<i>Cypraea noueli</i> Maury, 1917a	= <i>Muracypraea henekeni</i> (juvenile)	
<i>Cypraea zebra</i> Linnaeus, 1758	<i>Macrocypraea</i>	9
<i>Cypraea dominicensis</i> Gabb, 1872 (nom. inq.)	<i>Macrocypraea</i>	
<i>Cypraea cinerea</i> Gmelin, 1791	<i>Luria</i>	22
<i>Cypraea campbelliana</i> Pilsbry, 1922	= <i>Luria campbelliana</i>	
<i>Cypraea patrespatriae</i> Maury, 1917a	<i>Luria</i>	47
<i>Trona colossus</i> n. sp.		1
<i>Cypraea raymondrobertsi</i> Pilsbry, 1922	<i>Pseudozonaria</i>	63
<i>Pseudozonaria</i> sp.		1
<i>Cypraea spurcoides</i> Gabb, 1872	<i>Zonaria</i>	70
<i>Zonaria</i> cf. <i>pseudotumulus</i> Landau and Groves, 2011		1
<i>Zonaria vokesae</i> n. sp.		1

Gurabo Formation (Table 1). No cypraeids were present in the collection consulted from upper lower Pliocene to middle Pliocene beds of the Mao Formation. Six species still occur in Caribbean waters: *Naria acicularis*, *Macrocypraea zebra*, *Luria cinerea*, *Cyphoma intermedium*, *Simnialena uniplicata*, and *Pusula pediculus*.

Cypraeids are relatively uncommon in the Dominican Republic assemblages, with the exception of one locality on Río Cana (locality NMB 16844), where *Naria acicularis* is unusually abundant. Undoubtedly some degree of taphonomic bias is involved in the total numbers given (Table 2), and robust species such as *Muracypraea henekeni* and *Pseudozonaria raymondrobertsi* are better represented than thin-shelled species such as *Luria patrespatriae* (Maury 1917a) and *Macrocypraea zebra*, which are often found crushed and cannot be collected (BL, personal observation). Ovulids are uncommon in all the Dominican deposits. Triviids and eratooids are only abundant at the same Río Cana deposit discussed above (locality NMB 16844); elsewhere they are extremely uncommon.

PALEOECOLOGY

Members of the family Cypraeidae inhabit intertidal to tropical bathyal coral reefs and sand bottoms where they graze the substrate; some are generalists, others specialists on coralline algae or sponges. Depth and bottom condition records for living relatives of the species reported here are provided in the

systematic section of this paper. Occurrence and abundance of cypraeoideans are influenced by paleoenvironmental factors in the northern Dominican Republic; they are primarily recorded from two paleoenvironments, very shallow marine (coral/algal reef at 0–20 m) and shallow marine (sand flats at 10–50 m) areas, as documented in Saunders et al. (1982, 1986), van den Bold (1988), and Anderson (1994). Ovulids inhabit tropical to temperate oceans and are commensal or parasitic on soft corals, gorgonians, and other sessile anthozoans. Triviids and eratooids are also tropical to temperate dwellers and feed on colonial tunicates and ascidians.

PALEOBIOGEOGRAPHY

Herein, eighteen of the 31 confirmed and/or newly described species included in this study (= 58%) are endemic to the Dominican Republic: *Cypraeorbis alisonkayae*, *Muracypraea henekeni*, *Luria patrespatriae*, *Trona colossus*, *Pseudozonaria* sp., *Zonaria vokesae*, *Cyphoma guraboensis*, *Cyphoma* sp., *Neosimnia wisewoodae*, *Neosimnia* sp., *Jenneria dominicensis*, *Jenneria gabbiana*, *Jenneria pilsbryi*, *Niveria sanctidominici* (Maury, 1917a), *Niveria* sp., *Hespererato canae*, *Hespererato domingensis*, and *Hespererato praeclusa*. Some of these species, such as *M. henekeni*, have been recorded from other Caribbean Neogene assemblages, but many of these records are based on incorrect or unreliable identifications. None of the six extant species are endemic. At the generic level, the cypraeids *Macrocypraea* and *Pseudozonaria*, the ovulids

Cyphoma and *Simnialena*, the triviid *Pusula*, and the eratoid *Hespererato* are currently extant in the Caribbean and eastern Pacific. The living cypraeid genus *Muracypraea* is restricted to the Caribbean but also has an extensive fossil record in the eastern Pacific. The cypraeid genera *Naria*, *Cypraeorbis*, *Luria*, *Trona*, and *Zonaria*, the ovulid genera *Neosimnia* and *Jenneria*, the triviid genera *Trivia* and *Niveria*, and the eratoid genus *Hespererato* all originated in the Paleogene and/or Neogene of Europe and/or the Mediterranean region.

Of note is the presence of the ovulid genus *Jenneria*, represented by three species in the Dominican Republic assemblages. This genus is an example of a paciphile genus; that is a genus that was distributed on both sides of the Isthmus of Panama prior to the closure of the Central American Seaway (CAS), but subsequent to the closure became restricted to the Pacific side of its originally wider distribution (Landau et al., 2009). Indeed, *Jenneria* is one of the last paciphiles to disappear from the Caribbean at the end of the late Pleistocene. It is therefore part of the small stock of Gatunian Neogene Paciphilic Molluscan Unit 2 (GNPMU2) paciphiles (Landau et al., 2009).

RELATIONSHIPS OF THE DOMINICAN REPUBLIC CYPRAEIDS

Of the eight cypraeid genera represented in the northern Dominican Republic fauna, only four (*Naria*, *Muracypraea*, *Macrocypraea*, and *Luria*) are extant in the Caribbean, and only three (*Naria*, *Macrocypraea* and *Luria*) are extant in the Pacific Panamic Province. Cypraeid affinities to other Miocene through Pleistocene faunas throughout the Caribbean include: two species in the Pliocene Bowden Member of the Layton Formation of Jamaica (Woodring, 1928; F. A. Schilder, 1939a); two species in the Neogene to Pleistocene deposits of the Limon Basin, Costa Rica (Dall 1890; Olsson 1922; Robinson, 1991); and two species in the Miocene Chipola Formation of Florida (Dolin, 1991). Moore (1850), introducing Sowerby's molluscan notes, remarked on the close relationships between these Dominican mollusks and those in Europe. Guppy (1874) also stressed a close alliance between the faunas of the Caribbean Miocene and Pliocene and the European beds of Malta, Bordeaux, Dax, Vienna, and Piedmont and living faunas of eastern Asia. He argued for a migration eastward across the Atlantic, a position strongly supported by Forbes (1844). Maury (1917b, 1918) remarked on resemblances between the Santo Domingo (now, Dominican Republic) faunas and those of the Pliocene Bowden Member of the Layton Formation of Jamaica (see James-Williamson and Mitchell, 2012; Locatelli et al., 2018), the Miocene of Trinidad (unspecified), the Cumaná Formation of Venezuela, the Gatun beds of Panama, and the Chipola and *Silex* beds of Florida. She also noted Vaughan's inferred "interoceanic connection, which permitted the Atlantic fauna to extend into the Gulf of California ... probably in the region of the Isthmus of Tehuantepec, or farther southeast"

(Vaughan, 1917, p. 369). Vermeij and Rosenberg (1993: p. 187) estimated that at least 28 species of mollusks have dispersed eastward across the Atlantic but no cypraeoideans were noted.

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA
BPBM	Bernice P. Bishop Museum, Honolulu, Hawai'i, USA
CASIZ	California Academy of Sciences, Invertebrate Zoology, San Francisco, California, USA
CASG	California Academy of Sciences, Geology, San Francisco, California, USA
CPP	California Polytechnic University, Pomona, California, USA
CSUN	California State University, Northridge, California, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
HNC	Haus der Natur, Cismar, Germany
LACM	Natural History Museum of Los Angeles County, Malacology Department, Los Angeles, California, USA
LACMIP	Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles, California, USA
NHMK	The Natural History Museum, London, United Kingdom
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
NMB	Naturhistorisches Museum Basel, Switzerland
PRI	Paleontological Research Institution, Ithaca, New York, USA
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, USA
TU	Tulane University, New Orleans, Louisiana, USA [collections now at PRI and USNM]
UCD	University of California, Davis, USA
UCMP	University of California, Museum of Paleontology, Berkeley, California, USA
UHI	University of Hawai'i, Mānoa, Honolulu, Hawai'i, USA
USC	University of Southern California, Los Angeles, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZSM	Zoologische Staatssammlung München, Germany

SYSTEMATIC PALEONTOLOGY

Phylum **MOLLUSCA** Cuvier, 1795

Class **GASTROPODA** Cuvier, 1795

Subclass **CAENOGASTROPODA** Cox, 1960

Cohort **SORBEOCONCHA** Ponder and Lindberg, 1997

Subcohort **HYPGASTROPODA** Ponder and Lindberg, 1997

Superorder **LATROGASTROPODA** Riedel, 2000

Superfamily **CYPRAEOIDEA** Rafinesque, 1815

Cypraeoidea Rafinesque, 1815: pp. 145, 146 (as subfamily Cypridia).

Description.—Shells of large to small size, shape globular or elongate, shell glossy, mostly smooth and bilaterally symmetrical. Aperture long, usually narrow, nearly straight, in most species lined with denticles ('teeth') and usually extending the entire length of the ventral surface. Terminal anterior and posterior canals present. Periostracum lacking. Mantle bilobed, thin, contractile. Radula taenioglossate. Operculum lacking in adults but present in veliger specimens (F. Lorenz, pers. comm., 2020). Protoconch cancellate, concealed in mature shells.

Remarks.—M. Schilder and F. A. Schilder (1971) developed a classification scheme based on radula, osphradium, and shell characteristics, much of which was published in F. A. Schilder (1936). Bouchet and Rocroi (2005) and Ponder and Lindberg (2020) separated the superfamilies Cypraeoidea (Cypraeidae and Ovulidae) from Velutonoidea (Eratoidae and Triviidae). However, herein higher-level systematics above superfamily follow those of Bouchet et al. (2017).

Family **CYPRAEIDAE** Rafinesque, 1815

Cypraeidae Rafinesque, 1815: pp. 145, 146 (as subfamily Cypridia).

Description.—Shells of large to small size, usually smooth, pear-shaped, elongate, or globular; spotted, sometimes highly colorful, appearing polished; covered by bilobed mantle with papillae. Aperture narrow, usually with denticles ('teeth') lining labral and columellar margins. Juvenile shell (= bulla stage) thin with wide aperture without denticles. Spire callused over in mature shells. Operculum lacking in adults but present in veliger specimens (F. Lorenz, pers. comm., 2020), radula taenioglossate with central tooth (rachidian), three marginal teeth on either side.

Remarks.—These are the true cowries. The earliest cypraeid species, *Palaeocypraea tithonica* (Stefano, 1882) and *Palaeocypraea gemmellaroi* (Stefano, 1882), appeared in Upper Jurassic strata (Tithonian) of Sicily from apparent stromboidean ancestors (Groves, 1994). They had a limited worldwide distribution in the Early Cretaceous (Barremian and Albian) of western North America, France, and Brazil, and became widespread in the Late Cretaceous (Cenomanian through Maastrichtian) of North America, Europe, North Africa, India, Pakistan, South America, South Africa, and Australia. Over 400 fossil and Recent species are currently recognized (Lorenz, 2017). Cowries were traditionally classified primarily on the basis of conchological characters until the mid-nineteenth century when Troschel (1863) devised a classification scheme based primarily on radular characters. F. A. Schilder (1932a) and M. Schilder and F. A. Schilder (1971) utilized radular and other anatomical characters in their definitive accounts of the family. A recent summary of the radula of 200 species by Bradner and Kay (1996) recognized seven of the thirteen Schilderian genera.

Fossil cypraeids are a notoriously difficult group to work on, especially as the vast majority of specimens have lost their color patterns. Cypraeid systematics has been greatly enhanced by the works of Meyer (2003, 2004), in particular his molecular database for the family. The phylogenetic implications of these data outlined by Meyer (2004) and the systematic arrangement presented by López Soriano (2006) based on Meyer's work are loosely followed here. Higher-level systematics above superfamily rank follow those of Bouchet et al. (2017) for the most part. Darragh (2011) and Lorenz (2017) are followed for lower systematics.

Two major taxonomic studies have been undertaken in recent years on the tropical American Neogene cypraeid assemblages. Dolin (1991) revised the Cypraeoidea from the lower Miocene Chipola Formation of northern Florida and Landau and Groves (2011) revised the cypraeids from the roughly contemporaneous Cantaure Formation of Venezuela.

The shell formula proposed by F. A. Schilder (1935: p. 327) has not been given for each species in this work. This formula is derived from measurements taken from all available fully mature and normally formed specimens. It consists of the following elements:

[L (W-H) LT: CT], where:

L = average length in mm

W = average width/length ratio in percent

H = average height/length ratio in percent

LT = normalized number of labral teeth

CT = normalized number of columellar teeth

The normalized number of teeth (T) in relation to a shell of 25 mm length is calculated as follows:

$$T = 7 + [(c-7) \times \sqrt{(25/L)}], \text{ where:}$$

T: normalized number of teeth.

c: teeth counted.

L: length (in mm).

Schilder's shell formula is useful to highlight differences and similarities between species, but should not be used on its own to distinguish between species. Herein, the authors are not convinced the shell formula is useful enough for specific differentiations.

Most living species are generalized omnivores, with a few more specialized genera, such as *Zoila*, feeding on sponges (Taylor and Walls, 1975; Wilson and Clarkson, 2004). The radula is taenioglossate (Ponder and Lindberg, 2020), which separates the Cypraeidae from the other allied groups (Lorenz and Fehse, 2009). Synonymies and chresonymies cite fossil and Recent accounts of each species.

Subfamily **EROSARIINAE** F. A. Schilder, 1924

Erosariinae F. A. Schilder, 1924: p. 182.

Genus *Naria* Broderip, 1837

Naria Broderip, 1837: p. 256. Type species (by original designation): *Cypraea (Naria) irrorata* (Gray, 1828), Recent, southwest Pacific.

Erosaria Troschel, 1863: pp. 205, 210. Type species (by subsequent designation of Jousseaume, 1884a: p. 96): *Cypraea erosa* Linnaeus, 1758, Recent, Indo-Pacific.

Ocellaria Weinkauff, 1881a: p. 148. Type species (by original designation): *Cypraea spurca* Linnaeus, 1758, Recent, Mediterranean Sea and western Africa, not *Ocellaria* Ramond, 1801.

Paulonaria Iredale, 1930: p. 83. Type species (by original designation): *Cypraea beekii* Gaskoin, 1836, Recent, Indo-Pacific.

Albacypraea Steadman and Cotton, 1946: p. 508. Type species (by original designation): *Cypraea eburnea* Barnes, 1824, Recent, southwest Pacific.

Original description.—"Front of columella narrow dilated into a sharp-toothed ridge; shell smooth. Shell ovate, purplish, yellow dotted; base white; teeth large." (Broderip, 1837: p. 256).

Revised description.—"Small to medium sized, often solid shells with paler lacunae and often ocellated spots, occasionally all white. Usually with distinct marginal pitting along the labrum and above the extremities. Teeth and terminal ridge angular." (Lorenz, 2017: p. 237).

Remarks.—Described as a subgenus by Broderip (1837). Lorenz (2017: p. 237) noted that this genus is better known by the name *Erosaria* and further noted that the conchologically extreme type species, *Naria irrorata* (Gray, 1828), and all species formerly assigned to *Erosaria* now belong in *Naria* according to molecular analysis. The conchological and malacological communities have readily accepted this reassignment and no case has been submitted to the International Commission on Zoological Nomenclature for conservation of *Erosaria*. Several groups within *Naria* were recognized by Lorenz (2017: p. 237) based on molecular data, and *Naria acicularis* is included within his *Paulonaria* group. These species are small to medium in size and elongate to oval in shape. They have fine columellar teeth sometimes connected by a ridge of callus anteriorly.

Geographic range.—Pacific Panamic Province to the Indo-Pacific, Caribbean, West Africa and the Mediterranean.

Stratigraphic range.—Oligocene to Recent.

Naria acicularis (Gmelin, 1791)

Text-figs. 2.1–2.19, 3.1–3.4

Cypraea spurca Linnaeus, 1758: p. 724.

Cypraea acicularis Gmelin, 1791: p. 3421.

Cypraea spurca Linnaeus. Gabb, 1872: p. 235.

Cypraea near *spurca* Linnaeus. Dall, 1903: p. 1584.

Cypraea acicularis Gmelin. Hidalgo, 1906–1907: pp. 245–247.

Cypraea spurca Linnaeus. Maury, 1917a: p. 115, pl. 19, fig. 6.

Cypraea spurca Linnaeus. Maury, 1917b: pp. 10, 28.

Cypraea (Erosaria) spurca Linnaeus. Vredenburg, 1920: p. 112.

Cypraea spurca Linnaeus. Maury, 1922: p. 113.

Cypraea spurca Linnaeus. Pilsbry, 1922: p. 365.

Cypraea spurca Linnaeus. Vaughan and Woodring, 1921: pp. 125, 141.

Erosaria acicularis (Gmelin). F. A. Schilder, 1928: pp. 283, 284.

Cypraea flaveola Linnaeus. Rutten, 1931: p. 664.

Erosaria (Erosaria) acicularis (Gmelin). F. A. Schilder, 1932a: p. 164.

Cypraea spurca Linnaeus. Johnson, 1934: p. 421, pl. 140.

Erosaria (Ravitrona) spurca acicularis (Gmelin). F. A. Schilder and M. Schilder, 1938–1939: pp. 133, 198.

Erosaria (Ravitrona) spurca acicularis (Gmelin). F. A. Schilder, 1939a: pp. 6, 9, 21.

Cypraea spurca Linnaeus. Ingram, 1939b: pp. 336, 337, pl. 22, fig. 2.

Cypraea gurabonis Ingram, 1939b: pp. 329, 330, pl. 22, figs. 6, 7.

Cypraea spurca Linnaeus. Patterson, 1944: p. 38.

Cypraea spurca flaveola Linnaeus. Jaume, 1946: p. 105.

Cypraea spurca Linnaeus. Ingram, 1947a: pp. 59–61, 80, 81, pl. 7, fig. 8.

Cypraea spurca Linnaeus. Ingram, 1947c: p. 149.

Cypraea spurca Linnaeus. Ingram, 1951: pp. 159–161, pl. 1, figs. 3, 4.

Cypraea spurca Linnaeus. Ramírez, 1956: pp. 17, 25.

Text-figs. 3.1–3.4. Holotype, *Naria acicularis* (Gmelin, 1791) specimen formerly assigned to *Cypraea gurabonis* Ingram, 1939a, USNM 483461, length 17 mm, width 11 mm, height 9.25 mm; locality USNM 8737, District of Monte Cristi, Gurabo River about 5 miles above Gurabo Adentro at base of coral limestone and above conglomerate; ?Gurabo Formation, lower Pliocene.

Ravitriona spurca acicularis (Gmelin). Allan, 1956: p. 95.
Cypraea (Erosaria) spurca acicularis Gmelin. Abbott, 1958: p. 48.
Cypraea spurca acicularis (Gmelin). Nowell-Usticke, 1959: p. 53.
Cypraea spurca acicularis (Gmelin). Warmke and Abbott, 1961: p. 92, pl. 16, fig. 1.
Cypraea spurca acicularis (Gmelin). Weber, 1961: p. 56.
Cypraea (Erosaria) spurca acicularis Gmelin. Weisbord, 1962: pp. 16, 22, 232–234, pl. 21, figs. 15, 16.
Cypraea spurca acicularis (Gmelin). Merrill and Petit, 1965: p. 62.
Erosaria (spurca) acicularis [sic] (Gmelin). F. A. Schilder, 1966b: p. 212.
Cypraea spurca Linnaeus. Ranson, 1967: p. 120.
Cypraea spurca acicularis (Gmelin). Richards et al., 1969: p. 6.
Cypraea acicularis Linnaeus. Burgess, 1970: pp. 156, 157, pl. 10, fig. L (as *Cypraea acicularis*).
Cypraea spurca Linnaeus. Vilas and Vilas, 1970: pp. 71, 72, pl. 9, fig. 4.
Cypraea spurca acicularis Gmelin. Kaufman and Götting, 1970: fig. 67.
Pustularia (Pustularia) gurabonis (Ingram). M. Schilder and F. A. Schilder, 1971: p. 57.
Erosaria (Erosaria) spurca acicularis (Gmelin). M. Schilder and F. A. Schilder, 1971: pp. 62, 91.
Cypraea spurca acicularis Gmelin. Abbott, 1974: p. 150, color pl. 5, fig. 1643.
Cypraea spurca Linnaeus. Briton, 1975: p. 36.
Cypraea spurca Linnaeus. Taylor and Walls, 1975: p. 182, 2 unnumbered figs.
Cypraea spurca Linnaeus. Lozet and Pétron, 1977: p. 50, fig. 38.
Cypraea spurca Linnaeus. Fast, 1978: p. 83.
Cypraea spurca Linnaeus. Walls, 1979: p. 182, 2 unnumbered figs.

Erosaria (Erosaria) acicularis (Gmelin). Raybaudi, 1982: pp. 11–14, figs. A–F, 1 unnumbered fig.
Cypraea (Erosaria) spurca acicularis Gmelin. H. E. Vokes and E. H. Vokes, 1983: p. 21, pl. 8, fig. 12.
Cypraea spurca acicularis Gmelin. Bandel, 1984: p. 84, fig. 139, pl. 7, fig. 5 (radula).
Cypraea spurca Linnaeus. Burgess, 1985: pp. 218, 219, 2 unnumbered figs.
Cypraea spurca acicularis Gmelin. Jensen et al., 1986: p. 421, pl. 140.
Cypraea spurca Linnaeus. Bertsch, 1987: p. 25.
Cypraea (Erosaria) spurca acicularis Gmelin. Robinson, 1991, p. 255, pl. 10, fig. 6.
Naria (Erosaria) acicularis (Gmelin). Cossignani and Passamonti, 1991: pp. 20, 25.
Erosaria acicularis acicularis (Gmelin). Lorenz and Hubert, 1993: p. 197, pl. 85, figs. 17–27.
Cypraea spurca acicularis Gmelin. Díaz and Puyana, 1994: p. 166, fig. 613.
Cypraea (Erosaria) spurca acicularis Gmelin. Espinosa et al., 1988: p. 20.
Cypraea spurca acicularis Gmelin. Carlos and Joaquín, 1998: p. 126.
Erosaria acicularis acicularis (Gmelin). Lorenz and Hubert, 2000: p. 197, pl. 85, figs. 17–27.
Cypraea (Erosaria) spurca acicularis Gmelin. Espinosa and Ortea, 2001: p. 17.
Cypraea (Erosaria) spurca acicularis Gmelin. Macsotay and Campos Villaroel, 2001: p. 57.
Erosaria acicularis (Gmelin). Redfern, 2001: p. 51, pl. 26, fig. 218.
Erosaria acicularis (Gmelin). Köhler, 2003: p. 36.

Text-fig. 2. *Naria acicularis* (Gmelin, 1791). 1–5, NHMW 2017/0124/0042, length 20.0 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 6–10, NHMW 2017/0124/0069, length 17.8 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 11–13, NHMW 2017/0124/0063, length 18.1 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 14, 15, NHMW 2017/0124/0068, length 18.5 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 16–19, NHMW 2017/0124/0075, length 17.5 mm; locality TU 1442–1444, López Section, Río Yaque del Norte, Dominican Republic, unnamed formation of Cercado or Gurabo age, upper Miocene to lower Pliocene. 20–23, holotype, *Erosaria aliena* F. A. Schilder, 1939a, NMB H 11268 (NMB coll.), length 15 mm, greatest diameter 9.7 mm; Matura Bay, Trinidad, Matura shell bed, Talparo Formation, Pleistocene.

Cypraea spurca Linnaeus. Absalão et al., 2006: p. 236.
Cypraea acicularis Gmelin. Absalão et al., 2006: p. 236.
Erosaria acicularis (Gmelin). Simone and Gonçalves, 2006: pp. 13, 14, fig. 1.
Cypraea acicularis Gmelin. Rios, 2009: p. 132, fig. 313.
Erosaria acicularis (Gmelin). Jensen and Pearce, 2009: pp. 61, 62.
Erosaria acicularis (Gmelin). Lee, 2009: p. 77.
Erosaria acicularis (Gmelin). Massemin et al., 2009: p. 99, 2 unnumbered figs.
Erosaria acicularis (Gmelin). Tunnell et al., 2010: p. 172, unnumbered fig.
Erosaria acicularis (Gmelin). Brunner and Brunner, 2011: p. 8.
Erosaria acicularis (Gmelin). Daccarett and Bossio, 2011: p. 65, fig. 177.
Erosaria acicularis (Gmelin). Petuch and Sargent, 2011: pp. 47, 80, 101, 135, fig. 3.2D.
Erosaria acicularis (Gmelin). Zhang, 2011: p. 89, fig. 235.
Erosaria acicularis (Gmelin). Simone, 2011: pp. 166, 215.
Erosaria acicularis (Gmelin). Petuch, 2013: pp. 26, 27, 36, fig. 2.8A.
Erosaria acicularis (Gmelin). Redfern, 2013: p. 42, fig. 118.
Erosaria acicularis (Gmelin). Petuch and Myers, 2014: pp. 141, 150, 189, 254, figs. 7.5I, J.
Erosaria acicularis (Gmelin). Lamy and Pointier, 2017: p. 168, unnumbered fig., pl. 49, figs. 8a–8d, pl. 50, fig. 7.
Naria acicularis (Gmelin). Lorenz, 2017: p. 190, pl. H7, fig. 23, p. 245, unnumbered figs.
Naria acicularis (Gmelin). Lorenz, 2018: p. 54, pl. 23, figs. 1–9, 26, 27.

Type material.—*Cypraea acicularis*, holotype whereabouts unknown; *Cypraea gurabonis*, holotype USNM 483461, length 17 mm, width 11 mm, height 9.25 mm.

Type locality.—*Cypraea acicularis*, unknown (Schilder, 1966b: p. 212); *Cypraea gurabonis*, USNM loc. 8737, District of Monte Cristi, Gurabo River about 5 miles above Gurabo Adentro at base of coral limestone and above conglomerate, Pliocene, Gurabo Formation (see note under remarks).

Previously figured material.—Hypotype (Maury, 1917a: p. 115, pl. 19, fig. 6), PRI 28777; Fast (1978: p. 83) provided the previously unpublished type number.

Other examined material.—16 lots NMB collection, comprising 50+ specimens; NHMW 2017/0124/0042–0050 (9 specimens; locality TU 1215); 2017/0124/0051 (5 specimens; locality TU 1215); NHMW 2017/0124/0052–0057 (6 specimens; locality TU 1357); 2017/0124/0058 (10 specimens; locality TU 1357); NHMW 2017/0124/0059, 0060 (2 specimens; locality TU 1219); NHMW 2017/0124/0061 (1 specimen; locality TU 1219); NHMW 2017/0124/0062–0071 (10 specimens; locality NMB 16844); NHMW 2017/0124/0072 (17 specimens; locality NMB 16844); NHMW 2017/0124/0073–

0078 (6 specimens; locality TU 1363/1364); NHMW 2017/0124/0079 (1 specimen; locality TU 1363/1364); NHMW 2017/0124/0080 (1 specimen; locality TU 1449); PRI 84462 (1 specimen; locality TU 1363); PRI 84463 (1 specimen; locality TU 1297); PRI 84464 (25 specimens; locality TU 1230); PRI 84480 (4 specimens; locality TU 1219); PRI 84481 (1 specimen; locality TU 1250); PRI 84482 (2 specimens; locality TU 1210); PRI 84483 (1 specimen; locality TU 1211); PRI 84484 (7 specimens; locality TU 1354); PRI 84485 (1 specimen; locality TU 1231); PRI 84490 (1 + 1 incomplete specimens; locality TU 1215); PRI 84492 (2 specimens; locality TU 1296); PRI 84493 (9 specimens; locality TU 1293); PRI 84495 (5 specimens; locality TU 1422); PRI 84496 (2 specimens; locality TU 1278); PRI 84769 (3 specimens; locality TU 1277).

Measurements.—See Table 3.

Original description.—"C. testa solida supra flavescente fusco punctata: linea horizontali pallida, subtrus lactea, punctis ad marginem impressis." (Gmelin, 1791: p. 3421).

Revised description.—Shell small, pyriform-inflated, in lateral profile dorsal curvature regularly attenuated abapically, dorsal line absent, spire umbilicate, covered by adapical callus; labial margin upturned, bearing row of pits; pitting continuous over anterior canal and to columellar margin; base convex; aperture of medium width, weakly to moderately curved, anterior portion slightly wider; siphonal and exhalant canals slightly upturned, moderately produced; columella denticulate along entire length, bearing 11–18 pronounced teeth that do not extend onto the columellar peristome, teeth extend across abapertural half of venter; anterior columellar teeth usually very strongly developed, short, solid, and elevated; terminal fold strongly developed, broad, and elevated, bordering siphonal canal, internal lamina elevated (sensu Dolin and Lozouet, 2004); fossula poorly developed, vertical, smooth except for ridge arising from first anterior columellar tooth and running obliquely and posteriorly, delimiting lateral border of fossula; outer lip rounded, 13–16 sharp, elevated labral teeth extending onto labrum and slightly less than mid-labral width. Finely spotted dorsal color pattern rarely preserved in some specimens.

Remarks.—*Naria acicularis* is found in all the Gurabo Formation localities in the Dominican Republic but is never common, whereas in the Cercado Formation deposits on the Río Cana *Naria acicularis* is locally abundant. The shells of the slightly earlier upper Miocene Cercado Formation populations are somewhat different from those found in the Gurabo Formation; they are smaller and more globular with

Table 3. Measurements of *Naria acicularis* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable; * = measurement unreliable due to specimen being incomplete or distorted/crushed.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0042	20.0	11.8	9.8	16	18	TU 1215
NHMW 2017/0124/0043	18.9	12.3	10.2	16	16	TU 1215
NHMW 2017/0124/0044	23.1	14.1	11.4	16	15	TU 1215
NHMW 2017/0124/0045	21.3	13.2	10.9	15	18	TU 1215
NHMW 2017/0124/0046	20.5	12.1	9.9	16	17	TU 1215
NHMW 2017/0124/0047	19.4	11.7	9.4	14	16	TU 1215
NHMW 2017/0124/0048	20.4	12.6	9.6	18	16	TU 1215
NHMW 2017/0124/0049	17.9	11.2	9.5	18	12	TU 1215
NHMW 2017/0124/0050	13.8	9.4	7.5	16	14	TU 1215
NHMW 2017/0124/0052	22.3	15.1	12.2	14	15	TU 1354
NHMW 2017/0124/0053	19.6	12.7	10.0	16	15	TU 1354
NHMW 2017/0124/0054	17.8	12.1	9.8	15	14	TU 1354
NHMW 2017/0124/0055	19.8	13.1	10.7	16	17	TU 1354
NHMW 2017/0124/0056	18.2	12.6	10.2	17	14	TU 1354
NHMW 2017/0124/0057	18.1	12.0	9.6	15	13	TU 1354
NHMW 2017/0124/0059	20.2	12.5	10.5	16	17	TU 1219
NHMW 2017/0124/0060	17.0	11.6	9.2	13	13	TU 1219
NHMW 2017/0124/0062	17.2	12.0	9.6	16	13	NMB 16844
NHMW 2017/0124/0063	18.1	12.8	10.1	13	11	NMB 16844
NHMW 2017/0124/0064	18.3	12.9	10.3	13	12	NMB 16844
NHMW 2017/0124/0065	19.9	14.0	11.0	16	15	NMB 16844
NHMW 2017/0124/0066	18.7	12.6	10.2	15	12	NMB 16844
NHMW 2017/0124/0067	18.9	13.4	10.0	15	11	NMB 16844
NHMW 2017/0124/0068	18.5	13.2	10.7	15	13	NMB 16844
NHMW 2017/0124/0069	17.8	11.9	9.3	14	12	NMB 16844
NHMW 2017/0124/0070	19.3	12.9	10.5	16	14	NMB 16844
NHMW 2017/0124/0071	18.1	12.4	10.5	14	15	NMB 16844
NHMW 2017/0124/0073	21.7	14.3	11.5	18	16	TU 1363/1364
NHMW 2017/0124/0074	17.9	12.2	9.1	16	18	TU 1363/1364
NHMW 2017/0124/0075	17.5	10.7	9.3	18	16	TU 1363/1364
NHMW 2017/0124/0076	25.3	17.2	12.6	19	19	TU 1363/1364
NHMW 2017/0124/0077	23.6	16.8	12.8	18	20	TU 1363/1364
NHMW 2017/0124/0078	25.3	17.3	12.5	18	18	TU 1363/1364
NHMW 2017/0124/0080	21.5	13.6*	11.7*	n/c	n/c	TU 1449
USNM 483461	17	11	9.3	n/c	n/c	

fewer columellar and labral teeth (Text-figs. 2.6–2.16). There is, however, some overlap. The Baitoa Formation specimens are quite variable in shape, from pyriform to oval, and tend to have a slightly larger number of teeth (see measurements for specimens from locality TU 1363/1364). Some specimens are somewhat rhomboidal with a weakly angular left margin

(Text-figs. 2.6–2.15), reminiscent of but not as strongly developed as in typical *N. acicularis*. The radula is of the ‘Erosa Pattern’ of Bradner and Kay (1996); it has relatively small, crowded teeth, with laterals and marginals overlapping each other and the central tooth. Bradner and Kay (1996) noted no differences between the radula of the Caribbean *N.*

acicularis and *N. spurca* of the Mediterranean. *Naria acicularis* is common in upper sublittoral to deep water, usually under rocks and coral slabs from 3 to 150 m (Lorenz, 2017).

Comparisons.—The *Naria acicularis*/*Naria spurca* species group is present both in the western and eastern Atlantic, Atlantic islands, and the Mediterranean and has been interpreted in various ways. Dodge (1953: pp. 102–106) gave an excellent summary regarding the use of this name in the early literature and the confusion surrounding the name due to the closely similar eastern and western Atlantic species. Although Dodge noted “It cannot be stated categorically which of the two widely separated races Linnaeus was describing, nor even whether he knew that the western American race existed” (Dodge, 1953: p. 102), Linnaeus, 1758 gave the Mediterranean as the locality of his shell. Burgess (1985, p. 218) noted that “on the basis of the consistently white color of the base of *C. [Cypraea] acicularis* Gmelin, serious consideration should be given to separating this shell as a species;” however, he considered it as a synonym of *Cypraea spurca* Linnaeus.

F. A. Schilder and M. Schilder (1938–1939) considered *Naria acicularis* to differ from *Naria spurca* in having a more reduced fossula with 1–3 teeth (instead of 2–5 in *N. spurca*), a more deltoidal shell shape, and an angular rather than rounded left margin. The eastern Atlantic populations, *Naria spurca verdensium* (Melvill, 1888) [= *Naria spurca atlantica* (Monterosato, 1897), = *Naria spurca cascabelorum* (Talavera et al., 1986)], were said to differ from those of the Mediterranean in having a less convex base and a narrower aperture; they also have slightly more close-set and less sharply cut labial teeth (F. A. Schilder and M. Schilder, 1938–1938). F. A. Schilder and M. Schilder (1938–1939) gave the shell formula for the Mediterranean *N. spurca* (27.62.20.15), for the Atlantic *N. spurca* (22.62.20.16), and for *N. acicularis* (21.66.19.15). Ingram (1951: p. 159) considered *Cypraea spurca*, *Erosaria spurca santaehelenae* Schilder, 1932a, and *Erosaria spurca acicularis* a single species. M. Schilder and F. A. Schilder (1971) recognized several living subspecies of *N. spurca* with distinct geographic distributions.

Gmelin (1791), Hidalgo (1906–1907), and F. A. Schilder (1928, 1932a) all considered *Naria acicularis* distinct from *Naria spurca*, but F. A. Schilder and M. Schilder (1938–1939) and M. Schilder and F. A. Schilder (1971) recanted and returned *N. acicularis* to the synonymy of *N. spurca*. Later, Raybaudi (1982) clearly demonstrated that *N. acicularis* was a distinct species. Lorenz and Hubert (1993, 2001) considered the western Atlantic *Erosaria acicularis* distinct from the eastern Atlantic *N. spurca* at the species level, with the populations from St. Helena and Ascension islands more closely resembling the western Atlantic *N. acicularis*. The small differences between the eastern Atlantic populations and

those of the Mediterranean do not warrant formal taxonomic separation according to Lorenz and Hubert (2001: p. 197). Heimann (2006) performed a statistical analysis of *N. spurca* and *N. acicularis* using the diagnostic shell characters of shell color and angularity of the left side. He concluded that the base coloration was a good diagnostic shell character, allowing the distinction of the two taxa at specific level, but the angularity of the left side could only be used as an auxiliary shell character. Lastly, molecular data revealed that the two taxa can be separated at the species level (Lorenz, 2017: p. 245).

It is widely agreed that the western Atlantic *Naria acicularis* can usually be separated from the eastern Atlantic and Mediterranean *Naria spurca* by its shape. However, only their consistent color differences reliably separate the two species. This causes a dilemma when dealing with the fossil populations from the Dominican Republic, in which the color pattern is rarely preserved, and, if so, does not correspond to the original colors. The Dominican Republic shells from the Gurabo Formation are most like *N. spurca* in having a more oval shape and a rounded rather than angular left margin. Some of the specimens approach the rhomboidal shape of the Recent western Atlantic *N. acicularis*, which has a slightly angular left margin, but still fall within the variability seen in the eastern Atlantic and Mediterranean *N. spurca* (see Heimann, 2006: fig. 2b). The Dominican Republic specimens are on average smaller shelled than those of Recent populations of *N. spurca*, and a constant character by which to differentiate them is lacking.

This lower Miocene earliest record (Baitoa Fm.) for *Naria acicularis* indicates that the eastern Atlantic and Mediterranean populations migrated eastwards fairly late, possibly in the late Pleistocene, as *Naria spurca* has not been found in the Mediterranean Pliocene (Sacco, 1894; Pavia and Demagistris, 1970; Inzani, 1985, 1995a, 1995b; Landau and Fehse, 2004), the Atlantic Pliocene (Silva, 2001; Landau et al., 2011), nor in the Italian Pleistocene (Cerulli-Irelli, 1911). As the early Miocene-Pliocene records of *N. acicularis* are intermediate in shape, the rhomboidal shape in *N. acicularis* must have evolved later, so that the Atlantic and Mediterranean populations developed slightly different morphotypes with local variations. Interestingly, the eastern Atlantic forma *verdensium* differs from the Mediterranean shells in having a narrower aperture and thicker teeth, not unlike the Dominican shells. Dodge (1953, p. 103) noted that Gmelin’s use of “*subtus lactea, punctis ad marginem impressis*” tied his shell to the American race of the species. Vermeij and Rosenberg (1993: p. 187) estimated that at least 28 species of mollusks may have dispersed eastward across the Atlantic, but no cypraeoideans were noted. Further examples of late Neogene west to east migration in marginellids were given by

Silva et al. (2011). It is therefore clear from the fossil record that the *N. acicularis*/*N. spurca* group first appeared in the western Atlantic and extended its range to the eastern Atlantic relatively late. In the absence of consistent shell characters to separate the two in the fossil state, the name *N. acicularis* for the Caribbean Neogene populations is used herein. It is interesting to note that Ingram (1951: p. 159) erroneously reported that “this species is the only Afro-European cowry to enter the fauna of the Western Hemisphere.”

Erosaria (Ravitrona) aliena Schilder, 1939a (Text-figs. 2.20–2.23; holotype) was described from a single worn specimen found in the Matura shell bed, Talparo Formation of Trinidad, now known to be Pleistocene. Although undoubtedly related to the *Naria spurca*/*N. acicularis* species group, the teeth seem to be less strongly developed and shorter. However, it does not seem to be entirely adult and additional specimens are required to confirm its characteristics.

Ingram (1939b) described *Cypraea gurabonis* from the Gurabo Formation (Text-figs. 3.1–3.4). Despite the fact that he gave a fairly detailed description of the only known specimen, it is a poorly preserved specimen that is herein included within the synonymy of *Naria acicularis*. It appears to closely resemble the wider specimens from the Cercado Formation. Indeed, if the type locality is correct, 5 miles above Gurabo Adentro would be Cercado Formation and not Gurabo Formation. M. Schilder and F. A. Schilder (1971) erroneously placed *C. gurabonis* in the genus *Pustularia* following Ingram’s comparison to *Cypraea semen* Cooke, 1919. The assignment of *C. semen* to *Propustularia* by the Schilders is also erroneous, as it likely represents a species of the genus *Pustularia*.

Occurrence.—Río Cana (localities NMB 16820, NMB 16821, NMB 16828, NMB 16831, NMB 16832, NMB 16833, NMB 16834, NMB 16835, NMB 16836, NMB 16839, NMB 16842, NMB 16844, NMB 16852; TU 1230); Arroyo Bellaco (locality TU 1422); Río Gurabo (localities NMB 15856, NMB 15888, TU 1210, TU 1211, TU 1215, TU 1231, TU 1277, TU 1278, TU 1296, TU 1297); Río Amina (locality TU 1219); Cañada de Zamba (locality TU 1354); Río Yaque del Norte (localities TU 1363/1364, TU 1357, TU 1443, TU 1449); Río Verde (locality TU 1250); Río Mao (locality TU 1293).

Fossil distribution.—Miocene (indeterminate): Dominican Republic (Gabb, 1872; Fast, 1978). Lower Miocene: Baitoa Formation, Dominican Republic (this paper). Upper Miocene: Cercado Formation (Maury, 1917a, 1917b; Ingram, 1939b; Ingram, 1947a; Ingram, 1947c; Ingram, 1951). Lower Pliocene: Gurabo Formation, Dominican Republic (Vaughan and Woodring, 1921; Pilsbry, 1922; Ingram, 1939b, 1951;

Ramírez, 1956). Pleistocene (indeterminate): Barbados and Guadelupe (F. A. Schilder, 1932a). Lower Pleistocene: Moin Formation, Costa Rica (Robinson, 1991). Upper Pleistocene: Spencer’s Point Formation, Bermuda (Richards et al, 1969); Britton Hill and Hastings, Barbados (F. A. Schilder, 1939a; Ingram, 1947c, 1951); St. Eustatius, Caribbean Netherlands (Rutten, 1931).

Recent distribution.—Bermuda (Jensen and Pearce, 2009), South Carolina (Merrill and Petit, 1965), southern Florida, the Bahamas, the southern Gulf of Mexico to northeastern México, and the entire Caribbean Sea to southern Brazil.

Subfamily **CYPRAEORBINAE** F. A. Schilder, 1927

Cypraeorbinae F. A. Schilder, 1927: p. 97 (as tribe Cypraeorhini) (as per Darragh, 2011: p. 1).

Remarks.—Cypraeorbinae ranges from the late Eocene (Auversian) to the late Miocene (Messinian) (newly documented herein). The earliest appearance of the Cypraeorbinae is *Cypraeorbis alabamensis* (de Gregorio, 1890: p. 59) from the late Eocene (Claibornian, Auversian) of Alabama, USA.

Genus **CYPRAEORBIS** Conrad, 1865

Cypraeorbis Conrad, 1865: p. 31. Type species (by original designation): *Cypraea sphaeroides* Conrad, 1847, Oligocene, Vicksburg, Mississippi, USA.

Floradusta Petuch, 2004: p. 279. Type species (by original designation): *Cypraea heilprini* Dall, 1890, Chipola Formation, Alum Bluff Group, Miocene, Florida, USA.

Loxacypraea Petuch, 2004: p. 279. Type species (by original designation): *Cypraea chilona* Dall, 1900, Chipola Formation, Alum Bluff Group, Miocene, Florida, USA.

Original description.—Conrad’s (1847: p. 113) description of the type species *Cypraea sphaeroides*: “Short ovate, subglobose; posterior end narrow; base rounded; aperture narrow, the margins with numerous teeth.”

Revised description.—“Medium sized to large. Rather inflated. Extremities slightly produced, rounded posteriorly, pointed or spatulate anteriorly. Teeth strong and distant. Fossula smooth, usually slightly projecting, fossular gap rather shallow, terminal pleat distinct. Labrum often sloping anteriorly. Dorsum with darker mottling or blotching, margins densely spotted. Intracapsular development.” (Lorenz, 2017: p. 277).

Remarks.—Conrad (1865: p. 31) introduced *Cypraeorbis* as a subgenus of *Cypraea* for *Cypraea sphaeroides* Conrad, 1847, from the Vicksburg, Mississippi, Oligocene without

a description. Lorenz (2017: p. 277) noted that there was “convincing conchological evidence that *Muracypraea*, and later *Siphocypraea*, evolved from *Cypraeorbis* ancestry.” He further stated that “it seems obvious that *Cypraeorbis* was not closely related to the modern *Zoila*: they were confined to a different area, and lived in a different period.” Dolin (2015) assigned several similar European and Floridian species of *Cypraeorbis* to the synonym genus *Loxacypraea* and the living *Barycypraea fultoni* (G. B. Sowerby III, 1903) based on conchological features alone. This attribution to *B. fultoni* is an assumption, as molecular data are not available for extinct taxa, and such conclusions should be made with caution. Darragh (2011) argued that *Bernaya* F. A. Schilder, 1927, was a synonym of *Cypraeorbis*. He further noted that “if subfamilies are regarded as useful in classification, Cypraeorbinæ should be used instead” (Darragh, 2011, p. 1). Bouchet and Rocroi (2005) and Bouchet et al. (2017) included Cypraeorbinæ in the synonymy of Gisortinae F. A. Schilder, 1927; however, as Darragh (2011, p. 1) noted, “species within *Gisortia* have an obsolete fossula, quite different form species of *Cypraeorbis* and *Zoila*, so this synonymy is unlikely.”

According to Dolin (1991: p. 18), *Cypraeorbis chilona* (Dall, 1900) is a widespread species with a range including the Baitoa Formation of the Dominican Republic; he added that “it is one of the more abundant species.” Thus far the authors are unaware of any *C. chilona* specimens from the Dominican Republic. Herein, the authors disagree with Dolin’s inclusion of *Siphocypraea angustirima hyaena* F. A. Schilder, 1939a, from the lower to middle Miocene Cantaure Formation and middle Miocene Urumaco Formation of Venezuela, in the synonymy of *C. chilona*. *Muracypraea hyaena* (F. A. Schilder, 1939a) is considered a valid species (see Landau and Groves, 2011: pp. 3, 4). Dolin (1991: p. 18) considered six specimens from the early Miocene (Aquitainian) of France “unquestionably” conspecific with *C. chilona*, although none were figured. In 2015, Dolin (p. 9, pl. 2, figs. 4–6) described *Cypraeorbis testudinea* from the Chipola Formation and designated USNM 438596 as the holotype; he had previously identified this specimen as *C. chilona* in 1991. The holotype is remarkably similar to a specimen he also figured as *C. chilona* (Dolin, 1991: pl. 1, figs. 4–6) from the Chipola Formation. If *C. chilona* is indeed verified from Florida and France, it would join a short list of early Miocene amphiatlantic species including *Eudolium subfasciatum* Sacco, 1890 (J. Gibson-Smith and W. Gibson-Smith, 1988), and *Muricopsis (Risomurex) crassica* (Benoist, 1873) (E. H. Vokes and Houart, 1986).

Geographic range.—Europe including Italy, France, Hungary, Germany; the southeastern United States, including Florida, Alabama, and Mississippi; northern South America including Colombia and Venezuela; and the Dominican Republic, as documented herein.

Stratigraphic range.—Late Eocene to late Miocene (late Miocene documented herein).

***Cypraeorbis alisonkayae* n. sp.**

Text-figs. 4.1–4.16

Siphocypraea chilona (Dall, 1900). Dolin, 1991: p. 18 [not *Cypraeorbis chilona* (Dall, 1900)].

Type material.—Holotype NHMW 2017/0124/0081; paratype 1, NHMW 2017/0124/0082; paratype 2, NHMW 2017/0124/0083; paratype 3, NHMW 2017/0124/0084; paratype 4, NHMW 2017/0124/0085; paratype 5, NHMW 2017/0124/0086; paratype 6, NHMW 2017/0124/0087; paratype 7, NHMW 2017/0124/0088; paratype 8, PRI 84763.

Type locality.—Locality TU 1443, unnamed formation probably of Cercado age, east bank at López, just upstream from mouth of Arroyo López, Río Yaque del Norte, Dominican Republic, probably upper Miocene.

ZooBank LSID.—urn:lsid:zoobank.org:act:86A29994-BB99-43A1-B2B8-C791C3E493EB.

Other material.—NHMW 2017/0124/0089-0100 (12 specimens; locality TU 1443); NHMW 2017/0124/0101 (10 specimens; locality TU 1443); PRI 84764 (1 incomplete specimen; locality TU 1443).

Measurements.—See Table 4.

Diagnosis.—*Cypraeorbis* species medium sized for genus, dorsum strongly inflated, strongly callused, venter flattened, aperture almost straight, anterior canal deep, delimited by small spatulate expansions of lips, posterior channel very deep, columella denticulate along entire length, 15–20 teeth not extending onto peristome, but across abapertural quarter of venter, terminal ridge strongly developed, fossula poorly developed, outer lip bearing 16–22 short teeth restricted to lip edge. Finely spotted dorsal color pattern with larger spots on marginal callus.

Description.—Shell medium sized for genus, solid, rotund, dorsum strongly inflated, evenly rounded, not humped; no dorsal sulcus; spire depressed, covered by adapical callus; sides rounded, strongly callused, callus ascending adapically to between 1/3 and 1/2 shell height, right slightly higher than left; venter flattened, slightly convex in profile; aperture almost straight, anterior third weakly dilated, posterior third weakly curved to the left; anterior canal deep, abaxially asymmetrical and abapically orthogonally truncated, flanked on either side

Text-fig. 4. *Cypraeorbis alisonkayae* n. sp. 1–4, holotype, NHMW 2017/0124/0081, length 48.8 mm. 5–8, paratype 1, NHMW 2017/0124/0082, length 45.2 mm. 9–12, paratype 2, NHMW 2017/0124/0083, length 42.6 mm. 13–16, paratype 3, NHMW 2017/0124/0084, length 40.6 mm. Locality of all specimens: TU 1443, east bank at López, just upstream from mouth of Arroyo López, Río Yaque del Norte, Dominican Republic, unnamed formation probably of Cercado age, upper Miocene.

by small spatulate horizontal expansions produced from the abapical tips of the inner and outer lips; posterior channel very deep, limited by parallel lips; columella denticulate along entire length, bearing 15–20 pronounced teeth, teeth not extending onto the columellar peristome, teeth extending across abapertural quarter of venter; anterior columellar teeth slightly stronger, short, solid and elevated; terminal ridge strongly developed, elevated, bordering siphonal canal, separated from first anterior columellar tooth by wide, shallow

groove; elevated internal lamina (sensu Dolin and Lozouet, 2004); fossula poorly developed, vertical, smooth except for ridge arising from first anterior columellar tooth and running obliquely posteriorly, delimiting lateral border of fossula; outer lip rounded, slightly flattened, and flared abapically, 16–22 short, sharp, elevated labral teeth restricted to lip edge. Finely spotted dorsal color pattern with larger spots on marginal callus preserved in some specimens.

Table 4. Measurements of *Cypraeorbis alisonkayae* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable; * = measurement unreliable due to specimen being incomplete or distorted/crushed.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0081 (Holotype)	48.8	33.3	25.9	21	15	TU 1443
NHMW 2017/0124/0082 (Paratype 1)	45.2	30.6	24.9	20	18	TU 1443
NHMW 2017/0124/0083 (Paratype 2)	42.6	28.6	22.9	20	20	TU 1443
NHMW 2017/0124/0084 (Paratype 3)	40.6	28.1	22.3	18	17	TU 1443
NHMW 2017/0124/0085 (Paratype 4)	49.4	33.6	24.9	22	18	TU 1443
NHMW 2017/0124/0086 (Paratype 5)	46.2	32.7	25.7	22	16	TU 1443
NHMW 2017/0124/0087 (Paratype 6)	47.1	31.5	25.3	22	17	TU 1443
NHMW 2017/0124/0088 (Paratype 7)	38.4	27.8	21.5	18	18	TU 1443
NHMW 2017/0124/0089	45.2	30.8	24.6	22	18	TU 1443
NHMW 2017/0124/0090	47.0	31.1	24.9	n/c	n/c	TU 1443
NHMW 2017/0124/0091	38.3	25.0	20.9	21	18	TU 1443
NHMW 2017/0124/0092	47.8	31.0	25.1	n/c	16	TU 1443
NHMW 2017/0124/0093	37.1	26.9	20.8	19	15	TU 1443
NHMW 2017/0124/0094	42.1	29.1	22.6	19	20	TU 1443
NHMW 2017/0124/0095	41.6	29.2	21.8	21	16	TU 1443
NHMW 2017/0124/0096	37.4	25.3	20.4	n/c	n/c	TU 1443
NHMW 2017/0124/0097	39.4	27.9	21.8	18	15	TU 1443
NHMW 2017/0124/0098	41.1	28.8	22.5	20	17	TU 1443
NHMW 2017/0124/0099	39.0	26.6	21.6	16	16	TU 1443
NHMW 2017/0124/0100	40.5	27.6	21.5	16	18	TU 1443

Dimensions.—Holotype: length 48.8 mm, width 33.3 mm, height 25.9 mm; paratype 1: length 45.2 mm, width 30.6 mm, height 24.9 mm; paratype 2: length 42.6 mm, width 28.6 mm, height 22.9 mm; paratype 3: length 40.6 mm, width 28.1 mm, height 22.3 mm; paratype 4: length 49.4 mm, width 33.6 mm, height 24.9 mm; paratype 5: length 46.2 mm, width 32.7 mm, height 25.7 mm; paratype 6: length 47.1 mm, width 31.5 mm, height 25.3 mm; paratype 7: length 38.4 mm, width 27.8 mm, height 21.5 mm; paratype 8: height 43.4 mm, width 30.7 mm, height 23.8 mm.

Remarks.—Despite the relatively large number of specimens at hand from the Río Yaque del Norte, they are only found at one small outcrop in the López section that has been exposed only twice in the ten visits to the locality. The presence of *Cypraeorbis* in the Dominican Republic was noted by Dolin (1991: p. 18), who recorded two specimens found by E. H. and H. E. Vokes, one at TU 1226, Baitoa Formation, and one at TU 1443, unnamed formation probably of Cercado age. These records probably represent *Cypraeorbis alisonkayae*, but, unfortunately, the specimens are now missing from the Vokes collection at PRI. This species has not been found in the Baitoa Formation by the present authors, and its presence in

the upper Miocene Cercado Formation is the stratigraphically youngest occurrence of the genus.

Comparisons.—*Cypraeorbis alisonkayae* superficially resembles three of the highly inflated *Cypraeorbis* species figured by Dolin (1991) from the Chipola Formation, and this is particularly evident in the lateral views. Specifically, these include *Cypraeorbis emilyae* Dolin, 1991 (holotype USNM 438580; Dolin 1991: fig. 2c), *Cypraeorbis hertleini* (Ingram, 1948) (hypotype USNM 438581; Dolin 1991: fig. 3b), and *Cypraeorbis ballista* (Dall, 1915) (hypotype USNM 438585; Dolin 1991: fig. 7b). However, in ventral view *C. alisonkayae* is much less inflated, has a wider aperture, and is much more narrowly constricted anteriorly than all three of Dolin's specimens. With regard to the ventral view of Dolin's *Cypraeorbis wilcoxi* (Dall, 1890), *C. alisonkayae* is also more narrowly constricted anteriorly and significantly more inflated dorsally. In dorsal view, Petuch's (1997) and Lorenz's (2018) specimens of *C. wilcoxi* are similar to *C. alisonkayae* in shape, but *C. alisonkayae* has much deeper terminal canals and a much narrower overall shape. *Cypraeorbis alisonkayae* is not similar to any of the European species.

Etymology.—Named after E. Alison Kay (1928–2008) in recognition of her many contributions to malacology and the preparation of an unpublished monograph on Dominican Republic cypraeids, which formed the basis of this work. *Cypraeorbis* is gender masculine.

Occurrence.—Río Yaque del Norte (localities TU 1443, TU 1226).

Distribution.—Lower to middle Miocene: Baitoa Formation (Dolin, 1991). Upper Miocene: Cercado Formation (herein), Dominican Republic.

Subfamily **CYPRAEINAE** Rafinesque, 1815

Cypraeinae Rafinesque, 1815: pp. 146, 147 (as subfamily Cypridia).

Remarks.—Cypraeinae ranges from the Miocene to Recent.

Tribe **CYPRAEINI** Rafinesque, 1815

Cypraeini Rafinesque, 1815: pp. 146, 147 (as subfamily Cypridia).

Genus **MURACYPRAEA** Woodring, 1957

Muracypraea Woodring, 1957: pp. 88, 89. Type species (by original designation): *Cypraea mus* Linnaeus, 1758, Recent, Venezuela, Colombia, and Aruba.

Original diagnosis.—"Pyriform cowries of medium size to moderately large (45 to 75 mm). Posterior part of dorsal surface smooth, roughened, warty or bituberculate. Outer lip wide, slightly constricted near anterior end; teeth short, moderately strong. Terminal ridge (bordering siphonal canal) narrow. Fossula indistinct, wide, shallow, smooth. Teeth on inner lip weak to strong. Posterior outlet long, wide, deep" (Woodring, 1957: p. 89).

Description.—As described by Woodring (1957: p. 89), as a subgenus of *Cypraea*.

Remarks.—Placement of these tropical American species within the genus *Muracypraea* Woodring, 1957, rather than *Barycypraea* F. A. Schilder, 1927, and the usage of *Muracypraea* at full generic rank was fully discussed by Landau and Groves (2011). The authors noted the geographical separation of the two genera: *Muracypraea* is only tropical American, whereas *Barycypraea* is fossil and recent from East Africa to Indonesia. Although some of the shells of the Indonesian fossil *Barycypraea* group are extremely similar conchologically to those of *Muracypraea* in the tropical American Neogene,

their similarity could represent a convergent evolutionary process. A prominent morphological feature that separates *Muracypraea* from *Barycypraea* is the flattened spatulate horizontal expansions on either side produced from the abapical tips of the inner and outer lips, which occurs in *Muracypraea henekeni* and many related species. However, this feature is lacking entirely in some living *Muracypraea mus*. Occasionally these spatulate expansions are hyper developed in the Caribbean forms, whereas they are somewhat obsolete in the Indonesian taxa. Although the two genera may have a common Tethyan ancestor, consistent shell differences and their vast geographic separation justify different genera. Most *Muracypraea* shells are lightweight and less callused with a broad aperture and less developed, widely spaced dentition. In contrast, the shells of *Barycypraea* are heavy and strongly callused with a narrow aperture; their dentition may be distinct and close-set (as in *Barycypraea fultoni amorimi* Raybaudi, 1989) or entirely absent [as in *Barycypraea teulerei* (Cazenavette, 1845)]. The dorsal callosities of both genera can be variable even within the same species. However, in *Muracypraea* they tend to be restricted to the posterior portion of the dorsal surface, whereas in *Barycypraea* there may be a second set located slightly anterior to the dorsum center. *Barycypraea zietsmani* (Liltved and Le Roux, 1988), from the Pliocene of South Africa, is a remarkably similar fossil species to the topical American *Muracypraea* group, particularly in the dorsal aspect, but it lacks the high dorsal profile as in most fossil *Muracypraea*. Because the Miocene fossil record for the central Pacific islands is incomplete—and until a conclusive answer to whether two genera should be used for the two seemingly geographically separated species groups—the classification of M. Schilder and F. A. Schilder (1971) for *Muracypraea* is used for the Caribbean species.

Geographic range.—Circum-Caribbean to Brazil, and Peru to southeastern California.

Stratigraphic range.—Early Miocene to Recent.

Muracypraea henekeni (G. B. Sowerby I, 1850) Text-figs. 5.1–5.15, 6.1–6.4

Cypraea henikeri [sic] G. B. Sowerby I, 1850: p. 45, pl. 9, fig. 3 [error for *henekeni*].

Cypraea henekeni G. B. Sowerby I. Guppy, 1867: p. 160.

Cypraea henikeni [sic] G. B. Sowerby I. Gabb, 1872: p. 235 [error for *henekeni*].

Cypraea henekeni G. B. Sowerby I. Guppy, 1874: p. 440.

Cypraea henekeni G. B. Sowerby I. Guppy, 1876: p. 528.

Cypraea henekeni G. B. Sowerby I. Dall, 1890: p. 165.

Not *Cypraea henikeni* G. B. Sowerby I, var. Brown and Pilsbry, 1911: pp. 356, 357, pl. 26, figs. 9, 10 [= *Muracypraea isthmica* (Schilder, 1927)].

Text-fig. 6. *Muracypraea henekeni* (G. B. Sowerby I, 1850), juvenile specimens, formerly assigned to *Cypraea noueli* Maury, 1917a. 1, 2, holotype, PRI 28776, length 61 mm; Bluff 1, Cercado de Mao, Dominican Republic (= locality TU 1293), Gurabo Formation, lower Pliocene. 3, 4, NHMW 2017/0124/0038, length 44.7 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Not *Cypraea henekeni* G. B. Sowerby I. Guppy, 1912: p. 3 [= *Muracypraea caroniensis* (Maury, 1925)].
 Not *Cypraea henekeni* G. B. Sowerby I. Brown and Pilsbry, 1912: p. 501 [= *Muracypraea isthmica* (Schilder, 1927)].
Cypraea henekeni G. B. Sowerby I. Maury, 1917a: p. 114, pl. 19, fig. 4.
Cypraea henekeni G. B. Sowerby I. Maury, 1917b: pp. 10, 22, 24, 27, 28.
Cypraea noueli Maury, 1917a: pp. 114, 115, pl. 19, fig. 5 (juvenile specimen).
Cypraea noueli. Maury, 1917b: p. 10.
 Not *Cypraea henekeni* G. B. Sowerby I, var. Vaughan, 1919: p. 561 [= *Muracypraea isthmica* (Schilder, 1927)].
Cypraea blandiana Vredenburg, 1920: p. 95.
Cypraea noueli Maury. Vaughan and Woodring, 1921: p. 141.
Cypraea henikeri [sic] G. B. Sowerby I. Vredenburg, 1920: p. 95 [error for *henekeni*].
Cypraea henekeni G. B. Sowerby I. Vaughan and Woodring, 1921: pp. 125, 129, 141, 160.
Cypraea henekeni G. B. Sowerby I. Pilsbry, 1922: p. 365.
Cypraea henekeni G. B. Sowerby I. Olsson, 1922: p. 196.
Cypraea henekeni G. B. Sowerby I. Maury, 1925: pp. 371, 372, pl. 48, fig. 1.
Cypraea henekeni var. *lacrimula* Maury, 1925: p. 372, pl. 48, fig. 2.
Cypraeorbis (*Siphocypraea*) *blandiana* (Vredenburg). F. A. Schilder, 1927: p. 99.
Cypraeorbis (*Siphocypraea*) *henikeri* [sic] (G. B. Sowerby I). F. A. Schilder, 1927: p. 99.
 Not *Cypraea henekeni* (G. B. Sowerby I). Anderson, 1927: p. 89 [= *Muracypraea andersoni* (Ingram, 1948)].

Not *Cypraea henekeni* (G. B. Sowerby I). Anderson, 1929: p. 139 [= *Muracypraea andersoni* (Ingram, 1948)].
Siphocypraea (*Siphocypraea*) *henikeri* [sic] *lacrimula* (Maury). F. A. Schilder, 1932a: p. 118.
Siphocypraea (*Siphocypraea*) *henikeri* [sic] *henikeri* (G. B. Sowerby I). F. A. Schilder, 1932a: p. 118.
Cypraea henekeni var. *potreronis* Ingram, 1939b: pp. 331, 332, pl. 22, figs. 8, 9.
Cypraea henekeni G. B. Sowerby I. Ingram, 1939b: pp. 334, 335, pl. 22, fig. 3.
Cypraea noueli Maury. Ingram, 1939b: pp. 335, 336, pl. 22, fig. 5.
Siphocypraea henikeri [sic] (G. B. Sowerby I). F. A. Schilder, 1939a: pp. 5, 9, 24.
Siphocypraea noueli (Maury). F. A. Schilder, 1939a: pp. 7, 9, 24.
Cypraea henekeni G. B. Sowerby I. Pilsbry and Olsson, 1941: p. 42.
Cypraea henikeri [sic] *potreronis* Ingram. Ingram, 1947a: p. 53, pl. 5, figs. 1, 2.
Cypraea henikeri [sic] G. B. Sowerby I. Ingram, 1947a: pp. 53, 93–95, pl. 5, fig. 3 [error for *henekeni*].
Cypraea noueli Maury. Ingram, 1947a: p. 53; pl. 7, fig. 13.
Cypraea henikeri [sic] *potreronis* Ingram. Ingram, 1947b: p. 130.
Cypraea henikeri [sic] G. B. Sowerby I. Ingram, 1947c: p. 146 [error for *henekeni*].
Cypraea henikeri [sic] *potreronis* Ingram. Ingram, 1947c: p. 146.
Cypraea noueli Maury. Ingram, 1947c: p. 147.
Cypraea henikeri [sic] G. B. Sowerby I. Ingram, 1951: p. 136 [error for *henekeni*].
Cypraea noueli Maury. Ingram, 1951: pp. 136, 137.
 Not *Cypraea* cf. *C. henekeni* G. B. Sowerby I. Marks, 1951: p. 376 [= *Muracypraea woodringi* Landau and Groves, 2011].

Text-fig. 5. *Muracypraea henekeni* (G. B. Sowerby I, 1850). 1, 2, lectotype, NHMUK G83940, length 58 mm, collected Col. T. S. Heneken, ('J. S. Heniker'), c. 1848; Yaque River, St. Domingo, Miocene. 3–5, NHMW 2010/0036/0027, length 53.6 mm; locality TU 1219, Río Amina, Dominican Republic, Gurabo Formation, lower Pliocene. 6–8, NHMW 2010/0036/0028, length 51.7 mm; locality TU 1219, Río Amina, Dominican Republic, Gurabo Formation, lower Pliocene. 9–12, unnumbered specimen, length 63.8 mm; locality NMB 15899, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 13–15, NHMW 2017/0124/0016, length 67.3 mm; locality TU 1379, Río Mao, Dominican Republic, Gurabo Formation, lower Pliocene.

- Cypraea henekeni* G. B. Sowerby I. Ramírez, 1956: p. 13.
Cypraea henekeni potreronis Ingram. Ramírez, 1956: p. 13.
Cypraea henekeni G. B. Sowerby I. Woodring, 1957: pp. 88, 89.
Cypraea (*Muracypraea*) *henekeni* G. B. Sowerby I. Woodring, 1959 (in part only, see below): pp. 152, 194–196.
 Not *Cypraea* (*Muracypraea*) *henekeni* G. B. Sowerby I. Woodring, 1959: pp. 152, 194–196, pl. 32, figs. 1, 4, 6, 9 [= *Muracypraea woodringi* Landau and Groves, 2011].
 Not *Cypraea* (*Muracypraea*) *henekeni* G. B. Sowerby I. Woodring, 1959: pp. 194–196, pl. 31, figs. 6–10 [= *Muracypraea isthmica* (Schilder, 1927)].
Cypraea henekeni potreronis Ingram. Woodring, 1959: p. 194.
Cypraea henekeni lacrimula Maury. Woodring, 1959: p. 194.
Cypraea henekeni G. B. Sowerby I. Brann and Kent, 1960: p. 305.
Cypraea henekeni lacrimula Maury. Brann and Kent, 1960: p. 305.
Cypraea (*Muracypraea*) *henekeni* G. B. Sowerby I. Pflug, 1961: pp. 11, 14, 30, 31, pl. 5, figs. 1–8.
 Not *Cypraea* (*Muracypraea*) *henekeni* (G. B. Sowerby I). Weisbord, 1962: pp. 236–238, pl. 22, figs. 5, 6 [= *Muracypraea mus bicornis* f. *tristensis* (Petuch, 1987)].
Siphocypraea (*Muracypraea*) *henekeni* (G. B. Sowerby I). Olsson 1964: pp. 9, 176, 177.
 Not *Siphocypraea* (*Muracypraea*) *henekeni* (G. B. Sowerby I). Olsson, 1964: p. 176, pl. 31, figs. 3, 3a [= *Muracypraea woodringi* Landau and Groves, 2011].
Cypraea (*Muracypraea*) *henekeni* G. B. Sowerby I. Perez Nieto, 1965: p. 17.
Siphocypraea (*Muracypraea*) *henekeni* (G. B. Sowerby I). Olsson and Petit, 1968: p. 280, pl. 18, fig. 4.
Siphocypraea (*Muracypraea*) *amandusi potreronis* (Ingram). M. Schilder and F. A. Schilder, 1971: p. 29, 145.
Siphocypraea (*Muracypraea*) *henekeni henekeni* (G. B. Sowerby I). M. Schilder and F. A. Schilder, 1971: pp. 29, 121.
Siphocypraea (*Muracypraea*) *henekeni lacrimula* (Maury). M. Schilder and F. A. Schilder, 1971: pp. 29, 126.
Siphocypraea (*Muracypraea*) *noueli* (Maury). M. Schilder and F. A. Schilder, 1971: pp. 29, 137.
 Not *Siphocypraea* (*Muracypraea*) *henekeni* (G. B. Sowerby I). J. Gibson-Smith, 1976: pp. 9, 10 [= *Muracypraea mus mus* (Linnaeus, 1758)].
Cypraea henekeni G. B. Sowerby I. Fast, 1978: p. 83.
 Not *Siphocypraea* (*Muracypraea*) *henekeni* (G. B. Sowerby I). J. Gibson-Smith and W. Gibson-Smith, 1979: p. 25 [= *Muracypraea mus mus* (Linnaeus, 1758)].
Siphocypraea henekeni (G. B. Sowerby I). Petuch, 1979: pp. 216, 217.
Siphocypraea noueli (Maury). Petuch, 1979: p. 217.
Siphocypraea potreronis (Ingram). Petuch, 1979: p. 217.
Siphocypraea noueli (Maury). Petuch, 1981: p. 316.
 Not *Siphocypraea henekeni* (G. B. Sowerby I). Petuch, 1981: p. 319 [= *Muracypraea mus bicornis* f. *tristensis* (Petuch, 1987)].
Cypraea henekeni G. B. Sowerby I. Burgess, 1985: pp. 270, 272, pl. 20, fig. H₃.
 Not *Cypraea* (*Muracypraea*) *henekeni* G. B. Sowerby I. Pitt and Pitt, 1993: p. 3, pl. 1, fig. 7 [= *Muracypraea woodringi* Landau and Groves, 2011].
 Not *Barycypraea* (*Muracypraea*) *henekeni* (G. B. Sowerby I): Groves, 1993: p. 12 [= *Muracypraea woodringi* Landau and Groves, 2011].
Barycypraea henekeni (G. B. Sowerby I). Doneddu and Manunza, 1996: pp. 1, 2, 4, 5, pl. 1, figs. A, B.
Muracypraea henekeni (G. B. Sowerby I). Arnold, 1997: p. 11 (in part).
Muracypraea henekeni (G. B. Sowerby I). Groves, 1997: p. 8.
 Not *Muracypraea* “*henekeni*” (G. B. Sowerby I). Groves, 1997: p. 152, pl. 1, figs. 4–6 [= *Muracypraea woodringi* Landau and Groves, 2011].
 Not *Muracypraea henekeni* (G. B. Sowerby I). Arnold, 1997: p. 11 [= *Muracypraea woodringi* Landau and Groves, 2011].
 Not *Muracypraea henekeni* (G. B. Sowerby I). Arnold, 1998: p. 89 [= *Muracypraea woodringi* Landau and Groves, 2011].
Muracypraea henekeni (G. B. Sowerby I). Arnold, 1998: pp. 89, 90 (in part).
Cypraea henekeni G. B. Sowerby I. Kugler, 2001: p. 123.
 Not *Muracypraea henekeni* (G. B. Sowerby I). Petuch, 2004: pp. 38, 39, pl. 4, figs. C, D [= *Muracypraea hyaena* (Schilder, 1939a)].
Muracypraea henekeni (G. B. Sowerby I). Landau and Silva, 2010: pp. 36–39 pl. 7, figs. 5a–c [+ 5a on cover].
 Not *Siphocypraea henekeni* (G. B. Sowerby I). Diaz and García-Llano, 2010: pp. 109, 113 (erroneously as Guppy, 1867) [possibly = *Muracypraea woodringi* Landau and Groves, 2011].
Muracypraea henekeni (G. B. Sowerby I). Landau and Groves, 2011: pp. 2, 3, figs. 15–20.
Barycypraea henekeni (Sowerby III, 1903 [*sic*]). Fehse, 2016a: p. 53, figs. 13.5, 14.3, 16.2.
Muracypraea henekeni (G. B. Sowerby I). Lorenz, 2017: p. 178, pl. G6, fig. 13, p. 279 (erroneously as Gabb, 1873).
Muracypraea henekeni (G. B. Sowerby I). Lorenz, 2018: p. 670, pl. 331, fig. 7 (refigured from Landau and Groves, 2011, figs. 18, 19).
- Type material*.—*Cypraea henekeni* G. B. Sowerby I, 1850: lectotype (of Pflug, 1961: p. 31, pl. 5, figs. 1–3) NHMUK G83940, length, 58.9 mm, width 44.2 mm, height, 33.4 mm; paralectotypes (as syntypes): NHMUK GG 20022-3, GG 20024-5, GG 20025, GG 20026, GG 20027; *Cypraea noueli* Maury, 1917a; holotype PRI 28776, length 61 mm, width 45.5 mm, height 30.9 mm; *Cypraea henekeni* var. *lacrimula* Maury, 1925, holotype PRI 1064, length 45.6 mm, width 47.1 mm, height 25.4 mm; *Cypraea henekeni* var. *potreronis* Ingram, 1939b: holotype USNM 559683, length 61 mm, width 48 mm, height 31.25 mm.
- Type locality*.—*Cypraea henekeni*, Yaque del Norte River, Sto. Domingo, Miocene; *Cypraea noueli*, Bluff 1, Cercado de Mao, Dominican Republic (= TU locality 1293), Gurabo Formation, lower Pliocene; *Cypraea henekeni* var. *lacrimula* Maury, 1925, Eastern E 24, 407 (central Trinidad), Machapoorie (= Machapure), Miocene, Trinidad; *Cypraea henekeni* var. *potreronis* Ingram, 1939b, bluff on the right bank of Río Amina at ford near Potrero, Provincia de Santiago, Santo Domingo, Gurabo Formation, lower Pliocene.
- Previously figured material*.—Hypotype (Maury, 1917a: p. 114, pl. 19, fig. 4), PRI 28775 (refigured by Ingram 1939b: p. 334, pl. 1, fig. 3; Ingram, 1947a: pp. 93–95, pl. 5, fig. 3);

hypotype (Maury, 1925: p. 219, pl. 37, fig. 1), PRI 1063; hypotype (Olsson, 1964: pp. 176–177, pl. 31, figs. 3, 3a), USNM 644046; hypotype (Olsson and Petit, 1968: p. 278, pl. 18, fig. 4), USNM 64782; hypotype (Burgess, 1985: p. 270, pl. 20, fig. H₃), USNM 113788; hypotypes (Doneddu and Manunza, 1996: pp. 1, 2, 4, 5, pl. 1, figs. A, B), ANSP 3007; hypotypes (Landau and Silva, 2010: pp. 38, 39, pl. 7, fig. 5 + cover) NHMW 2010/036/0027; hypotypes (Landau and Groves, 2011: pp. 2, 3, 8, figs. 15–20), NHMW 2010/0036/0027, 2010/0036/0028 (refigured in Lorenz, 2017: pl. G6, fig. 13; Lorenz, 2018: pl. 331, fig. 7).

Other material.—*Muracypraea henekeni*: 23 unnumbered lots NMB coll., comprised of 31 specimens; NHMW 2017/0124/0004–0013 (10 specimens; locality TU 1378); NHMW 2017/0124/0014–0016 (3 specimens; locality TU 1379); NHMW 2010/0036/0027, 0028, NHMW 2017/0124/0017–0023 (9 specimens; locality TU 1219); NHMW 2017/0124/0024–0035 (12 specimens; locality TU 1293); NHMW 2017/0124/0036, 0037 (2 specimens; locality NMB 16844); PRI 84429 (4 specimens; locality TU 1293); PRI 84430 (2 specimens; locality TU 1412); PRI 84431 (3 specimens; locality TU 1278); PRI 84432 (3 specimens; locality TU 1225); PRI 84433 (2 specimens; locality TU 1211); PRI 84434 (1 incomplete specimen; locality TU 1227A); PRI 84435 (12 specimens; locality TU 1231); PRI 84436 (6 specimens; locality TU 1277); PRI 84438 (7 specimens; locality TU 1230); PRI 84440 (4 steinkerns; locality TU 1255); PRI 84441 (2 juveniles of the ‘*noueli*’ morphotype; locality TU 1293); PRI 83919 (2 specimens; locality TU 1422); ANSP 3007 (8 specimens, Gabb Collection, Santo Domingo); ANSP 31682 (8 specimens, no locality data); PRI 84442 (1 adult, 1 fragment, 1 young adult, 1 juvenile ‘*noueli*’ morphotype; locality TU 1219); PRI 84443 (4 fragments; locality TU 1250); PRI 84444 (1 juvenile ‘*noueli*’ morphotype; locality TU 1293); PRI 84448 (1 juvenile ‘*noueli*’ morphotype; locality TU 1354); PRI 84449 (2 fragments; locality TU 1405); PRI 84450 (1 juvenile ‘*noueli*’ morphotype; locality TU 1379); PRI 84451 (2 juveniles of the ‘*noueli*’ morphotype; locality TU 1296); PRI 84452 (1 specimen; locality TU 1352); PRI 84453 (1 specimen; locality TU 1214); PRI 84456 (1 incomplete subadult; locality TU 1206); PRI 84465 (1 incomplete specimen; locality TU 1297); PRI 84777 (2 specimens; locality TU 1455); PRI 84762 (1 specimen + 1 fragment; locality TU 1375). ‘*Cypraea noueli*’ juvenile morphotype: NHMW 2017/0124/0038–0041 (4 specimens; locality TU 1215).

Measurements.—See Table 5 (*Muracypraea henekeni*) and Table 6 (*Cypraea noueli* juvenile morphotype).

Original description.—“Testa obovata, ventricosa, inflata, laevis, dorso postice irregulariter tuberculifero, lateribus, praecipue sinistro, obsolete granosis; extremitatibus, posticâ brevissimâ, anticâ subproductâ, aperturâ angustâ, marginibus dentatis, dentibus paucis, magnis, rotundatis, canali brevissimo, reflexo” (G. B. Sowerby I, 1850: p. 45).

Revised description.—Shell medium sized for genus, solid, roundly triangular shaped, dorsum very strongly humped slightly anterior to mid-dorsum, bearing two discrete tubercles, left slightly anterior to right; shallow dorsal sulcus/depression between tubercles in medio-dorsal line; spire depressed, covered by adapical callus; sides rounded, strongly callused, callus ascending rapidly adapically, enveloping the dorsal tubercles with margin just posterior to apex of dorsal hump (in some specimens, a small strip of uncallused dorsum occurs between tubercles), callus edge usually but not always delimited; venter flattened, slightly convex in profile; aperture almost straight, anterior third weakly dilated, posterior third weakly curved to the left; anterior canal deep, abaxially asymmetrical and abapically orthogonally truncated, flanked on either side by flattened spatulate horizontal expansions produced from the abapical tips of the inner and outer lips, developed to a variable degree; posterior channel very deep, limited by parallel lips; terminal ridge narrow, flattening abapically; 12–17 columella teeth, five stout short teeth above fossula, teeth weakening and more elongated posteriorly, almost restricted to columellar edge, not extending onto the venter and posteriorly only a very short distance into the aperture; fossula small, concave, smooth, poorly delimited; columellar peristome convex, smooth; outer lip broad, narrowing anteriorly, with 14–20 rounded teeth on inner edge, becoming stouter and slightly more widely spaced posteriorly, where the teeth extend as raised ridges to two-thirds labral width in some specimens. Most shells without color pattern preserved, callus golden-brown to cream; a few shells with large pigmented spots preserved on margins.

Remarks.—*Muracypraea henekeni* has a somewhat variable shell; the dorsal tubercles can be well developed and elevated to almost absent, the dorsal sulcus or depression between the tubercles present or absent, and the spatulate extensions of the anterior channel more or less developed. All these characters tend to become more marked in larger specimens, but this is not always the case. *Cypraea henekeni* var. *potreronis* was described from the Potrero Dam outcrop on the Río Amina, where this large gerontic morphotype occurs. The differences stated by Ingram (1939b: p. 331)—a deep pit between the dorsal tubercles, a deeply cut posterior channel, well-developed spatulate extensions at the anterior channel, and a heavy shell—are characters seen in the gerontic shells

Table 5. Measurements of *Muracypraea benekeni* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable.

Specimen	Length	Width	Height	LT	CT	Locality
NHMuK G83940 (lectotype)	58.9	44.2	33.4	19	14	Yaqui River Sto. Domingo
NHMuK GG20022-3 (paralectotype)	71.3	52.3	39.4	17	15	Yaqui River Sto. Domingo
NHMuK GG20024-5 (paralectotype)	54.9	45.1	29.4	15	14	Yaqui River Sto. Domingo
NHMuK GG20026 (paralectotype)	48.9	38.8	28.4	12	n/c	Yaqui River Sto. Domingo
NHMuK GG20027 (paralectotype)	49.6	34.7	29.2	15	15	Yaqui River Sto. Domingo
NMB coll. unnumbered	68.3	47.3	33.4	19	14	NMB 15899
NHMuW 2017/0124/0004	63.4	51.1	33.0	19	15	TU 1378
NHMuW 2017/0124/0005	59.8	44.4	31.2	20	15	TU 1378
NHMuW 2017/0124/0006	61.5	45.2	31.0	18	14	TU 1378
NHMuW 2017/0124/0007	57.6	42.2	30.5	18	16	TU 1378
NHMuW 2017/0124/0008	55.5	40.8	29.3	15	13	TU 1378
NHMuW 2017/0124/0009	57.6	43.4	27.9	n/c	n/c	TU 1378
NHMuW 2017/0124/0010	51.9	38.5	26.0	17	12	TU 1378
NHMuW 2017/0124/0011	49.0	39.3	27.2	18	15	TU 1378
NHMuW 2017/0124/0012	44.5	32.0	23.5	14	n/c	TU 1378
NHMuW 2017/0124/0013	45.1	35.7	23.8	16	14	TU 1378
NHMuW 2017/0124/0014	62.9	50.4	35.7	19	16	TU 1379
NHMuW 2017/0124/0015	66.8	52.3	38.6	18	14	TU 1379
NHMuW 2017/0124/0016	67.3	53.6	37.3	17	16	TU 1379
NHMuW 2010/0036/0027	51.5	40.3	28.0	16	16	TU 1219
NHMuW 2010/0036/0028	53.5	43.3	29.2	19	17	TU 1219
NHMuW 2017/0124/0017	61.0	41.0	32.1	19	18	TU 1219
NHMuW 2017/0124/0018	66.7	49.3	34.6	19	17	TU 1219
NHMuW 2017/0124/0019	62.5	46.4	35.0	n/c	n/c	TU 1219
NHMuW 2017/0124/0020	60.7	43.7	31.2	19	16	TU 1219
NHMuW 2017/0124/0021	66.9	45.1	34.3	18	16	TU 1219
NHMuW 2017/0124/0022	64.5	44.6	35.1	17	16	TU 1219
NHMuW 2017/0124/0023	63.1	46.3	35.1	n/c	n/c	TU 1219
NHMuW 2017/0124/0024	59.5	39.4	27.8	18	15	TU 1293
NHMuW 2017/0124/0025	48.3	36.4	26.4	16	15	TU 1293
NHMuW 2017/0124/0026	56.7	45.6	33.7	16	12	TU 1293
NHMuW 2017/0124/0027	52.6	36.7	28.4	15	13	TU 1293
NHMuW 2017/0124/0028	51.4	37.7	29.0	18	13	TU 1293
NHMuW 2017/0124/0029	58.6	42.0	33.1	16	18	TU 1293
NHMuW 2017/0124/0030	51.2	36.9	29.5	16	14	TU 1293
NHMuW 2017/0124/0031	50.3	35.1	27.9	18	13	TU 1293
NHMuW 2017/0124/0032	49.5	35.4	26.7	n/c	n/c	TU 1293

Table 5, continued. Measurements of *Muracypraea henekeni* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0033	43.8	33.8	24.0	18	14	TU 1293
NHMW 2017/0124/0034	44.1	34.2	23.9	16	15	TU 1293
NHMW 2017/0124/0035	39.1	28.0	21.2	17	15	TU 1293
NHMW 2017/0124/0036	70.9	51.2	37.9	17	15	NMB 16844
NHMW 2017/0124/0037	54.2	39.8	30.0	17	15	NMB 16844

Table 6. Measurements of '*Cypraea noueli*' juvenile morphotype specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable; * = measurement unreliable due to specimen being incomplete or distorted/crushed.

Specimen	Length	Width	Height	LT	CT	Locality
PRI 28776 (holotype)	60	44	39	n/c	n/c	TU 1293
NHMW 2017/0124/0038	44.7	33.5	26.9	n/c	17	TU 1215
NHMW 2017/0124/0039	44.6	32.7	25.7	18	16	TU 1215
NHMW 2017/0124/0040	39.6	30.3	24.0	17	14	TU 1215
NHMW 2017/0124/0041	39.6*	30.7	24.8	n/c	n/c	TU 1215

from all localities. Therefore, *Cypraea henekeni* var. *potreronis* is considered a junior subjective synonym of *M. henekeni*. As with most cypraeids, there is an enormous variation in adult size, and there is also some difference in the maximum size reached within a population. In the Dominican Republic, the largest specimens are found at locality TU 1379 (Arroyo Bajón, Río Mao), whereas specimens found at locality TU 1293 (Maury Bluff 1, Río Mao) tend to be smaller. The largest and smallest specimens with some dorsal tubercle developed are 71.3 mm and 39.1 mm in length, respectively.

Cypraea noueli is based on a juvenile specimen of *Muracypraea henekeni*. The differences between the two species given by Maury (1917a: p. 115)—that *C. noueli* is "...more globose and with no traces of dorsal tubercles, nor lateral corrugations, with a different color pattern, and with the apex of the spire visible"—are all features of juvenile or subadult cypraeids. Shell size cannot be used for the separation of the juvenile form, *C. noueli*, which lacks dorsal tubercles, from the adult tuberculate *M. henekeni*, as full adult size is highly variable. 'Dwarf' adult *M. henekeni* with tubercles can be smaller than the juvenile *C. noueli* form without tubercles.

Many species of *Muracypraea* have been described from the tropical American Neogene, some of which await validation. Landau and Groves (2011) suggested that the fossil *Muracypraea* species may have had intracapsular larval development like the extant *Muracypraea mus* complex (Ranson, 1967; Hoeblich, 1979). This assumption cannot be validated with the fossil taxa; however, this type of development would favor a restricted distribution of species

and a high degree of variability between populations. This helps explain the difficulty encountered with the Caribbean Neogene *Muracypraea* populations and may be analogous to the situation among Recent species of the genus *Zoila* in Australia, which also show intracapsular development. Numerous species of *Zoila* are not only geographically restricted, but numerous intermediate forms are common off the western and southern coasts of Australia (Lorenz and Hubert, 2000; Lorenz, 2001).

Comparisons.—The problems surrounding the classification of the "*Muracypraea henekeni* group" have been discussed at length by almost every author who attempted to determine how many species are present in the Neogene tropical American assemblages (Woodring, 1959; Groves, 1997; Landau and Silva, 2010; Landau and Groves, 2011). These taxonomic problems are not helped by the relative scarcity of well-preserved specimens in some of these deposits, especially the southern Caribbean, Colombian, and Trinidadian assemblages. Nevertheless, extensive recent collections from Panama (Panama Paleontology Project, PPP), Ecuador (Groves, 1997), and Venezuela (Landau and Silva, 2010; Landau and Groves, 2011) have allowed for species to be clearly identified.

Muracypraea hyaena (Schilder, 1939a) is a lower and middle Miocene southern Caribbean species found in Venezuela. It is characterized by having a relatively small shell that is rounded in outline and a strongly humped dorsum placed mid-length. It has poorly developed dorsal tubercles,

with the right tubercle larger and anterior to left. A color pattern of large spots occurs over the margins and dorsum.

Muracypraea isthmica (Brown and Pilsbry, 1911, p. 356 as “*Cypraea henikeni* Sowb., var.”) is from the middle and upper Miocene Gatun Formation of Panama. It is characterized by a medium-sized shell that is rounded in outline with a centrally placed, smoothly rounded, and poorly delimited dorsal hump; the dorsal tubercles are absent or hardly developed. A striped dull red-orange and tan color pattern is present on the ventral and dorsal zones; the marginal callus is lighter in color.

Muracypraea woodringi Landau and Groves, 2011, is from the late Miocene of Ecuador, Panama, and Colombia. It is characterized by a medium-sized, solid shell that is triangular in outline; the dorsum is strongly humped two-thirds the distance from the anterior end. The dorsal tubercles are small and warty; they are arranged in two groups, the left group larger and slightly anterior to right. A spike-like projection arises from the center of the apex in most specimens. A striped dull red-orange and tan color pattern is present on the ventral and dorsal zones; the marginal callus is lighter in color.

Muracypraea grahami (Ingram, 1947b) is from the lower Pliocene southern Caribbean of Cubagua, Venezuela. It is characterized by a very large, heavy shell that is strongly triangular in outline. The posterior margin is strongly crenulated, and the dorsum is strongly humped two-thirds the distance from the anterior end. The dorsal tubercles are well developed and close to the midline, with the right tubercles placed significantly anterior to the left. There is an indication of a striped color pattern.

Muracypraea caroniensis (Maury, 1925: p. 373, pl. 37, figs. 3, 5, 6) is from the lower Pliocene Springvale Formation, Trinidad. It differs from *Muracypraea henikeni* by its heavier, more elongate shell that lacks prominent dorsal tubercles; it also has more numerous and larger apertural teeth. The two syntypes of *Cypraea caroniensis* (PRI 1065, 1067)—despite a detailed description by Maury—are poorly preserved but clearly *Muracypraea*. The two line drawings of F. A. Schilder (1939a: figs. 26, 27) and a non-figured specimen of H. E. Vokes (1938: p. 4, AMNH 024680), also from Springvale, Trinidad, clearly demonstrate that the species differs from *M. henikeni*.

Muracypraea henikeni is easily separated from *Muracypraea hyaena* by its larger, more triangular shell, more strongly developed dorsal tubercles, and relative absence of color pattern. It is easily separated from *Muracypraea isthmica* by its less elevated dorsal gibbosity and the presence of well-developed dorsal tubercles. *Muracypraea henikeni* is distinguished from *Muracypraea woodringi* by its more anteriorly placed dorsal gibbosity and in having discrete dorsal tubercles rather than a group of warty tubercles; it also lacks a dorsal spike. It differs from *M. grahami* in having a smaller

average size and less triangular outline with a smooth rather than crenulated posterior edge. Furthermore, in *M. henikeni* the dorsal gibbosity is lower and more anterior and the dorsal tubercles are more widely spaced and less staggered than in *M. grahami*. The left tubercle is anterior to the right in *M. henikeni*, whereas the right is strongly anterior to the left in *M. grahami*.

Several other related taxa have been described from the tropical American Neogene: *Cypraea henikeni* var. *lacrimula* Maury, 1925 (pl. 37, fig. 2), from Machapoorie (= Machapure) Quarry, Brasso Formation, Trinidad, middle Miocene; *Cypraea tuberae* Ingram, 1947a and *Cypraea andersoni* Ingram, 1947a, both from the lower Pliocene of Tubará Hill, Colombia; *Cypraea almirantensis* Olsson, 1922, from the Pliocene Cayo Agua Formation of the Bocas del Toro area, Panama; and *Cypraea cayapa* Pilsbry and Olsson, 1941, from the lower Pliocene Jama Formation of Ecuador. All of these species are represented by poorly preserved or scant material and await validation.

The shells of the living *Muracypraea mus* (Linnaeus, 1758) differ from those of its fossil congeners in the character of the columellar dentition, which is obsolete in the central portion, whereas the dentition is always well-developed throughout in all the fossil species. The color pattern of *M. mus* is also different from that of any of the fossil taxa. In the Recent populations of *Muracypraea*, there are tuberculate and non-tuberculate specimens, the significance of which has produced much debate. Doneddu and Manunza (1996) separated the *M. mus* complex into two species and one subspecies; *Muracypraea mus mus*, *Muracypraea mus tristensis* (Petuch, 1987) and *Muracypraea donmoorei* (Petuch, 1979). Lorenz and Hubert (2000) and Lorenz (2017) recognized two subspecies, the shallow water *M. mus mus* (non-tuberculate) and *Muracypraea mus bicornis* (G. B. Sowerby II, 1870) (tuberculate), which is restricted to deeper water. They stated that *M. mus bicornis* was isolated from populations of *M. mus mus*. These populations have been split further into several geographical and ecological variants (Petuch, 1979, 1987), taxa of dubious taxonomic significance. The living *M. mus* and *M. mus bicornis* commonly live in infralittoral to upper sublittoral zones, in shallow water on smooth muddy bottoms among seaweed and sponges (Lorenz, 2017). It is likely that the fossil species lived in similar habitats.

Occurrence.—Río Cana (localities NMB 16817, NMB 16835, NMB 16842, NMB 16844, NMB 16865, TU 1230); Cañada de Zamba (TU 1354); Río Gurabo (localities NMB 15865, NMB 15867, NMB 15869, NMB 15870, NMB 15878, NMB 15883, NMB 15899, NMB 15901, NMB 15903, NMB 15905, NMB 15906, NMB 15908, NMB 15909, NMB 15910, TU, 1211, TU 1214, TU 1215, TU 1231, TU

1277, TU 1278, TU 1296, TU 1297, TU 1352, TU 1375, TU 1378); Río Amina (localities NMB 16807, TU 1219); Río Guanajuma, tributary of Río Amina (localities TU 1412, TU 1455); Río Mao (localities NMB 16901, NMB 16912, NMB 16914, NMB 16931, TU 1225, TU 1293, TU 1379); Arroyo Zalaya (locality TU 1227A); Río Yaque del Sur (TU 1255); Río Verde (TU 1250); Arroyo Babosico, tributary of Río Yaque del Norte (TU 1405); roadcut between Santiago and San Jose de las Matas (TU 1206).

Distribution.—Miocene (indeterminate): Haiti (Guppy, 1867, 1876); Dominican Republic (G. B. Sowerby I, 1850; Gabb, 1872; Pilsbry, 1922; Ingram, 1947a, 1947c; Pflug, 1961). Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; F. A. Schilder, 1932a; Ingram, 1939b; Woodring, 1959). Pliocene (indeterminate): Bowden Member of the Layton Formation, Jamaica (Woodring, 1928; Ingram, 1939b, 1947c; F. A. Schilder, 1939a). Lower Pliocene: Gurabo Formation, Dominican Republic (Maury, 1917a; Vaughan and Woodring, 1921; F. A. Schilder, 1932a; Ingram, 1939b; Ramírez, 1956; Woodring, 1959; Fast, 1978; Landau and Silva, 2010; Landau and Groves, 2011).

Tribe MAURITIINI Steadman and Cotton, 1946

Mauritiini Steadman and Cotton, 1946: p. 504 (as subfamily Mauritiinae).

Genus *MACROCYPRAEA* F. A. Schilder, 1930

Macrocypraea F. A. Schilder, 1930: p. 55. Type species (by original designation): *Cypraea exanthema* Linnaeus, 1767 [= *Cypraea zebra* Linnaeus, 1758], Recent, Bermuda, Florida, the Bahamas, the southern Gulf of Mexico, the entire Caribbean Sea to Trinidad, eastern to southern Brazil.

Macrocypraea (*Lorenzocypraea*) Petuch and Drolshagen, 2011: pp. 121, 122. Type species (by original designation): *Cypraea cervus* Linnaeus, 1771, Recent, southeastern United States, Florida and the Bahamas to the southern Gulf of Mexico and southern Cuba and Pleistocene of Florida.

Original diagnosis.—"The generic name *Erythraea*, Mörch (1877), being preoccupied by Sowerby (1839), I propose to call the genus *Macrocypraea*, with *Cypraea exanthema*, Linn, (1767), as genotype, which is the adult shell of *C. zebra*, Linn. (1758)" F. A. Schilder (1930: p. 55).

Description.—Medium to very large sized cowries, cylindrical shape, anterior aperture wide, narrows posteriorly.

Remarks.—This tropical American genus comprises at least three extant species: *Macrocypraea cervus* (Linnaeus, 1771)

and *Macrocypraea zebra* (Linnaeus, 1758) in the western Atlantic and *Macrocypraea cervinetta* (Kiener, 1843) in the Panamic Province. Recently, Simone and Cavallari (2020) described *Macrocypraea mammoth* from Trinidad, a remote oceanic island off Espírito Santo, Brazil. It is very similar to *M. cervus* but is wider and heavier and has anatomical differences. Some Caribbean fossil records occur, such as *Macrocypraea anguillana* (Cooke in Vaughan, 1919) and *M. cervus peilei* Schilder, 1932a; others ascribed by some authors (M. Schilder and F. A. Schilder, 1971; Lorenz and Hubert, 2000) to *Macrocypraea*—i.e., *Cypraea fossula* Ingram, 1947b, and *Cypraea trinitatensis* Mansfield, 1925—are best placed in the genus *Trona* Jousseume, 1884a (Landau and Groves, 2011). The erection of the subgenus *Lorenzocypraea* Petuch and Drolshagen, 2011, for *Cypraea cervus* Linnaeus, 1771, is not supported by the molecular phylogeny of Meyer (2004: p. 135, fig. 4).

Geographic range.—Southeastern United States, circum-Caribbean to Brazil, Ecuador and Islas Galápagos to the Golfo de California, México.

Stratigraphic range.—Miocene to Recent.

Macrocypraea zebra (Linnaeus, 1758)

Text-figs. 7.1–7.8

Cypraea zebra Linnaeus, 1758: p. 719.

Cypraea exanthema Linnaeus, 1767: pp. 1172, 1174.

Cypraea exanthema Linnaeus. d'Orbigny, 1845: p. 202.

Cypraea (*Tigris*) *exanthema* Linnaeus. Troschel, 1863: pp. 207, 208, pl. 17, fig. 7 (radula).

Cypraea exanthemata [sic] (v. *cervinella* [sic]) Kiener, 1843. Gabb, 1873: p. 572.

Cypraea carneola Linnaeus. Gabb, 1881: p. 360. [not *Lyncina carneola* (Linnaeus, 1758)]

Cypraea [sic] cf. *exanthema* Linnaeus. Loricé, 1889: pp. 133, 134, 142, pl. 2, fig. 20.

Cypraea exanthema Linnaeus. Fluck, 1905: p. 55.

Cypraea exanthema Linnaeus. Verrill, 1905: pp. 180, 348, pl. 36, fig. 19.

Cypraea exanthema Linnaeus. Hidalgo, 1906–1907: pp. 345–348.

Cypraea exanthema Linnaeus. Vredenburg, 1920: p. 88.

Cypraea exanthema Linnaeus. Maury, 1922: p. 113.

Cypraea exanthema Linnaeus. Vayssière, 1923: pp. 54, 55, pl. 1, figs. 7–11 (papillae and radula).

Cypraea (*Cypraea*) *zebra* var. *dissimilis* F. A. Schilder, 1924: p. 194.

Cypraea exanthema Linnaeus. Earle, 1928: p. 184.

Cypraea cf. *exanthema* Linnaeus. Rutten, 1931: p. 664.

Trona (*Macrocypraea*) *zebra* (Linnaeus). F. A. Schilder, 1932a: p. 134.

Trona (*Macrocypraea*) *zebra zebra* (Linnaeus). F. A. Schilder and M. Schilder, 1938–1939: pp. 179, 198.

Trona (*Macrocypraea*) *zebra zebra* (Linnaeus). F. A. Schilder 1939a: pp. 6, 9, 31.

Text-fig. 7. *Macrocypraea zebra* (Linnaeus, 1758). 1–4, NHMW 2017/0124/0001, length 81.2 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 5–8, NHMW 2017/0124/0003, length 64.7 mm; locality TU 1354, Cañada de Zamba, Dominican Republic, Gurabo Formation, lower Pliocene.

Cypraea (Trona) zebra Linnaeus. Jaume, 1946: p. 105.

Cypraea (Trona) zebra var. *vallei* Jaume and Borro, 1946: pp. 21, 22.

Cypraea zebra Linnaeus. Ingram, 1947a: pp. 82, 83.

Cypraea zebra Linnaeus. Ingram, 1947c: p. 150.

Cypraea zebra Linnaeus. Ingram, 1951: pp. 162, 163, pl. 1, figs. 9, 10.

Cypraea exanthema Linnaeus. Shetrone, 1954: p. 14.

Macrocypraea zebra zebra (Linnaeus). Allan, 1956: p. 40, pl. 5, figs. 5, 6.

Macrocypraea zebra dissimilis (Schilder). Allan, 1956: p. 40.

Cypraea (Trona) zebra Linnaeus. Abbott, 1958: p. 48.

Cypraea zebra Linnaeus. Nowell-Usticke, 1959: p. 53.

Cypraea zebra Linnaeus. Warmke and Abbott, 1961: pp. 91, 92, pl. 2, fig. e, pl. 16, fig. n.

Cypraea zebra Linnaeus. Weber, 1961: p. 56.

Cypraea (Trona) zebra Linnaeus. Weisbord, 1962: pp. 16, 22, 234–236, pl. 22, figs. 3, 4 (juvenile).

Macrocypraea zebra (Linnaeus). Schilder, 1966b: pp. 197, 198.

Cypraea zebra Linnaeus. Ranson, 1967: pp. 95, 105, pl. 11, fig. 2 (protoconch).

Cypraea zebra Linnaeus. Sarasura, 1968: p. 2, figs. 1, 2.

Cypraea zebra Linnaeus. Richards et al., 1969: p. 6.

Cypraea zebra Linnaeus. Burgess, 1970: p. 229, pl. 21, figs. B, C, C₁.

Cypraea zebra Linnaeus. Kaufman and Götting, 1970: p. 362, fig. 65.

- Cypraea zebra* Linnaeus. Crovo, 1971: pp. 292–295.
 Not *Macrocypraea* aff. *zebra* (Linnaeus). Jung, 1971: p. 181, pl. 8, figs. 1–3 [= *Trona trinitatis* (Mansfield, 1925)].
Macrocypraea zebra (Linnaeus). M. Schilder and F. A. Schilder, 1971: p. 33.
Cypraea zebra Linnaeus. Brunt et al., 1973: p. 218.
Cypraea zebra Linnaeus. Abbott, 1974: p. 149, color pl. 5, fig. 1638.
Cypraea zebra Linnaeus. Zeiller, 1974: p. 37, unnumbered fig.
Cypraea (Trona) zebra Linnaeus. Regteren Altena, 1975: p. 35.
Cypraea zebra Linnaeus. Briton, 1975: p. 36.
Cypraea zebra Linnaeus. Taylor and Walls, 1975: p. 189, 2 unnumbered figs.
Cypraea zebra Linnaeus. Lozet and Pétron, 1977: p. 49, fig. 36.
Cypraea zebra Linnaeus. Manjarres, 1979: p. 36.
Cypraea zebra Linnaeus. Taylor, 1979: p. 189, 2 unnumbered figs.
Cypraea zebra Linnaeus. Macha, 1982: p. 176.
Cypraea (Macrocypraea) zebra Linnaeus. H. E. Vokes and E. H. Vokes, 1983: p. 21, pl. 8, fig. 10.
Cypraea zebra Linnaeus. Bandel, 1984: pp. 82, 83, fig. 135, pl. 7, fig. 3 (radula).
Cypraea zebra Linnaeus. Burgess, 1985: p. 100, 3 unnumbered figs.
Cypraea zebra Linnaeus. Bertsch, 1987: p. 25.
Cypraea (Macrocypraea) zebra Linnaeus. Robinson and Montoya, 1988: p. 386.
Cypraea (Macrocypraea) zebra Linnaeus. Cossignani and Passamonti, 1991: pp. 8, 123.
Cypraea (Macrocypraea) zebra Linnaeus. Robinson, 1991: p. 250, pl. 10, figs. 3a, b.
Cypraea zebra Linnaeus. Donovan and Littlewood, 1993: p. 36.
Macrocypraea zebra (Linnaeus). Lorenz and Hubert, 1993: p. 53, pl. 10, figs. 12, 14, 17, 20.
Cypraea zebra Linnaeus. Díaz and Puyana, 1994: p. 166, fig. 615.
Cypraea zebra Linnaeus. Ramos and Robaina, 1994: p. 101.
Macrocypraea zebra (Linnaeus). Bradner and Kay, 1996: p. 72, fig. 117 (radula).
Cypraea zebra Linnaeus. Fernández Milera, 1998: pp. 116, 206, unnumbered fig.
Cypraea zebra Linnaeus. Carlos and Joaquín, 1998: p. 126.
Cypraea (Macrocypraea) zebra Linnaeus. Espinosa et al., 1988: p. 20.
Macrocypraea zebra (Linnaeus). Lorenz and Hubert, 2000: p. 53, pl. 10, figs. 12, 14, 17, 20.
Cypraea (Trona) zebra Linnaeus. Macsotay and Campos Villaroel, 2001: pp. 56, 57.
Cypraea (Macrocypraea) zebra Linnaeus. Espinosa and Ortea, 2001: p. 17.
Macrocypraea zebra (Linnaeus). Redfern, 2001: p. 51, pl. 26, figs. 219A–C.
Cypraea zebra Linnaeus. López and Mijail Pérez, 2004: pp. 54, 55, figs. 1, 2.
Cypraea zebra Linnaeus. Rios, 2009: p. 132, fig. 314.
Macrocypraea zebra (Linnaeus). Jensen and Pearce, 2009: pp. 62, 63.
Macrocypraea zebra (Linnaeus). Tunnell et al., 2010: p. 172, unnumbered fig.
Cypraea cf. *zebra* Linnaeus. Díaz and García-Llano, 2010: p. 110.
Macrocypraea zebra (Linnaeus). Petuch and Sargent, 2011: pp. 47, 80, 135, fig. 3.2A.
Macrocypraea zebra (Linnaeus). Zhang, 2011: pp. 89, 90, fig. 236.
Cypraea (Trona) zebra var. *vallei* Jaume and Borro. Zhang, 2011: pp. 89, 90, fig. 237.
Macrocypraea zebra dissimilis (Schilder). Zhang, 2011: pp. 89, 90, fig. 238.
Macrocypraea zebra (Linnaeus). Daccarett and Bossio, 2011: p. 65, fig. 176.
Macrocypraea zebra (Linnaeus). Simone, 2011: pp. 166, 215.
Macrocypraea zebra (Linnaeus). Redfern, 2013: p. 42, figs. 117A–E.
Macrocypraea (Macrocypraea) zebra (Linnaeus). Petuch, 2013: pp. 26, 27, 37, figs. 2.8C, D.
Macrocypraea (Macrocypraea) zebra dissimilis (Schilder). Petuch, 2013: pp. 154, 159, figs. 10.12D, E.
Macrocypraea zebra (Linnaeus). Petuch and Myers, 2014: pp. 141, 150, 254, fig. 7.5D.
Macrocypraea zebra (Linnaeus). Lamy and Pointier, 2017: p. 170, pl. 48, figs. 3a–d.
Macrocypraea zebra zebra (Linnaeus). Lorenz, 2017: pp. 191, 288, pl. H8, fig. 59.
Macrocypraea zebra (Linnaeus). Massemin et al., 2017: p. 100, 2 unnumbered figs.
Macrocypraea zebra zebra (Linnaeus). Lorenz, 2018: p. 126, pl. 59, figs. 5–14.
Cypraea zebra (Linnaeus). Bergonzoni, 2019: p. 57, fig. 13.
Cypraea exanthema (Linnaeus). Bergonzoni, 2019: p. 58, fig. 14.
- Type material.*—*Cypraea zebra* Linnean Society of London (Hanley, 1855), lectotype (Schilder, 1966a: p. 92); Linnean Society of London, figured by Bergonzoni (2019: p. 57, fig. 13); *Cypraea exanthema* Linnean Society of London, lectotype (Schilder, 1966a: p. 92; figured by Bergonzoni, 2019: p. 58, fig. 14); *Cypraea (Cypraea) zebra* var. *dissimilis*, in Schilder collection?; *Cypraea zebra* var. *vallei*, holotype (?) in Jaume collection, Museo Poey de la Universidad de la Habana, Cuba 20,813.
- Type locality.*—*Cypraea zebra*, not given by Linnaeus (Dodge, 1953: p. 69; Schilder, 1966b: p. 197), India [= West Indies?] (Schilder, 1966b: p. 197); *Cypraea exanthema*, unknown (Schilder, 1966b: p. 197), *Oceanus americanus*, *atlanticus* (Schilder, 1966b: p. 197); *Cypraea (Cypraea) zebra* var. *dissimilis*, unknown (Schilder, 1966b: p. 198), S.E. Brazil (Schilder, 1966b: p. 198); *Cypraea zebra* var. *vallei*, Bacuranas (Habana), Cuba (Schilder, 1966b: p. 198).
- Other material.*—NMB unnumbered specimens (2 fragments; localities NMB16818, NMB 16865); NHMW 2017/0124/0001, 0002 (2 specimens; locality TU 1215); NHMW 2017/0124/0003 (1 specimen; locality TU 1354); PRI 84437 (2 specimens; locality TU 1215); PRI 84439 (2 steinkerns; locality TU 1415); PRI 84455 (1 steinkern; locality TU 1281).

Table 7. Measurements of *Macrocypraea zebra* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable; * = measurement unreliable due to specimen being incomplete or distorted/crushed.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0001	81.2	45.4*	33.6*	n/c	n/c	TU 1215
NHMW 2017/0124/0002	76.6*	44.0	35.8*	n/c	n/c	TU 1215
NHMW 2017/0124/0003	64.7*	37.5	31.4	25	31	TU 1354

Measurements.—See Table 7.

Original description.—*Macrocypraea zebra*: “C. testa turbinata cinerea fasciis fuscis ... Statura Carneolae, sed duplo major, spira majore evidentiore quam in reliquis. Denticuli aperturae fuscis. Venter ocellis obsoletes” (Linnaeus, 1758: p. 719; Linnaeus, 1767: p. 1174).

Macrocypraea exanthema: “C. testa subturbinata ferruginea maculis pallidis rotundis adspersa, llines longitudinali subramosa. Similis C. Mappae, sed color atro s. rufo ferrugineus; linea longitudinalis recta uno alterove ramo; caeterum adspersa punctis latis pallidis. Spira mucrone prominens, Subtus pallida, immaculate ” (Linnaeus, 1767: pp. 1172, 1173).

Revised description.—Shell large, solid, subovate, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides angular, strongly callused, callus ascending to $\frac{1}{2}$ – $\frac{1}{3}$ shell height, left callus higher than right; venter flattened, weakly convex; aperture of medium width, parasigmoidal, posteriorly curving to left, anterior portion slightly wider; siphonal canal narrow, abaxially asymmetrical, anterior termini barely constricted, blunt; exhalant channel weakly produced, relatively shallow; columella denticulate along entire length, bearing 31 well developed, narrow denticles extending as folds deep within columellar peristome, on venter denticles stopping abruptly at angulation; terminal fold strongly developed and elevated, bordering siphonal canal, where it is strengthened and keel-like with a prominent, elevated internal lamina (sensu Dolin and Lozouet, 2004), separated from columellar teeth by deep groove; fossula shallow, poorly delimited from rest of columella, steep, bearing strong ridges extending to inner edge, ending in denticle; 25 narrow labral teeth, outer lip bevelled inwards with teeth extending across bevelled inner portion to slightly less than mid-labral width (based on Dominican fossil specimens).

Remarks.—Linnaeus (1758) based this species on a juvenile specimen and later described an adult under the name *Cypraea exanthema* Linnaeus, 1767.

Macrocypraea zebra is uncommon in the Dominican Republic assemblages, occurring in deposits of upper Miocene

Cercado and lower Pliocene Gurabo age. The venter is exposed in only one of the three specimens at hand. The teeth on the outer lip and columella fit within the range observed in present-day specimens. The radula is of the ‘Mauritiana Pattern’ of Bradner and Kay (1996) and is large with a central tooth with a pair of denticles that project below the basal platform. The apex of the rectangular central tooth is straight rather than curved, and all teeth on the ribbon overlap. Living specimens are commonly found in infralittoral to medium deep water, under rocks and in crevices; they often live in turbid water (Lorenz, 2017).

Comparisons.—*Macrocypraea cervus* (Linnaeus, 1771) co-occurs sympatically with *Macrocypraea zebra* in the northern Caribbean but does not occur in the southern Caribbean. It differs from *M. zebra* in having a greater maximum length, although as in most cowries adult size is highly variable. *Macrocypraea cervus* also has a more inflated shell, and the anterior portion of the aperture is wider. Crovo (1971) raised the possibility that the two species were simply sexually dimorphic forms of the same species, as they occur together in many Florida localities. However, she concluded that they are separate species based on radular differences and shell shape differences. *Macrocypraea cervinetta* (Kiener, 1843), from the tropical American Pacific, attains the smallest maximum size of the three congeners, has a more cylindrical depressed shell form, and also has a wider anterior aperture. López and Pérez (2004) presented evidence of ‘zebra-like’ specimens in the Panamic Province of Nicaragua. In a multivariate analysis they concluded that 20 of their 22 specimens were *M. cervinetta*, but two remained dubious. Because all of their specimens were collected in Pacific Nicaragua, it is unlikely that there is a valid case for *M. zebra* living in that region.

Occurrence.—Río Cana (localities NMB 16818, NMB 16865); Cañada de Zamba (locality TU 1354); Río Gurabo (localities TU 1215, TU 1415); Quarry south side Río Yaque (TU 1281).

Fossil distribution.—Upper Miocene: Cercado Formation, Dominican Republic (herein). Miocene–Pliocene (indeterminate): San Andrés Formation, Isla de San Andrés, Colombia (Díaz and García-Llano, 2010). Lower Pliocene:

Gurabo Formation, Dominican Republic (herein). Pliocene: Haiti (F. A. Schilder, 1939a; Ingram, 1947a, 1947c, 1951); Curaçao and Aruba (F. A. Schilder, 1932a). Lower Pleistocene: Moin Formation, Costa Rica (Robinson, 1991). Upper Pleistocene: La Isabella Formation, Dominican Republic (NHMW coll.); Boca Chica Formation, Isla Margarita, Venezuela (NHMW coll.); Coulibstre and Morne Daniel, Dominica (Earle, 1928); Ironshore Formation, Grand Cayman (Brunt et al., 1973); Falmouth Formation, Jamaica (Donovan and Littlewood, 1993); Devonshire Formation, Bermuda (Verrill, 1905; Ingram, 1951; Richards et al., 1969); Hastings, Barbados (F. A. Schilder, 1932a, 1939a; Ingram, 1947a, 1947c, 1951); Aruba and Curaçao (Lorié, 1889; Rutten, 1931); Cuba, Trinidad, and Bermuda (F. A. Schilder, 1932a). Holocene: Hopewell burial mound, Ohio (Shetrone, 1954).

Recent distribution.—Bermuda (Jensen and Pearce, 2009), Florida, the Bahamas, the southern Gulf of Mexico, and the entire Caribbean Sea to Trinidad and southern Brazil.

Macrocypraea dominicensis* (Gabb, 1872) *nomen inquirendum
Text-fig. 8

Cypraea dominicensis Gabb, 1872: p. 236.

Cypraea dominicensis? Gabb. Maury, 1917a: p. 116, pl. 19, fig. 11.

Cypraea dominicensis? Gabb. Maury, 1917b: p. 21.

Cypraea (Bernayia) dominicensis Gabb. Vredenburg, 1920: p. 93.

Cypraea dominicensis Gabb. Vaughan and Woodring, 1921: p. 141.

Cypraea dominicensis Gabb. Olsson, 1922: p. 196.

Cypraea cf. dominicensis Gabb. Olsson, 1922: p. 312.

Cypraea dominicensis Gabb. Pilsbry, 1922: p. 364, pl. 30, figs. 7, 8.

Talparia (Luria) dominicensis (Gabb). F. A. Schilder, 1927: p. 101.

Luria (Luria) dominicensis (Gabb). F. A. Schilder, 1932a: p. 147.

Luria (Luria) dominicensis (Gabb). F. A. Schilder, 1939a: pp. 4, 9, 28.

Cypraea dominicensis Gabb. Ingram, 1939b: pp. 333, 334.

Cypraea dominicensis Gabb. Richards, 1968: p. 125.

Luria dominicensis dominicensis (Gabb). M. Schilder and F. A. Schilder, 1971: pp. 40, 111.

Not *Cypraea dominicensis?* Gabb. Fast, 1978: p. 83 [= *Luria patrespatriae* (Maury, 1917a)].

Not *Talparia (Talparia) dominicensis* (Gabb). Dolin, 1991: p. 23 (in part), figs. 23a–c [= *Luria (Tessellata) dockeryi* Dolin and Lozouet, 2004].

Not *Talparia (Talparia) dominicensis* (Gabb). Dolin, 1991: p. 23 (in part), figs. 24a, b [= *Luria (Tessellata) pseudotalpa* Dolin and Lozouet, 2004].

Luria (Luria) dominicensis (Gabb). Kugler, 2001: p. 269.

Luria dominicensis (Gabb). Kugler, 2001: p. 270.

Luria dominicensis (Gabb). Landau and Groves, 2011: p. 8.

Macrocypraea dominicensis (Gabb). Lorenz, 2017: p. 286.

Luria dominicensis (Gabb). Groves and Squires, 2018: p. 76.

Text-fig. 8. *Macrocypraea dominicensis* (Gabb, 1872); specimen illustrated by Pilsbry (1922: pl. 30, figs. 7, 8) Santo Domingo, Miocene. Type lost, considered *nomen inquirendum* herein.

Type material.—Holotype ANSP 3003 (Richards, 1968: p. 125 as ‘type’), currently missing (K. Estes-Smargiassi, pers. comm. to LG, 2020).

Type locality.—Santo Domingo, Miocene (Maury, 1917a).

Original description.—“Shell very similar to *C. lurida* and *C. pulchra* in form, sides-subparallel, anterior end tapering more than the posterior, base slightly flattened; inner lip flexuous in advance; teeth small, very numerous and not extending over the base” (Gabb, 1872: p. 236). He goes on to note that “This shell is closely allied to *C. lurida* and *C. pulchra*, but differs from both in that its teeth are small, regular, uniform and end abruptly along a straight line. This last character at once separates it from the latter, while the size of the crenulations equally distinguish [*sic*] it from the former. The largest specimen is 1.5 inch long.”

Remarks.—This species is based solely on its missing holotype. Because of this, a scanned figure of Pilsbry (1922: pl. 30, figs. 7, 8) is included herein (Text-fig. 8).

The present authors suggest that this species be considered a *nomen inquirendum* or a name that requires further investigation. Maury’s (1917a) hypotype of *Cypraea dominicensis?* is actually her own species *Luria patrespatriae*. Olsson (1922: p. 312) noted a fragmentary shell of *Cypraea dominicensis* from Limon, Costa Rica, but did not figure it; F. A. Schilder (1939a) did not figure any specimens of *C. dominicensis* from two localities in Trinidad, although he compared the specimens to *L. patrespatriae*. Therefore, the records of Olsson (1922) and F. A. Schilder (1939a) remain unsubstantiated for the time being.

Lorenz (2017) attributed his assignment of *Cypraea dominicensis* to *Macrocypraea* to his examination of the figures of *Talparia dominicensis* in Dolin (1991), but Lorenz disagreed with Dolin’s generic assignment. The authors concur with Lorenz’s assignment of the species to *Macrocypraea*.

Dolin (1991: p. 23) synonymized *Jousseamea joosi* Schilder, 1939a, with *Macrocypraea dominicensis*. The holotype of *J. joosi* is a poorly preserved internal mold from Trinidad. It was considered a *nomen dubium* by Landau and Groves (2011: p. 8) and possibly represents a specimen of *Luria*.

Distribution.—All reports need confirmation as *Macrocypraea dominicensis* is considered a *nomen inquirendum* herein. Miocene (indeterminate): Dominican Republic (Gabb, 1872; Maury, 1917a, 1917b; Vaughan and Woodring, 1921; Olsson, 1922; Pilsbry, 1922; Ingram, 1939b, 1947a, 1947c; Richards, 1968; Fast, 1978), Trinidad (Ingram, 1947c). Middle Miocene: Guaracara Limestone Member, Tamana Formation, Trinidad (Kugler, 2001). Miocene: Gurabo, Dominican Republic (F. A. Schilder, 1932a); Brasso Formation, Trinidad (F. A. Schilder, 1939a). Lower Pliocene: Gurabo Formation, Dominican Republic (F. A. Schilder, 1932a). Pliocene (indeterminate): Port Limon, Costa Rica (Olsson, 1922; F. A. Schilder, 1932a [as Panama]).

Subfamily **LURIINAE** F. A. Schilder, 1932a

Luriinae F. A. Schilder, 1932a: p. 145 (as tribe).

Tribe **LURIINI** F. A. Schilder, 1932a

Luriini F. A. Schilder, 1932a: p. 145.

Genus **LURIA** Jousseume, 1884a

Luria Jousseume, 1884a: p. 92; Jousseume, 1884b: p. 414.

Type species (by original designation): *Cypraea lurida* Linnaeus, 1758, Recent, Mediterranean Sea, West Africa, and the Canary Islands to Angola and Ascension and St. Helena islands.

Tessellata Jousseume, 1884a: p. 97. Type species (by original monotypy): *Cypraea tessellata* Swainson, 1822, Recent, Hawai'i and the West Pacific.

Basilitronea Iredale, 1930: p. 83. Type species (by original designation): *Cypraea isabella* Linnaeus, 1758, Recent, Indo-Pacific.

Original description.—"Coquille ovoïde, allongée, déprimée en dessous, arrondie en dessus, extrémité antérieure large et bilobée; spire recouverte d'un enduit; ouverture un peu sinuée à bords dentés, fossette antérieure du bord columellaire peu accentuée" (Jousseume, 1884a: p. 92).

Revised description.—"Elongate-oval shells with short, well developed, often very fine teeth" (Lorenz, 2017: p. 350).

Remarks.—Dolin (1991) synonymized the genera/subgenera *Tessellata* Jousseume, 1884a (type species *Cypraea tessellata*

Swainson, 1822), *Basilitronea* Iredale, 1930 (type species *Cypraea isabella* Linnaeus, 1758) and *Fossacypraea* Schilder, 1939b (type species *Cypraea hieroglyphica* Schilder, 1923) with *Talparia* Troschel, 1863. Lorenz and Hubert (2000) considered '*Basilitronea*' and '*Tessellata*' as species groups within the genus *Luria* Jousseume, 1884a. Dolin and Lozouet (2004) transferred the tropical American species included in *Talparia* by Dolin (1991) to *Luria* (*Tessellata*). Meyer's (2004) molecular data supports the systematic arrangement of Lorenz and Hubert (2000), on the basis of which López Soriano (2006) formally synonymized *Tessellata* with *Luria*.

Shells in the genus *Luria* differ from those in *Talparia* in having blunt extremities and short and deep anterior and posterior canals. The anterior canal is straight in *Luria* as opposed to slightly offset in *Talparia*. In *Luria* the angulation is more prominent, with the labral teeth developed at the angulation running into the aperture but not onto the venter. In *Talparia* the angulation is developed and raised in the anterior portion, but not in the mid and posterior portions; the teeth extend a short distance onto the venter. The character of the fossula is similar in both genera; it is spoon-like, smooth or weakly ribbed, with denticles on the inner margin.

The genus *Fossacypraea* Schilder, 1939b, based on a Paratethian middle Miocene type species, was considered a valid genus by Lozouet et al. (2001: p. 40), but later synonymized with *Luria* by Dolin and Lozouet (2004: p. 23). However, Lorenz (2017: p. 358) considered it a valid genus, which "seems to represent an ancestral group that inhabited the entire area between the western Atlantic and the Paratethys in the mid-Miocene." The authors concur with Lorenz's assignment.

Geographic range.—Indo-Pacific and entire Pacific Panamic Province, Mediterranean and West Africa, southeastern United States, Caribbean to Brazil.

Stratigraphic range.—Late Miocene to Recent.

Luria cinerea (Gmelin, 1791)

Text-figs. 9.1–9.11, 10.1–10.21

Cypraea cinerea Gmelin, 1791: p. 3402.

Cypraea sordida Lamarck, 1811: p. 90, fig. 22.

Cypraea sordida Lamarck. Lamarck, 1822: p. 386.

Cypraea cinerea Gmelin. Wood, 1825: p. 88, pl. 17, fig. 27.

Cypraea sordida Lamarck. Kiener, 1843: pl. 26, fig. 2.

Cypraea sordida Lamarck. Kiener, 1845: p. 84.

Cypraea cinerea Gmelin. Reeve, 1846: pl. 22, fig. 124.

Cypraea cinerea Gmelin. d'Orbigny, 1845: pl. 7, figs. 9, 12.

Cypraea isabella Linnaeus. Gabb, 1872: p. 235 [not *Luria isabella* (Linnaeus, 1758)].

Cypraea cinerea Gmelin. Weinkauff, 1881b: p. 25, pl. 7, figs. 9, 12.

Text-fig. 9. *Luria cinerea* (Gmelin, 1791). 1–3, holotype specimen formerly assigned to *Cypraea campbelliana* Pilsbry, 1922, ANSP 3000 (ex Gabb collection), length 30.3 mm; Santo Domingo, Miocene. 4–7, holotype specimen formerly assigned to *Luria (Luria) cinerea rutschi* Schilder, 1939a, H 11295 (NMB collection), length 32.7 mm; Jacmel, Haiti, Pliocene. 8–11, holotype specimen formerly assigned to *Luria (Basilitrona) moritura* Schilder, 1939a, H 11287 (NMB collection), length 31.9 mm; Jacmel, Haiti, Pliocene.

Cypraea cinerea Gmelin. Gabb, 1881: p. 360.
Cypraea cinerea Gmelin. Tryon, 1885: p. 166, pl. 2, figs. 15, 16.
Cypraea [sic] cf. *sordida* Linnaeus. Loric, 1889: pp. 134, 142.
Cypraea cinerea Gmelin. Baker, 1891: p. 52.
Cypraea cinerea Gmelin. Dall and Simpson, 1901: p. 420.
Cypraea cinerea Gmelin. Verrill, 1905: p. 180.
Cypraea fragilioides Hidalgo, 1906–1907: p. 356.
Cypraea (Bernayia) cinerea Gmelin. Vredenburg, 1920: p. 93.
Cypraea cinerea Gmelin. Olsson, 1922: p. 312, pl. 15, fig. 8.
Cypraea cinerea Gmelin. Pilsbry, 1922: p. 364.
Cypraea campbelliana Pilsbry 1922: pp. 365, 366, pl. 30, figs. 9, 10.
Cypraea cinerea Gmelin. Maury, 1922: p. 113.
Cypraea cinerea Gmelin. Earle, 1928: p. 184.
Cypraea cf. *sordida* Linnaeus. Rutten, 1931: p. 664.
Luria (Luria) cinerea campbelliana (Pilsbry). F. A. Schilder 1932a: p. 147.
Luria (Luria) cinerea cinerea (Gmelin). F. A. Schilder, 1932a: p. 148.
Cypraea cinerea Gmelin. Johnson, 1934: p. 112.
Cypraea cinerea Gmelin. M. Smith, 1937: p. 110.
Luria (Luria) cinerea cinerea (Gmelin). F. A. Schilder, 1939a: pp. 6, 9, 29, 30.

Luria (Luria) cinerea campbelliana (Pilsbry). F. A. Schilder 1939a: p. 29.
Luria (Luria) cinerea rutschi F. A. Schilder 1939a: pp. 6, 9, 28, fig. 31.
Luria (Basilitrona) moritura F. A. Schilder, 1939a: pp. 6, 9, 27, fig. 30.
Cypraea cinerea var. *morinis* Ingram 1939b: pp. 324, 325, pl. 21, figs. 8, 9.
Cypraea cinerea Gmelin. Ingram, 1939b: pp. 329, 333.
Cypraea campbelliana Pilsbry. Ingram, 1939b: p. 333.
Cypraea isabella Linnaeus. Ingram, 1939b: p. 335 [not *Luria isabella* (Linnaeus, 1758)].
Cypraea costaricensis Ingram 1940: p. 505, figs. 1, 2.
Cypraea cinerea var. *limonensis* Ingram, 1940: p. 505, figs. 3, 4.
Cypraea cinerea Gmelin. Ingram, 1942: p. 99.
Cypraea cinerea Gmelin. Patterson, 1944: p. 38.
Cypraea cinerea Gmelin. Jaume, 1946: p. 105.
Cypraea cinerea Gmelin. Ingram, 1947a: pp. 70, 71.
Cypraea cinerea limonensis Ingram. Ingram, 1947a: pp. 90, 91, pl. 7, fig. 12.
Cypraea cinerea morinis Ingram. Ingram, 1947a: p. 91, pl. 7, figs. 5, 6.
Cypraea costaricensis Ingram. Ingram, 1947a: pp. 91, 92.
Cypraea cinerea Gmelin. Ingram, 1947d: pp. 1, 2.

- Cypraea cinerea* Gmelin. Ingram, 1951: pp. 147–149, pl. 21, figs. 1, 2.
- Cypraea cinerea* Gmelin. Salisbury, 1953: p. 48.
- Cypraea cinerea* Gmelin. Abbott, 1954: p. 180, pl. 6, fig. C.
- Cypraea cinerea* Gmelin. Richards, 1955: p. 9.
- Luria cinerea* (Gmelin). Allan, 1956: p. 38, pl. 4, figs. 21, 22.
- Cypraea (Luria) cinerea* Gmelin. Abbott, 1958: p. 48.
- Cypraea (Luria) cinerea* Gmelin. Olsson and McGinty, 1958: p. 15.
- Cypraea cinerea* Gmelin. Nowell-Usticke, 1959: p. 53.
- Cypraea cinerea* Gmelin. Brann and Kent, 1960: p. 305.
- Talparia (Luria) cinerea* (Gmelin). Regteren Altena, 1961: p. 297.
- Talparia (Luria)* cf. *cinerea* (Gmelin). Regteren Altena, 1961: p. 297.
- Cypraea (Luria) cinerea* Gmelin. Weisbord, 1962: pp. 16, 22, 228, pl. 21, figs. 11, 12, pl. 22, figs. 1, 2 (juvenile).
- Cypraea cinerea* Gmelin. Warmke and Abbott, 1961: p. 92, pl. 16, fig. h.
- Cypraea cinerea* Gmelin. Weber, 1961: p. 56.
- Cypraea (Luria) cinerea catiana* Weisbord, 1962: pp. 44, 230, pl. 21, figs. 13, 14.
- Cypraea cinerea* Gmelin. Rehder, 1962: p. 584.
- Cypraea campbelliana* Pilsbry. Clench and Turner, 1962: p. 25.
- Luria cinerea* (Gmelin). Schilder, 1966b: p. 205.
- Cypraea cinerea* Gmelin. Ranson, 1967: pp. 95, 104, pl. 10, fig. 3 (protoconch).
- Cypraea campbelliana* Pilsbry. Richards, 1968: p. 110.
- Cypraea cinerea* Gmelin. Radwin, 1969: p. 231.
- Cypraea cinerea* Gmelin. Richards et al., 1969: p. 6.
- Cypraea (Luria) cinerea* Gmelin. Rios, 1970: p. 60, pl. 11.
- Cypraea cinerea* Gmelin. Burgess, 1970: p. 39, pl. 2, fig. A.
- Cypraea cinerea* Gmelin. Kaufman and Götting, 1970: p. 362, fig. 66.
- Luria cinerea campbelliana* (Pilsbry). M. Schilder and F. A. Schilder, 1971: pp. 40, 102.
- Luria cinerea morinis* (Ingram). M. Schilder and F. A. Schilder, 1971: pp. 40, 135.
- Cypraea cinerea* Gmelin. Bandel, 1973: p. 83, fig. 137, pl. 7, fig. 4 (radula).
- Cypraea (Luria) cinerea* Gmelin. Morris, 1973: p. 175, pl. 48, fig. 14.
- Cypraea (Luria) cinerea* Gmelin. Abbott, 1974: p. 149, color pl. 5, fig. 1639.
- Cypraea (Luria) cinerea* Gmelin. Rios, 1975: p. 71, pl. 20, fig. 292.
- Cypraea cinerea* Gmelin. Briton, 1975: p. 36.
- Cypraea cinerea* Gmelin. Humfrey, 1975: p. 106, pl. 9, fig. 3.
- Cypraea cinerea* Gmelin. Taylor and Walls, 1975: p. 101, 2 unnumbered figs.
- Cypraea cinerea* Gmelin. Lozet and Pétron, 1977: p. 50, fig. 40.
- Cypraea cinerea* Gmelin. Manjarres, 1979: p. 36.
- Cypraea cinerea* Gmelin. Walls, 1975: p. 101, 2 unnumbered figs.
- Cypraea cinerea* Gmelin. Abbott and Dance, 1982: p. 95, unnumbered fig.
- Cypraea (Luria) cinerea* Gmelin. H. E. Vokes and E. H. Vokes, 1983: p. 21, pl. 8, fig. 11.
- Cypraea cinerea* Gmelin. Bandel, 1984: p. 83, fig. 137, pl. 7, fig. 4 (radula).
- Cypraea cinerea* Gmelin. Burgess, 1985: p. 182, 3 unnumbered figs.
- Cypraea (Luria) cinerea* Gmelin. Rios, 1985: p. 65, pl. 23, fig. 287.
- Cypraea cinerea* Gmelin. Jensen et al., 1986: p. 421, pl. 140.
- Cypraea cinerea* Gmelin. Bertsch, 1987: p. 25.
- Cypraea cinerea* Gmelin. De Jong and Coomans, 1988: p. 64, 65, pls. 16, fig. 399 (protoconch), pl. 36, fig. 399 (juvenile shell).
- Cypraea (Luria) cinerea* Gmelin. Robinson and Montoya, 1987: p. 386.
- Cypraea (Luria) cinerea* Gmelin. Robinson, 1991: p. 253, pl. 10, figs. 4, 5.
- Mauritia (Mauritia) campbelliana* (Pilsbry). Dolin, 1991: p. 26 figs. 28a, b.
- Luria (Luria) cinerea* (Gmelin). Cossignani and Passamonti, 1991: pp. 11, 44, 45.
- Cypraea cinerea* Gmelin. Donovan and Littlewood, 1993: p. 36.
- Luria cinerea* (Gmelin). Lorenz and Hubert, 1993: p. 79, pl. 30, figs. 1–3, 7, 12–14.
- Cypraea cinerea* Gmelin. Diaz and Puyana, 1994: p. 166, fig. 613.
- Luria cinerea* (Gmelin). Bradner and Kay, 1996: p. 96, fig. 149 (radula).
- Cypraea cinerea* Gmelin. Carlos and Joaquín, 1998: p. 126.
- Cypraea (Luria) cinerea* Gmelin. Espinosa et al., 1988: p. 20.
- Cypraea (Luria) cinerea* Gmelin. Espinosa and Ortea, 2001: p. 17.
- Luria cinerea* (Gmelin). Lorenz and Hubert, 2000: p. 79, pl. 30, figs. 1–3, 7, 12–14.
- Talparia cinerea* (Gmelin). Redfern, 2001: p. 51, pl. 26, figs. 220A–C.
- Talparia cinerea* (Gmelin). Köhler, 2003: p. 36.
- Cypraea cinerea* Gmelin. Absalão et al., 2006: p. 236.
- Cypraea cinerea* Gmelin. Rios, 2009: p. 133, fig. 315.
- Luria cinerea* (Gmelin). Jensen and Pearce, 2009: p. 62.
- Luria cinerea* (Gmelin). Lee, 2009: p. 77, 2 unnumbered figs.
- Luria cinerea* (Gmelin). Massemin et al., 2009: p. 100, 2 unnumbered figs.
- Cypraea (Luria) cinerea* Gmelin. Rios, 2009: p. 133, fig. 315.
- Luria cinerea* (Gmelin). Tunnell et al., 2010: p. 172, unnumbered fig.
- Luria cinerea* (Gmelin). Daccarett and Bossio, 2011: p. 64, fig. 173.
- Luria cinerea* (Gmelin). Brunner and Brunner, 2011: p. 7, unnumbered fig.
- Luria cinerea* (Gmelin). Petuch and Sargent, 2011: pp. 47, 80, 132, fig. 3.2C.

Text-fig. 10. *Luria cinerea* (Gmelin, 1791). 1–4, NHMW 2017/0124/0162, length 33.8 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower-middle Miocene. 5–8, NHMW 2017/0124/0163, length 28.8 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 9–12, NHMW 2017/0124/0164, length 33.2 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower-middle Miocene. 12–16, NHMW 2017/0124/0165, length 25.2 mm. 17–21, NHMW 2017/0124/0269, length 33.8 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower-middle Miocene.

- Luria cinerea* (Gmelin). Zhang, 2011: p. 89, fig. 239.
Luria cinerea (Gmelin). Petuch, 2013: pp. 26, 27, 36, figs. 2.8E, F.
Luria cinerea (Gmelin). Redfern, 2013: p. 42, figs. 116A–D.
Luria cinerea (Gmelin). Petuch and Myers, 2014: pp. 141, 150, 254, figs. 7.5K, L.
Luria cinerea (Gmelin). Lamy and Pointier, 2017: p. 170, 2 unnumbered figs., pl. 148, figs. 2a–f.
Luria cinerea cinerea (Gmelin). Lorenz, 2017: p. 56 [radula], p. 192, pl. H9, fig. 126, p. 350, 351.
Luria cinerea cinerea (Gmelin). Lorenz, 2018: p. 260, pl. 126, figs. 1–7, 20–22.

Type material.—*Cypraea cinerea*, holotype not designated, referred to figures in Lister (1688: fig. 23), Gualtieri (1742: pl. 16, figs. H, L, M) and Martini and Chemnitz (1769: pl. 25, figs. 254, 255); *Cypraea sordida*, holotype not designated; *Cypraea campbelliana*, holotype ANSP 3000 (ex Gabb collection), length 30.3 mm, Santo Domingo, Miocene (Text-figs. 9.1–9.3), Richards (1968: p. 110 as ‘type’); *Luria* (*Basilitronea*) *moritura*, holotype NMB H 11287, length 31.9 mm, Jacmel, Haiti, Pliocene (Text-figs. 9.8–9.11); *Luria* (*Luria*) *cinerea rutschi*, holotype NMB H 11295, length 32.7 mm, Jacmel, Haiti, Pliocene (Text-figs. 9.4–9.7); *Cypraea cinerea* var. *morinis*, holotype USNM 559686, paratype USNM 559687, Moin Hill, railroad cut 2.5 miles outside of Limon, Costa Rica, USNM locality 8461, Pliocene; *Cypraea costaricensis*, holotype USNM 498682, second bed from top of Moin Hill, Costa Rica, USNM locality 5884b, Pliocene; *Cypraea cinerea* var. *limonensis*, holotype USNM 498683, lowermost bed in street cut on the outskirts of Limon, Costa Rica, USNM locality 5885d, Pliocene; *Cypraea* (*Luria*) *cinerea catiana*, holotype PRI 26165, Playa Grande Formation, Catia member, 125 m west of the intersection of Playa Grande Yachting Club and coast road, 95 m south of the shoreline, Venezuela, Pleistocene.

Type locality.—*Cypraea cinerea* and *Cypraea sordida*, unknown type locality (Schilder, 1966b: p. 205); *Cypraea campbelliana*, Santo Domingo, Miocene, type locality restricted to TU 1226, Miocene, Baitoa Formation, Río Yaque, below Baitoa, Dominican Republic (Dolin, 1991: p. 27); *Luria* (*Basilitronea*) *moritura*, Jacmel, Haiti, Pliocene; *Luria* (*Luria*) *cinerea rutschi*, Jacmel, Haiti, Pliocene; *C. cinerea* var. *morinis*, Morin [sic] Hill [= Moin Hill], railroad cut 2.5 miles outside of Limon, Costa Rica, USNM locality 8461, Pliocene; *Cypraea costaricensis*, second bed from top of Moin Hill, Costa Rica, USNM locality 5884b, Pliocene; *C. cinerea* var. *limonensis*, lowermost bed in street cut on the outskirts of Limon, Costa Rica, USNM locality 5885d, Pliocene; *C. (L.) cinerea catiana*, Playa Grande Formation, Catia member, 125 m west of the intersection of Playa Grande Yachting Club and coast road, 95 m south of the shoreline, Venezuela.

Previously figured material.—Hypotype PRI 21079 (Olsson, 1922), Rio Blanca, Costa Rica, Miocene.

Material.—NHMW 2017/0124/0162 (1 specimen; locality NMB 16844); NHMW 2017/0124/0168 (2 specimens; locality NMB 16844); NHMW 2017/0124/0163–0167 (6 specimens; locality TU 1363/1364); NHMW 2017/0124/0169 (7 specimens; locality TU 1363/1364); NHMW 2017/0124/0265, 0266 (2 specimens; locality TU 1363/1364); NHMW 2017/0124/0267 (1 specimen; locality TU 1354); PRI 84477 (1 specimen; locality TU 1215); PRI 84478 (1 specimen; locality TU 1354); PRI 84765 (1 specimen; locality TU 1374).

Measurements.—See Table 8.

Original description.—“C. testa tenui ventricosa ex rubello cinerea: fasciis dilutioribus, ore albo” (Gmelin, 1791: p. 3402).

Revised description.—Shell small for genus, solid, subcylindrical, slightly posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, callused, the callus extending to ¼ height; venter flattened, convex in profile, upturned at extremities; aperture straight, weakly curved to the left in posterior portion, anteriorly slightly dilated by weak hemispherical expansion on outer lip; terminals weakly produced; siphonal canal deep and narrow, curving strongly abaxially; exhalant channel moderately deep, narrow, limited by short parallel lips; 29–35 columellar teeth: five anterior teeth in fossular area shorter and stronger, 24–30 narrow posterior columellar teeth running some distance from angulation into aperture across columellar peristome, but not onto venter; angulation relatively sharp; terminal ridge strongly developed, elevated, bordering siphonal canal, separated from first anterior columellar tooth by narrow, shallow groove; fossula poorly delimited from columellar peristome by subobsolete oblique ridge, spoon-like, concave, irregularly and weakly ridged, ridges ending as strengthened denticles at inner edge; columellar peristome steep, ridged outer half; 29–34 short, sharp labral teeth restricted to inner edge of lip, not extending externally onto the labrum; no color pattern preserved (based on NHMW coll. specimens from the Dominican assemblages).

Remarks.—Although *Luria cinerea* is well known in the Caribbean today, it is poorly represented in the Neogene fossil record in the Dominican Republic. Alison Kay did not identify any specimens in the Tulane collections. G. B.

Table 8. Measurements of *Luria cinerea* specimens in mm. LT = labial tooth count; CT = columellar tooth count; n/c = not countable.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0163	33.8	20.5	16.7	32	30	TU 1363/1364
NHMW 2017/0124/0162	28.8	19.2	16.0	30	30	NMB 16844
NHMW 2017/0124/0164	33.2	20.0	16.8	34	35	TU 1363/1364
NHMW 2017/0124/0165	25.2	15.1	12.5	30	30	TU 1363/1364
NHMW 2017/0124/0166	25.5	15.9	13.3	n/c	n/c	TU 1363/1364
NHMW 2017/0124/0167	24.2	14.6	12.2	29	29	TU 1363/1364
NHMW 2017/0124/0265	17.9	11.7	9.1	22	22	TU 1363/1364
NHMW 2017/0124/0266	20.7	13.0	9.9	27	n/c	TU 1363/1364
NHMW 2017/0124/0269	30.4	19.3	15.5	20	21	TU 1363/1364

Sowerby I (1850) did not record *L. cinerea* in the Heneken collection, although there are six specimens collected by Heneken in the Natural History Museum, London (NHMUK 4357, 20409, 11085a, 11109a, and 20410; *fide* Alison Kay). Four specimens are in the Gabb (1872) collection, Academy of Natural Sciences, Philadelphia. One of these specimens was included in Gabb's lot of *Macrocypraea dominicensis* (Pilsbry, 1922); the others were left either as duplicates or in an unopened package and found by Pilsbry, who described one of the specimens as *Cypraea campbelliana*; he separated this specimen from *L. cinerea* as follows: "outer lip 24 teeth. Inner lip with 20 short teeth [5 anterior columellar teeth] not running inward as in *L. cinerea* ... less convex... the posterior slope of the dorsal outline less abrupt. ... the markings of the lateral calluses ... of a different character" (Pilsbry, 1922: p. 366).

The authors consider all these Caribbean Neogene forms to be junior subjective synonyms of *Luria cinerea*: *Cypraea campbelliana* Pilsbry, 1922, *Luria (Basilitronea) moritura* Schilder, 1939a, *Luria (Luria) cinerea rutschi* Schilder, 1939a, *Cypraea cinerea* var. *morinis* Ingram, 1939a, *Cypraea costaricensis* Ingram, 1940, *Cypraea cinerea* var. *limonensis* Ingram, 1940, and *Cypraea (Luria) cinerea catiana* Weisbord, 1962. If the synonymies and interpretation of the species are correct, *L. cinerea* has an unusually long stratigraphic record.

Recent specimens of *Luria cinerea* are typically associated with quiet lagoonal environments, with dead individuals occasionally falling into the forereef zone but not occurring there alive (Robinson, 1991). Bandel (1973) described egg masses, with each capsule having 200–400 embryos that hatch as planktotrophic veligers. Radula teeth are in the 'Isabella Pattern' of Bradner and Kay (1996) and characterized by their precise arrangement in rows, each row noticeably separate with no overlapping. The central tooth is conspicuously larger than lateral and marginal teeth. *Luria cinerea* is commonly found in shallow water to the upper sublittoral zone under rocks and coral slabs and is usually associated with black sponges (Lorenz, 2017).

Occurrence.—Río Yaque del Norte (locality TU 1363/1364), Río Cana (locality NMB 16844), Cañada de Zamba (locality TU 1354), Río Gurabo (locality TU 1215, TU 1374).

Fossil distribution.—Miocene (indeterminate): Dominican Republic (Gabb, 1872; Pilsbry, 1922; Ingram, 1939a, 1947a, 1947c, 1951; Weisbord, 1962); Haiti (Ingram, 1947c). Lower–middle Miocene: Chipola Formation, Florida (Dolin, 1991); Baitoa Formation, Dominican Republic (Dolin, 1991; herein). Upper Miocene: Cercado Formation, Dominican Republic (herein). Pliocene (indeterminate): Costa Rica (Brann and Kent, 1960; Weisbord, 1962), Morin [*sic*] Hill [= Moin Hill] and Limon, Costa Rica (Ingram, 1939a, 1940, 1947a, 1947c, 1951); Colombia (Ingram, 1947a, 1947c, 1951; Weisbord, 1962). Lower Pliocene: Gurabo Formation, Dominican Republic (herein). Lower Pleistocene: Moin Formation, Costa Rica (Olsson, 1922; Ingram, 1951; Robinson, 1991); Jacmel, Haiti (F. A. Schilder, 1939a). Upper Pleistocene: Coulibstre and Morne Daniel, Dominica (Earle, 1928); Falmouth Formation, Jamaica (Donovan and Littlewood, 1993); Ironshore Formation, Grand Cayman (Richards, 1955; Rehder, 1962); Bermuda unspecified (Weisbord, 1962), Belmont Formation and Devonshire Formation, Bermuda (Richards et al., 1969); Playa Grande Formation, Venezuela (Weisbord, 1962; Fast, 1978); La Isabella Formation, Dominican Republic (NHMW coll.). Pleistocene (indeterminate): Hastings, Barbados (F. A. Schilder, 1939a; Ingram, 1947a, 1947c, 1951; Weisbord 1962); St. Kitts and St. Eustatius (Regteren Altena, 1961); Cuba and Aruba (Weisbord 1962); Aruba (Lorié, 1889; Rutten, 1931); Bermuda (Heilprin, 1889; Verrill, 1905; Ingram, 1947a, 1951; Weisbord, 1962); Guadelupe, Bahamas, Bermuda, Costa Rica (F. A. Schilder, 1932a).

Recent distribution.—Bermuda (Jensen and Pearce, 2009) and North Carolina (Dall, 1889), Florida and the southern and eastern Gulf of Mexico, and the entire Caribbean Sea to southern Brazil.

***Luria patrespatriae* (Maury, 1917a)**

Text-figs. 11.1–11.11

Cypraea isabella Linnaeus, 1758. Gabb, 1872: p. 235 [not *Luria isabella* (Linnaeus, 1758)].

Cypraea patrespatriae Maury, 1917a: p. 116, pl. 19, fig. 10.

Cypraea dominicensis? Gabb. Maury, 1917a: p. 116, pl. 19, fig. 11 [not *Macrocypraea dominicensis* (Gabb, 1872) *nom. inq.*].

Cypraea dominicensis? Gabb. Maury, 1917b: p. 21 [not *Macrocypraea dominicensis* (Gabb, 1872) *nom. inq.*].

Cypraea patrespatriae Maury, 1917b: p. 10.

Cypraea patrespatriae Maury. Vaughan and Woodring, 1921: p. 146.

Cypraea cf. *C. dominicensis* Gabb. Olsson, 1922: p. 140.

Cypraea isabella Linnaeus. Pilsbry, 1922: p. 364 [not *Luria isabella* (Linnaeus, 1758)].

Talparia (*Luria*) *patrespatriae* (Maury). F. A. Schilder, 1927: p. 101.

Not *Cypraea* (*Talparia*) *isabella patrespatriae* Maury. Woodring, 1928: p. 317, pl. 21, fig. 9 [= *Luria cinerea* (Gmelin, 1791)].

Luria (*Basilitronea*) *patrespatriae* (Maury). F. A. Schilder 1932a: p. 146.

Not *Luria* (*Basilitronea*) *patrespatriae* (Maury). F. A. Schilder, 1939a: p. 26 [hypotype of Jung, 1965: pp. 501, 502, pl. 67, figs. 7, 8, NMB no. H 11286 = *Luria isabellaprimitiua* Landau and Groves, 2011].

Cypraea isabella Linnaeus. Ingram, 1939b (*partim*): p. 335 [not *Luria isabella* (Linnaeus, 1758)].

Cypraea isabella Linnaeus. Ingram, 1951 (*partim*): p. 135 [not *Luria isabella* (Linnaeus, 1758)].

Luria patrespatriae patrespatriae (Maury). M. Schilder and F. A. Schilder, 1971: pp. 40, 142.

Cypraea dominicensis? Gabb. Fast, 1978: p. 83 [not *Macrocypraea dominicensis* (Gabb, 1872) *nom. inq.*].

Luria patrespatriae (Maury). Landau and Groves, 2011: p. 12, figs. 54–57.

Luria patrespatriae (Maury). Lorenz, 2017: p. 350.

Luria patrespatriae (Maury). Lorenz, 2018: p. 690, pl. 341, fig. 2.

Type material.—Holotype PRI 28780, specimen from Gabb collection, labelled “*C. isabella* Linné from Santo Domingo” (Maury, 1917a), labral teeth and fossula covered by matrix.

Type locality.—Santo Domingo (may = Bluff 1, Cercado de Mao, = locality TU 1293), Gurabo Formation, lower Pliocene.

Previously figured material.—Hypotype (Maury, 1917a: pl. 19, fig. 11) PRI 28781 (as *Cypraea dominicensis?* Gabb, 1872).

Material.—4 unnumbered lots, NMB coll., comprised of 6 specimens; NHMW 2017/0124/0149 (1 specimen; locality TU 1293); NHMW 2010/0036/0030 (1 specimen; locality TU 1215); NHMW 2017/0124/0150–0157 (8 specimens; locality TU 1215); NHMW 2010/0036/0158 (1 specimen; locality TU 1215); NHMW 2010/0036/0159 (1 specimen; locality TU 1219); NHMW 2017/0124/0160, 0161 (2

specimens; locality TU 1210); NHMW 2010/0036/0264 (1 specimen; locality TU 1354); NHMW 2017/0124/0171, 0172, 0268 (3 specimens; locality TU 1363/1364); PRI 84446 (5 steinkerns; locality TU 1415); PRI 84454 (4 fragments; locality TU 1215); PRI 84459 (3 specimens; locality TU 1422); PRI 84460 (1 incomplete specimen + 1 fragment; locality TU 1250); PRI 84461 (1 specimen; locality TU 1438); PRI 84466 (1 specimen; locality TU 1231); PRI 84467 (1 specimen; locality TU 1211); PRI 84471 (2 specimens; locality TU 1354); PRI 84487 (1 specimen; locality TU 1293); PRI 84494 (2 incomplete specimens + 1 steinkern; locality TU 1352).

Measurements.—See Table 9.

Original description.—“The fossil is subcylindrical; aperture nearly straight, very narrow; teeth numerous, fine, thirty-three on the outer lip” (Maury, 1917a: p. 116).

Revised description.—Shell of medium size, thin-shelled for genus, subcylindrical, slightly posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute and covered by adapical callus; sides rounded, weakly callused; venter flattened, very slightly convex in profile at the extremities; aperture straight, weakly curved to the left in posterior portion, anteriorly slightly dilated; siphonal channel deep, narrow, abaxially asymmetrical and abapically orthogonally truncated; exhalant channel deep and narrow, limited by parallel lips; 26–39 short columellar teeth extending a short distance into aperture from angulation, but not onto venter; angulation relatively sharp; columellar peristome smooth; terminal ridge well developed; fossula well delimited from the columellar peristome by an oblique ridge, spoon-like, concave, weakly ridged, ridges ending as denticles at its inner edge; 29–40 very short, sharp labral teeth extending across rounded inner lip margin but not externally onto labrum; color pattern of orange-tinted terminals preserved in some specimens.

Remarks.—The shells available show the same range of variation in shape as those illustrated by Lorenz and Hubert (2000: p. 282, pl. 29) for Recent *Luria isabella*. Some specimens are markedly more inflated than others, but they are always cylindrical. This is the most fragile of the Dominican Republic fossil cypraeids and preservation is rarely perfect. Most specimens are crushed so that the lips are pushed into the aperture, obscuring their edges and making accurate tooth counts impossible.

Text-fig. 11. *Luria patrespatriae* (Maury, 1917a). 1, holotype, PRI 28780 (ex Gabb collection), length 27.9 mm; Santo Domingo (may = Bluff 1, Cercado de Mao, = locality TU 1293) (specimen figured by Maury, 1917a: pl. 19, fig. 10; adapical portion of outer lip seems to have been damaged since the original figure was taken). 2–5, NHMW 2017/0124/0149, length 34.0 mm; locality TU 1293 (= Bluff 1), Río Mao, Dominican Republic, Gurabo Formation, lower Pliocene. 6–9, NHMW 2010/0036/0030, length 30.0 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 10, 11, NHMW 2017/0124/0160, length 37.3 mm; locality TU 1210, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Comparisons.—*Luria patrespatriae* is very similar to, and clearly belongs within, the *Luria isabella* species group, with which it is almost identical. One specimen from the Dominican Republic has the color pattern preserved; it shows the same orange-colored terminals seen in present-day *L. isabella*, but no black striping. *Luria patrespatriae* differs from *L. isabella* in having a slightly more sinuous columella in ventral view, and terminals—especially the posterior terminal—that are slightly more produced. The relationship between the species within the *L. isabella* group is unclear, and they are, therefore, considered distinct at full species level. *Luria isabella* has a long geological history in the Indo-Pacific, first recorded from the early Miocene of Fiji (Ladd, 1977) as *Cypraea* (*Talparia*) *isabella lekalekana* Ladd, 1934. This taxon was synonymized with *L. isabella* by Lorenz and Hubert (2000).

Luria isabellaprimitiva, from the lower to middle Miocene Cantaure Formation of Venezuela, is the earliest known

member of the group in tropical America. The lower to middle Miocene shells from the Cantaure Formation were synonymized with *Luria patrespatriae* by F. A. Schilder (1939a). However, the two populations are different; the Cantaure shells are never as cylindrical or elongated as those of *Luria patrespatriae*, and the teeth are far less numerous and stronger than in *L. isabella*. The Cantaure shells are closer in shape to those of *Luria isabellamexicana* (Stearns, 1893), but differ in having less protracted terminals and fewer columellar and labral teeth. Interestingly, one of the generic characters of modern *Luria* species is a smooth fossula that is denticulate at its inner edge; however, *L. isabellaprimitiva* has a strongly ridged fossula, the ridges formed by extensions from the anterior columellar teeth. *Luria patrespatriae* also has a ridged fossula, although the ridges are less strongly developed than in *L. isabellaprimitiva*. It is possible that this character may have been lost over time in the *L. isabella* species group. A

Table 9. Measurements of *Luria patrespatriae* specimens in mm. LT = labial tooth count; CT = columellar tooth count; ; n/c = not countable.

Specimen	Length	Width	Height	LT	CT	Locality
PRI 28780 (holotype)	27.9	14.5	11.0	n/c	n/c	TU 1293
NMB unnumbered	32.9	20.1	15.8	38	37	NMB 15816
NHMW 2017/0124/0149	34.0	18.6	14.8	40	39	TU 1293
NHMW 2010/0036/0030	30.0	16.3	12.6	36	33	TU 1215
NHMW 2017/0124/0150	32.4	18.4	15.4	n/c	n/c	TU 1215
NHMW 2017/0124/0151	37.1	18.9	16.5	37	n/c	TU 1215
NHMW 2017/0124/0152	32.5	17.9	14.1	35	n/c	TU 1215
NHMW 2017/0124/0153	32.9	18.2	15.1	n/c	n/c	TU 1215
NHMW 2017/0124/0154	28.9	14.3	11.3	n/c	n/c	TU 1215
NHMW 2017/0124/0155	23.5	13.0	10.8	33	29	TU 1215
NHMW 2017/0124/0156	23.0	11.5	9.1	32	30	TU 1215
NHMW 2017/0124/0157	31.3	18.4	14.5	n/c	n/c	TU 1215
NHMW 2017/0124/0159	26.3	15.6	13.1	29	32	TU 1219
NHMW 2017/0124/0160	37.3	19.2	16.0	38	n/c	TU 1210
NHMW 2017/0124/0161	24.2	13.5	11.4	30	26	TU 1210
NHMW 2017/0124/0264	25.6	15.4	12.2	n/c	31	TU 1354

further *Luria* species occurs in the Cantaure assemblage: *L. cantaurana* Landau and Groves, 2011. However, this species is quite different; it has a larger, less cylindrical shell, more produced extremities, and a smooth fossula. It does not belong within the *L. isabella* species group.

The genus *Luria* has also been recorded from the mid-Atlantic middle Miocene Madeira Archipelago (Lorenz and Groh, 1998). The shell of *Luria santoensis* Lorenz and Groh, 1998, is not unlike that of *Luria isabellaprimitiva* in general shape, but with fewer columellar teeth, a wider aperture, and a smooth fossula.

This species group is represented today in the tropical American Pacific by *Luria isabellamexicana*, which differs from *Luria isabella* in having a more pyriform, less subcylindrical shell shape, fewer teeth on both inner and outer lips, more protracted terminals, and a somewhat different coloration. There are also minor radular differences (Burgess, 1985; Bradner and Kay, 1996; Lorenz, 2002).

It seems, therefore, that during the Pliocene *Luria patrespatriae* was present in the Caribbean portion of the Neogene Gatunian Province and *Luria isabella* was present in the Indo-Pacific. Following the closure of the Central American isthmus, the *L. isabella* group disappeared from the Caribbean, and its populations in the Pacific became fragmented into an uncertain number of Indo-Pacific species/subspecies with restricted geographic distributions (see Lorenz and Hubert, 2000; Lorenz, 2002, 2017); of these, *Luria isabellamexicana*, an unquestionably valid taxon, is restricted to the tropical American Pacific. Interestingly, *L. isabellamexicana* is present

and common in the lower Pleistocene Moin Formation of Costa Rica (NHMW collection). At this time connections still existed between the Pacific and Caribbean, albeit intermittently; *L. isabellamexicana* is an example of a paciphile species (see Landau et al., 2009). The *L. isabella* group has not so far been found in the neighbouring northern Atlantic Caloosahatchian Province.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364), Río Cana (locality NMB 16817), Cañada de Zamba (locality TU 1354), Arroyo Bellaco (locality TU 1422), Río Gurabo (localities NMB 15816, NMB 15847, TU 1210, TU 1211, TU 1215, TU 1231, TU 1352, TU 1415), Río Amina (locality TU 1219), Río Mao (localities NMB 16911, TU 1293), Río Verde (locality TU 1250), roadcut 0.5 km south of bridge at Guayubin (locality TU 1438).

Distribution.—Miocene (indeterminate): Dominican Republic (Pilsbry, 1922; Fast, 1978). Lower–middle Miocene: Baitoa Formation, Dominican Republic (this paper). Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a). Pliocene (indeterminate): Woodring (1928), F. A. Schilder (1939a). Lower Pliocene: Gurabo Formation, Dominican Republic (Vaughan and Woodring, 1921; Woodring, 1928; F. A. Schilder, 1939a).

Tribe **AUSTROCYPRAEINI** Iredale, 1935

Austrocypreaeini Iredale, 1935: p. 132 (as subfamily Austrocypreaeinae).

Genus **TRONA** Jousseume, 1884a

Trona Jousseume, 1884a: pp. 89, 90. Type species (by original designation): *Cypraea stercoraria* Linnaeus, 1758, Recent, West Africa to Angola.

Etrona Jousseume, 1884b: p. 414 (*nomen nudum*).

Basterotia Bayle in Jousseume, 1884a: p. 95. Type species (by original designation): *Cypraea leporina* Lamarck, 1810, Miocene, France. Junior homonym of *Basterotia* Hörnes, 1859 [Bivalvia] [= *Bastorotia* Jousseume, 1884b, misspelled].

Cavicypraea Cossmann, 1896: p. 48. Type species (by typification of replaced name): *Cypraea leporina* Lamarck, 1810, Miocene, France. Nom. nov. pro *Basterotia* Bayle in Jousseume, 1884a: p. 95, not Hörnes, 1859 [Bivalvia].

Original description.—"Coquille semi-ovoïde, plane en dessous, arrondie et plus ou moins gibbeuse en dessus; bords dilatés et aplatis aux extrémités. Absence de ligne d'intersection du manteau; spire saillante, placée au-dessus de l'extrémité du bord columellaire; ouverture sinueuse, large et évasée en avant; bords dentés, sillon longitudinal du bord columellaire superficial, fossette antérieure large et profonde, à lèvre interne, formant une très forte saillie dans l'intérieur de l'ouverture" (Jousseume, 1884a: pp. 89–90).

Revised description.—"Solid, cylindrical to oval, often calloused shells. Anterior extremity pointed. Aperture narrow, widening anteriorly. Teeth fine and dense, short. Fossula coarsely denticulate and strongly projecting" (Lorenz, 2017: p. 359).

Remarks.—The genera *Trona* Jousseume and *Macrocypraea*, traditionally considered to be closely related and within the Cypraeinae (Lorenz and Hubert, 2000; Lorenz, 2017), were shown by Meyer (2004) to belong to different subfamilies; *Trona* is within the Luriinae and *Macrocypraea* is within the Cypraeinae. The shell characters of the two genera are quite different. *Macrocypraea* has a rather light shell, as opposed to the very heavy shell of *Trona*. The shells of *Macrocypraea* are elongate rather than globose; they rarely have a marginal callus, as opposed to the heavy callus seen in most *Trona* species. Furthermore, in *Macrocypraea* the base is far less flattened than in *Trona*, the apertures are wide with spiny extremities not seen in *Trona*, and the shape of the anterior expansion of the aperture is different. The fossula in *Macrocypraea* is not as large as in *Trona*, is not spoon-shaped, and is not as strongly sculptured as in *Trona*. The terminal ridge is much more prominent in *Macrocypraea*. Based on molecular data (Lorenz,

2017), the closest living relative to *Trona stercoraria* (Linnaeus, 1758) is the much smaller *Annepona mariae* (Schilder, 1927).

The archaic genus *Trona* has a record extending back to the late Oligocene. Numerous species have been described, especially from the Tethyan Miocene—where *Trona* is a characteristic component within the European Miocene cypraeid fauna—but also from the Caribbean. *Trona trinitatis* (Mansfield, 1925) was the first Caribbean member described; it is from the lower to middle Miocene of Venezuela, Trinidad, and Carriacou, Grenadine Islands, and Lesser Antilles. Dolin (1991) described *Trona leporina calhounensis* from the lower Miocene Chipola Formation of Florida, and Landau and Groves (2011) added *Trona ingrami* from the lower to middle Miocene Cantaure Formation of Venezuela, but until now no species had been recorded from the Dominican deposits.

Geographic range.—West Africa to Angola and western Europe, Caribbean.

Stratigraphic range.—Late Oligocene to Recent.

Trona colossus n. sp.

Text-figs. 12.1–12.4

Type material.—Holotype NHMW 2017/0124/0260.

Type locality.—Locality TU 1363/1364, Arroyo Hondo on east bank of Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene.

ZooBank LSID.—urn:lsid:zoobank.org:act:A935DD15-D1DF-4F8A-B622-66A122F18A9F

Other material.—Known only from holotype.

Measurements.—See Table 10.

Diagnosis.—*Trona* species of very large size, rotund, with high dorsum, venter flattened, sloping inward towards aperture, anterior third strongly dilated by hemispherical expansion, exhalant channel deep, 5 + 22 columellar teeth; anterior teeth narrow, running over anterior expansion, teeth bordering fossula tubercular, not extending onto fossula, 27 coarse labial teeth restricted to inner edge.

Description.—Shell very large for genus, solid, rotund. Dorsum probably high, regularly rounded; sides rounded, callused; venter flattened, slightly convex in profile, sloping inwards towards aperture; aperture parasigmoidal, anterior third strongly dilated by hemispherical expansion, narrowing

Text-figs. 12.1–12.4. *Trona colossus* n. sp., holotype, NHMW 2017/0124/0260, length 116.4 mm; locality TU 1363/1364, Arroyo Hondo on east bank of Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower-middle Miocene.

Table 10. Measurements of the *Trona colossus* holotype specimen in mm. LT = labial tooth count; CT = columellar tooth count.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0178 (holotype)	116.4	79.2	71.0	27	27	TU 1363/1364

adapically; siphonal canal not preserved; exhalant canal deep, straight, and twisted slightly to the left on posterior view, limited by smooth parallel lips. Columella with five narrow, elongated anterior teeth, most anterior narrowest, strengthening adapically; 22 parallel posterior columellar teeth, tubercular over fossula, lengthening adapically, extending within the aperture. Terminal ridge not preserved. Fossula very deep, concave, spoon-like, smooth; tubercular anterior columellar teeth at fossular outer edge not extending onto fossula; inner margin obscured by matrix. Outer lip relatively broad, flattened ventrally, round-edged, with 27 labial teeth; on anterior third teeth stretched out on expanded, depressed, hemicircular area; remainder of teeth heavier, teeth extending around inner edge of lip into aperture, not extending onto flattened ventral part of lip.

Remarks.—Despite being represented by a single specimen missing most of the dorsum, this species is so impressive that it warrants description. The venter is complete, missing only the anterior portion of the expanded anterior terminal. The matrix is extremely hard, and, although much of it was excavated, most of the fossular area remains unexposed. Nevertheless, enough can be seen to characterize the species. The large, heavy shell, the aperture that is strongly expanded

in its anterior third, and the deep, spoon-like fossula place this species in the genus *Trona*.

Comparisons.—*Trona colossus* is the largest *Trona* species known. It is similar in shape to some of the large Tethyan Miocene species such as *Trona leporina* (Lamarck, 1810) and *Trona subovum* (d’Orbigny, 1852). Although these species are large, they are at most half the size of this Dominican species. In *T. colossus* the anterior dilatation of the aperture is more pronounced. Furthermore, the exhalant canal is sharply delimited by elongated parallel lips, a feature not seen in the European species but present in other New World species; both *Trona ingrami* and *Trona trinitatensis* show this same feature, *Trona leporina calhounensis* less so. The Caribbean species are easily separated from *T. colossus*, as all are smaller, less solid, and less rotund. The fossula is ribbed in all Caribbean species, whereas in *T. colossus* it is smooth.

Etymology.—Latin, ‘*colossus*, -i’, noun, large statue or figure, reflecting the huge size of this species. *Trona* gender feminine.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364).

Distribution.—Lower–middle Miocene: Baitoa Formation, Dominican Republic (this paper).

Subfamily **ZONARIINAE** F. A. Schilder, 1932a

Zonariinae F. A. Schilder, 1932a: p. 172 [as tribe Zonariini].

Tribe **PSEUDOZONARIINI** López Soriano, 2006

Pseudozonariini López Soriano, 2006: p. 54 [as subfamily Pseudozonariinae].

Genus **PSEUDOZONARIA** F. A. Schilder, 1927

Pseudozonaria F. A. Schilder, 1927: pp. 115, 116. Type species (by original designation): *Cypraea arabicula* Lamarck, 1810, Pleistocene and Recent, southern Golfo de California, México, to northern Peru and Islas Galápagos.

Plaziatia Dolin and Lozouet, 2004: pp. 52, 53. Type species (by original designation): *Cypraea robertsi* Hidalgo, 1906, Pleistocene and Recent, southern Golfo de California, México to northern Peru and Islas Galápagos.

Original diagnosis.—“Anatomie unbekant. —Schale mehr eifö, S. verdickt gerundet bis verbreitert-gerandet, M. mehr zentral, gerader, K. eng und tief, ALVE. und ILVE sehr decliv, gekielt, VAZ. verlängert, Z. scharf rippenartig, TZ. schrägfaltig, aber längerichtet und nur wenig vom VKIR. abgerückt, mittlere AZ. und IZ. meist kürzer, IRZ. kräftig, Col. Stets glatt. R. feingesprenkeit, mit Tendenz zur Verschmelzung in Längsstriche” (F. A. Schilder, 1927: pp. 115, 116).

Description.—“Small to medium in size. Elongate-oval, with well developed, often sharply cut teeth. Fossula section distinctly denticulate. Densely spotted margins and freckled dorsum. Extremities often prominent” (Lorenz, 2017: p. 399).

Remarks.—The group is represented by five tropical American Pacific species; *Pseudozonaria aequinoctialis* (Schilder, 1933a), *Pseudozonaria annettae* (Dall, 1909), *Pseudozonaria arabicula* (Lamarck, 1810), *Pseudozonaria nigropunctata* (Gray, 1828), and *Pseudozonaria robertsi* (Hidalgo, 1906) (Lorenz and Hubert, 2000; Meyer, 2003, 2004; Lorenz, 2017). Several fossil species belonging to *Zonaria* Jousseaume, 1884a, and *Pseudozonaria* Schilder, 1927, have been described from the Gatunian Neogene. *Zonaria* and *Pseudozonaria* are closely related groups, and not all cypraeid specialists are in agreement as to their rank or which species belong in which of the two groups. Groves (1997) considered *Pseudozonaria* a subgenus of *Zonaria*, Lorenz and Hubert (2000) used ‘*Pseudozonaria*’ as an informal group within *Zonaria*, and Landau and Silva

(2010) considered both valid genera. López Soriano (2006) justified the separation of a new subfamily Pseudozonariinae from the Zonariinae based on molecular data (Meyer, 2004), anatomical differences of the mantle and papillae, and some small differences in shell morphology. The groups also have distinct geographical distributions; Pseudozonariinae are tropical American, today restricted to the western side of Central America; Zonariinae are known since the Miocene in Europe and from the Recent of West Africa (Lorenz and Hubert, 2000; Lorenz, 2017).

Geographic range.—Recent: The entire Pacific Panamic Province. Fossil: Pacific Panamic Province, Florida and the Caribbean to northern South America.

Stratigraphic range.—Miocene to Recent.

***Pseudozonaria raymondrobertsi* (Pilsbry 1922)**
Text-figs. 13.1–13.16

- Cypraea raymondrobertsi* Pilsbry, 1922: p. 365, pl. 30, figs. 1–3.
Cypraea raymondrobertsi bowdenensis Pilsbry, 1922: p. 365, pl. 30, fig. 6.
Erronea (Zonaria) raymondrobertsi (Pilsbry). F. A. Schilder, 1927: p. 119.
Erronea (Zonaria) bowdenensis (Pilsbry). F. A. Schilder, 1927: p. 119.
Cypraea (Zonaria) raymondrobertsi bowdenensis Pilsbry. Woodring, 1928: p. 318, pl. 21, figs. 10, 11, pl. 22, fig. 1.
Zonaria (Zonaria) bowdenensis (Pilsbry). F. A. Schilder, 1932a: p. 180.
Zonaria (Zonaria) raymondrobertsi (Pilsbry). F. A. Schilder, 1932a: p. 180.
Zonaria (Zonaria) bowdenensis (Pilsbry). F. A. Schilder, 1939a: pp. 7, 9, 21.
Cypraea raymondrobertsi Pilsbry. Ingram, 1939b: p. 336.
Cypraea raymondrobertsi Pilsbry. Clench and Turner, 1962: p. 128.
Cypraea raymondrobertsi bowdenensis Pilsbry. Clench and Turner, 1962: p. 21.
Cypraea raymondrobertsi bowdenensis Pilsbry. Richards, 1968: p. 108.
Cypraea raymondrobertsi Pilsbry. Richards, 1968: p. 181.
Zonaria (Zonaria) raymondrobertsi (Pilsbry). M. Schilder and F. A. Schilder, 1971: p. 44, 150.
Zonaria (Zonaria) raymondrobertsi bowdenensis (Pilsbry). M. Schilder and F. A. Schilder, 1971: pp. 44, 100.
Zonaria (Zonaria) raymondrobertsi (Pilsbry). Landau et al., 2008: p. 457.
Cypraea bowdenensis (Pilsbry). Díaz and García-Llano, 2010: pp. 109, 113.
Pseudozonaria raymondrobertsi (Pilsbry). Lorenz, 2017: p. 399.

Type material.—*Cypraea raymondrobertsi*: Holotype ANSP 3995 (Pilsbry, 1922: pl. 30, figs. 1–3), length 27.0 mm,

width 19.2 mm, height 14.9 mm (Text-figs. 13.1–13.4), Richards (1968: p. 181, as ANSP 11146 ‘type’ error); *Cypraea raymondrobertsi bowdenensis*: Holotype ANSP 11146 (Pilsbry 1922: pl. 30, fig. 6), length 25.5 mm, width 17.3 mm (Text-figs. 13.13–13.16), Richards (1968: p. 108).

Type locality.—*Cypraea raymondrobertsi*, “Miocene,” Santo Domingo, Gabb collection. The type locality here restricted to: locality TU 1354, Cañada de Zamba, Dominican Republic, Gurabo Formation, lower Pliocene. *C. raymondrobertsi bowdenensis*, Bowden Member of the Layton Formation, Jamaica, Pliocene.

Previously figured material.—Hypotype (Woodring, 1928: pl. 21, figs. 10, 11) USNM 364968.

Material.—8 unnumbered lots, NMB coll., comprised of 17 specimens; NHMW 2017/0124/0108-0116 (9; locality TU 1354); NHMW 2017/0124/0117 (2; locality TU 1354); NHMW 2017/0124/0105-0107 (3; locality TU 1215); NHMW 2017/0124/0103 (1; locality TU 1210); NHMW 2017/0124/0117-0121 (5; locality NMB 16844); NHMW 2017/0124/0122 (4; locality NMB 16844); NHMW 2017/0124/0270-0272, NHMW 2017/0124/0130-0131, NHMW 2017/0124/0263 (6; locality TU 1363/1364). NHMUK G11108a and G11110 collected by T.S. Heneken, St. Domingo; USNM 8553, Gurabo, Dominican Republic, and comparative material in the Schilder Collection 5545 from Haiti, NHMUK GG4384 collected by Trechmann from Tobago, West Indies; PRI 84447 (7; locality TU 1354); PRI 84457 (1; locality TU 1210); PRI 84458 (1; locality TU 1213); PRI 84468 (1; locality TU 1231); PRI 84470 (1; locality TU 1211); PRI 84486 (1; locality TU 1278); PRI 84491 (1; locality TU 1422); PRI 84759 (1; locality TU 1447); PRI 84761 (1 incomplete; locality TU 1445).

Measurements.—See Table 11.

Original description.—“The shell is subovate in basal outline, solid, with the sides heavily callused, laterally angular, the callus rising high, especially on the left side, and covering the spire, which is marked by a shallow irregular pit. Ends but little produced. The outer lip has 19 strong teeth, narrower than their intervals. Inner lip with 17 teeth. The base is rather strongly convex” (Pilsbry 1922: p. 365).

Revised description.—Shell medium sized, solid, subovate, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides angular, strongly callused, callus ascending to $\frac{1}{2}$ – $\frac{2}{3}$ shell height, left callus higher than right; venter flattened, weakly convex; aperture of medium width, parasigmoidal, posteriorly strongly curving to the left, anterior portion very slightly wider; siphonal canal narrow, abaxially asymmetrical, anterior termini barely constricted, blunt; exhalant channel weakly produced, relatively shallow; columella denticulate along entire length, bearing 11–19 well-developed, narrow denticles extending as folds deep within the columellar peristome, on venter denticles stop abruptly at the angulation; terminal fold strongly developed and elevated, bordering the siphonal canal, where it is strengthened and keel-like with a prominent, elevated internal lamina (sensu Dolin and Lozouet, 2004), separated from columellar teeth by deep groove; fossula shallow, poorly delimited from rest of columella, very steep, bearing strong ridges extending to inner edge, ending in a denticle; 14–20 narrow labral teeth, outer lip bevelled inwards, teeth extending across bevelled inner portion and onto labrum to less than mid-labral width. Marginal callus cream colored, dorsal and marginal spotted color pattern present under UV light.

Remarks.—The shells of *P. raymondrobertsi* are distinguished from the other small cowries among the Dominican Republic fossils by their distinctly angular margins. There is some important range of variability seen in outline, with the callus strongly developed in some specimens giving the shells a broadly ovate shape, whereas in others the callus is not as strongly developed and the outline is slightly more elongate. The Cercado Formation specimens examined tend to be smaller, less solid, with the marginal calluses less developed than many of the Gurabo Formation specimens, but overlap between the forms exists.

Comparisons.—Pilsbry (1922) recognized a similar form with angular calluses in the Pliocene Bowden Member of the Layton Formation of Jamaica, *Cypraea raymondrobertsi bowdenensis* Pilsbry, 1922, but said it differed in having fewer teeth (LT 16, CT 13). As can be seen from the measurements (Table 11), this number of teeth is also present in Dominican specimens of a similar size to the Jamaican holotype. Pilsbry (1922: p. 365) also noted that in the Jamaican shell the teeth extended further onto the base, which was less convex. These

Text-fig. 13. *Pseudozonaria raymondrobertsi* (Pilsbry, 1922). 1–4, holotype, ANSP 3995, length 27.0 mm, Gabb collected, Sto. Domingo, Miocene. 5–8, NHMW 2017/0124/0108, length 32.5 mm; locality TU 1354, Cañada de Zamba, Dominican Republic, Gurabo Formation, lower Pliocene. 9–12, NHMW 2017/0124/0109, length 25.4 mm; locality TU 1354. 13–16, holotype specimen formerly assigned to *Cypraea raymondrobertsi bowdenensis* Pilsbry, 1921, ANSP 11146, length 25.5 mm; Bowden, Jamaica, Bowden Member of the Layton Formation, Pliocene.

Table 11. Measurements of *Pseudozonaria raymondrobertsi* specimens in mm. LT = labial tooth count; CT = columellar tooth count.

Specimen	Length	Width	Height	LT	CT	Locality
ANSP (Holotype 3995)	27.0	19.0	15.0	16	15	Sto. Domingo
ANSP (Paratype 11146)	25.5	17.5	11.5	14	11	Jamaica
USNM 8553	30.0	20.0	16.5	20	19	Gurabo, DR
NHMUK 11108	25.5	17.5	13.0			Sto. Domingo
NHMUK GG 4384	23.0	15.0	13.0			Tobago
Schilder coll. 5545	34	20.5	16.5	20	19	Haiti
NHMW 2017/0124/0108	32.5	23.5	16.1	17	17	TU 1354
NHMW 2017/0124/0109	25.4	19.0	12.9	16	14	TU 1354
NHMW 2017/0124/0110	30.0	20.6	15.2	20	14	TU 1354
NHMW 2017/0124/0111	28.0	18.6	13.7	18	15	TU 1354
NHMW 2017/0124/0112	27.4	18.2	13.1	17	12	TU 1354
NHMW 2017/0124/0113	25.4	18.1	12.9	18	14	TU 1354
NHMW 2017/0124/0114	28.2	19.5	14.0	19	16	TU 1354
NHMW 2017/0124/0115	25.9	18.5	13.1	17	14	TU 1354
NHMW 2017/0124/0116	25.5	17.9	13.2	16	13	TU 1354
NHMW 2017/0124/0105	27.1	17.2	13.0	19	14	TU 1215
NHMW 2017/0124/0106	22.9	16.3	11.8	17	14	TU 1215
NHMW 2017/0124/0107	19.3	13.6	10.5	16	16	TU 1215
NHMW 2017/0124/0103	24.3	17.4	12.9	18	14	TU 1210
NHMW 2017/0124/0117	24.1	16.9	12.9	17	14	NMB 16844
NHMW 2017/0124/0118	25.2	16.5	12.6	19	16	NMB 16844
NHMW 2017/0124/0119	22.9	15.0	11.5	16	15	NMB 16844
NHMW 2017/0124/0120	21.8	14.7	11.6	18	15	NMB 16844
NHMW 2017/0124/0121	22.0	14.5	11.3	17	16	NMB 16844
NHMW 2017/0124/0130	28.4	19.6	14.8	20	20	TU 1363/1364
NHMW 2017/0124/0131	25.2	16.6	13.2	22	19	TU 1363/1364
NHMW 2017/0124/0263	23.4	16.1	12.7	17	22	TU 1363/1364

small differences fit within the range of variability seen in the Dominican specimens, and *Cypraea raymondrobertsi bowdenensis* is considered to be a subjective junior synonym of *Pseudozonaria raymondrobertsi*.

The *Pseudozonaria* group is well represented in the tropical American Neogene and Recent faunas. However, *Pseudozonaria raymondrobertsi* is relatively easily distinguished from all its congeners. *Pseudozonaria primaroberti* Landau and Groves, 2011, from the lower to middle Miocene Cantaure Formation of Venezuela, *Pseudozonaria telembiensis* (Olsson, 1964) from the upper Miocene Angostura Formation of Ecuador, *Pseudozonaria fehsei* Landau and Silva, 2010, from the lower Pliocene Araya Formation of Venezuela, *Pseudozonaria raymondrobertsi*, *Pseudozonaria portelli* Petuch, 1990, from the Plio-Pleistocene of Florida, and the Recent tropical American Pacific *Pseudozonaria robertsi* (Hidalgo,

1906) belong within the *P. robertsi* species group. Species in this group are characterized by moderately small but solid shells, with a marginal callus developed to a variable degree; they have a strong, keel-like terminal ridge followed by a deep groove separating the most anterior columellar tooth. *Pseudozonaria raymondrobertsi* can be easily separated from the rest of the group by its well-developed angular marginal callus, giving the shell a broad, depressed shape. Additionally, the groove following the terminal ridge is well developed but shallower than in the other members of the group, and there are fewer and finer columellar teeth than in the other members of the group.

Pseudozonaria praeaequinocialis Landau and Groves, 2011, from the lower to middle Miocene Cantaure Formation of Venezuela, *Pseudozonaria frassinetti* (Groves and Nielsen, 2003) from the lower upper Miocene (Tortonian) of Chile,

Pseudozonaria aequinoctialis (Schilder, 1933a) from Recent tropical Pacific of Panama to Ecuador and *Pseudozonaria annettae* (Dall, 1909) found along the Recent Pacific coast of México all belong within a different group, the *Pseudozonaria annettae* group (of Landau and Groves, 2011). The *P. annettae* group is characterized by its very wide aperture and widely spaced and sharp denticles.

Pseudozonaria cathyae (Groves, 1997), from the lower Pliocene Esmeraldas beds of the Onzole Formation of Ecuador, belongs within yet a different group. The anterior third of the aperture is dilated by a small hemispherical expansion, and there is no deep groove separating the weaker terminal ridge from the relatively fine columellar teeth.

Occurrence.—Río Cana (localities NMB 16817, NMB 16818, NMB 16820, NMB 16828, NMB 16835, NMB 16837, NMB 16839, NMB 16844, NMB 16852); Arroyo Bellaco (locality TU 1422); Río Gurabo (localities TU 1210, TU 1211, TU 1213, TU 1215, TU 1231, TU 1278); Cañada de Zamba (locality TU 1354); Río Yaque del Norte (locality TU 1363/1364, TU, 1445, TU 1447).

Distribution.—Miocene (indeterminate): Dominican Republic (Ingram, 1947c). Lower–middle Miocene: Baitoa Formation (this paper). Upper Miocene: Cercado Formation, Dominican Republic (Pilsbry, 1922; F. A. Schilder, 1932a; Ingram, 1939b). Miocene–Pliocene (indeterminate): San Andrés formation, Isla de San Andrés, Colombia (Díaz and García-Llano, 2010). Lower Pliocene: Gurabo Formation, Dominican Republic (F. A. Schilder, 1932a; this paper). Pliocene: Bowden Member of the Layton Formation, Jamaica (Pilsbry, 1922; Woodring, 1928; F. A. Schilder, 1939a, 1939b; Ingram, 1947c).

***Pseudozonaria* sp.**

Text-figs. 14.1–14.4

Material.—NHMW 2017/0124/0102 (1 specimen; locality TU 1215).

Measurements.—See Table 12.

Description.—Shell medium sized, solid, cylindrical-pyriform, posteriorly moderately swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire forming small point covered by adapical callus; sides rounded, moderately callused, callus ascending to $\frac{1}{2}$ – $\frac{1}{3}$ shell height, not sharply delimited; venter flattened, weakly convex; aperture of medium width, evenly and weakly curved, anterior portion very slightly wider; siphonal channel narrow, abaxially asymmetrical; exhalant channel moderately produced and deep, limited by parallel lips; columella denticulate along entire length,

bearing 21 coarse, elevated denticles extending as folds onto columellar peristome, not extending over angulation onto venter, anterior columellar teeth larger, weakening gradually, so that anterior and posterior columellar teeth not delimited; terminal flattened, forming small spatulate process bordering siphonal channel, there somewhat strengthened internally and keel-like with a prominent, elevated internal lamina (sensu Dolin and Lozouet, 2004), separated from the columellar teeth by a moderately deep groove; fossula well developed, concave, very steep, bearing ridges extending to inner edge, ridges ending as denticles; outer lip broad, flattened ventrally, edge rounded, slightly flattened and concave opposite fossula, bearing 24 coarse teeth extending deep within labrum but not onto venter. An indication of spotted marginal color pattern preserved on left side.

Remarks.—Although represented by a well-preserved specimen, the authors hesitate to formally describe this species based on a single shell and await further material. Placement in the genus *Pseudozonaria* is based on the specimen's well-developed dentition (although it is not as sharply cut as in other members of the genus), distinctly denticulate fossula, and spotted margins. The terminals are not as produced as in other members of the genus.

Comparison.—This specimen is quite unlike the only other congener in the Dominican assemblages, *Pseudozonaria raymondrobertsi*. *Pseudozonaria raymondrobertsi* is smaller, far more globose and pyriform due to its strongly thickened marginal callus, and has a wider, more sinuous aperture and more sharply cut dentition. This specimen is more similar to the cylindrical form of *P. primarobertsi* from the lower to middle Miocene Cantaure Formation of Venezuela; however, it differs in being larger—almost twice the size (length 18.8–29.2 mm for *P. primarobertsi*; see Landau and Groves, 2011: p. 29, tables 12a, b)—with a narrower, straighter aperture that is not as bent to the left apically. In the Venezuelan species, the anterior columellar denticles are more differentiated from the posterior ones, and, in many specimens, fused, unlike in the unnamed Dominican species. *Pseudozonaria falconensis* Landau and Groves, 2011, also from the Cantaure assemblage, is even smaller with more produced terminals.

The *Pseudozonaria annettae* group now living in the tropical American Pacific includes *Pseudozonaria annettae* (Dall, 1909), found along the Pacific coast of México; the southern species *Pseudozonaria aequinoctialis* (Schilder, 1933a), found from Panama to Ecuador; and the fossil *Pseudozonaria praeaequinoctialis* Landau and Groves, 2011, from the Cantaure Formation of Venezuela. All differ from the Dominican *Pseudozonaria* sp. specimen in having very short teeth and wide apertures.

Text-figs. 14.1–14.4. *Pseudozonaria* sp., NHMW 2017/0124/0102, length 52.0 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Table 12. Measurements of *Pseudozonaria* sp. specimens in mm. LT = labial tooth count; CT = columellar tooth count.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0102	52.0	32.5	26.8	24	21	TU 1215

The shell also bears some similarity to the illustration of a specimen in the Gabb collection given by Pilsbry (1922: pl. 30, figs. 7, 8) of *Cypraea dominicensis*, which is here discussed under the genus *Macrocypraea*. Gabb’s shell is not conspecific with the Dominican specimen, as it is smaller with a more sinuous aperture. As discussed above, the present authors are not sure which species Gabb’s specimen belongs to and consider it a *nomen inquirendum*.

In shape, this Dominican specimen is also somewhat similar to the lower to middle Miocene, southern Caribbean *Trona trinitatis* (see Landau and Groves, 2011: figs. 7–77). However, *Trona* species are separated by their well-developed, spoon-shaped, strongly denticulate fossula.

Occurrence.—Río Gurabo (locality TU 1215).

Distribution.—Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Tribe **ZONARIINI** F. A. Schilder, 1932a

Zonariini F. A. Schilder, 1932a: p. 172.

Genus **ZONARIA** Jousseume, 1884a

Zonaria Jousseume, 1884a: pp. 92, 93. Type species (by original designation): *Cypraea zonaria* Gmelin, 1791, Recent, West Africa to Angola.
Zonaria Jousseume, 1884b: p. 414. Spelling *Zonaria* conserved under Art. 33.3.1. (ICZN, 1999).

Original diagnosis.—“Coquille ovoïde, déprimée en dessous, convexe et arrondie endessus, extrémité antérieure large, ligue d’intersection du manteau nulle, spire recouverte d’un enduit formant un biurrelet qui relie en arriè celui des bords. Ouverture légèrement sinueuse, étroite, un peu dilatée en avant. Bord externe denté. Bord columellaire lisse ou à dents peu saillantes, au centre et en arrière, sur la partie antérieure duquel existe une fossette peu apparente, à bord interne et à bord armés de dents saillantes.” (Jousseume, 1884a: pp. 92, 93).

Remarks.—The genus *Zonaria* is traditionally assigned to the subfamily Erroneinae Schilder, 1927. However, based on mitochondrial molecular data, Meyer (2004) demonstrated that the genus belongs within a separate group: Zonariinae Schilder, 1932a. *Zonaria* has been known in Europe since the early Miocene and is distributed today in the Mediterranean and West Africa (Lorenz and Hubert, 2000; Lorenz, 2017). The genus has also been recorded from the middle Miocene of the Madeira Archipelago (Lorenz and Groh, 1998). Groves (1997) reported the genus in Pacific tropical American Neogene assemblages with the description of *Zonaria pittorum* Groves, 1997, from the lower Pliocene Esmeraldas beds of the Onzole Formation of Ecuador; additionally, Groves and Nielsen (2003) described *Zonaria frassinetti* from the lower upper Miocene (Tortonian) of Chile. However, Lorenz (2017: p. 399) reassigned *Z. pittorum* to *Pseudozonaria*, and Landau and Groves (2011: p. 22) reassigned *Z. frassinetti* to the genus *Pseudozonaria*. Therefore, the presence of *Zonaria* in the

tropical American Pacific Neogene needs to be confirmed.

The '*Pseudozonaria* group' (of Lorenz and Huber, 2000: p. 129) is closely related to *Zonaria*. Groves (1997) considered *Pseudozonaria* a subgenus of *Zonaria*, whereas Lorenz and Hubert (2000) used '*Pseudozonaria*' as an informal group within *Zonaria*. Landau and Groves (2011) considered the two separate at full generic rank. *Pseudozonaria* has a fossil record in the tropical American Neogene and is today restricted to the Pacific side of its original wider distribution (i.e., western side of Central America). It is an example of a Paciphile taxon (Woodring, 1966; Landau et al., 2009).

Geographic distribution.—Fossil: Western Europe and the Mediterranean, West Africa, and the Caribbean. Recent: Mediterranean and West Africa to Angola.

Stratigraphic distribution.—Oligocene to Recent.

***Zonaria spurcoides* (Gabb, 1872)**

Text-figs. 15.1–15.16

- Cypraea spurcoides* Gabb, 1872: p. 235.
Cypraea spurcoides Gabb. Maury, 1917a: p. 115, pl. 19, figs. 7–9.
Cypraea spurcoides Gabb. Maury, 1917b: pp. 10, 21.
Cypraea spurcoides? Gabb. Hubbard, 1920: p. 148.
Cypraea (Bernayia) spurcoides Gabb. Vredenburg, 1920: p. 94.
Cypraea spurcoides Gabb. Vaughan and Woodring, 1921: p. 141.
Cypraea spurcoides Gabb. Pilsbry, 1922: p. 365, pl. 30, figs. 4, 5.
Erronea (Zonaria) spurcoides (Gabb). F. A. Schilder, 1927: p. 119.
Cypraea cf. *spurcoides* Gabb. Meyerhoff, 1931: p. 336.
Zonaria (Zonaria) spurcoides (Gabb). F. A. Schilder, 1932a: p. 180.
Zonaria (Zonaria) spurcoides (Gabb). F. A. Schilder, 1939a: pp. 5, 9, 21.
Cypraea spurcoides Gabb. Ingram, 1939b: p. 337, pl. 22, fig. 4.
Cypraea spurcoides Gabb. Ingram 1947a: p. 56, pl. 6, fig. 17.
Cypraea spurcoides Gabb. Ingram, 1947c: p. 149.
Cypraea spurcoides? Gabb. Mitchell, 1954: p. 150.
Cypraea cf. *supurcoides* [sic] Gabb. Mitchell, 1954: p. 155.
Cypraea spurcoides Gabb. Ramírez, 1956: p. 13.
Cypraea spurcoides Gabb. Weisbord, 1962: p. 231.
Cypraea spurcoides Gabb. Richards, 1968: p. 190.
Zonaria (Zonaria) spurcoides (Gabb). M. Schilder and F. A. Schilder, 1971: pp. 45, 157.
Cypraea spurcoides Gabb. Fast, 1978: p. 83.
Erronea (Adusta) spurcoides (Gabb). Dolin, 1991: pp. 34–36, figs. 36–38.
Zonaria (Zonaria) spurcoides (Gabb). Kugler, 2001: p. 19.
Zonaria (Zonaria) cf. spurcoides (Gabb). Landau et al., 2008: p. 457.
Zonaria spurcoides (Gabb.). Landau and Groves, 2011: p. 25, figs. 140–143.
Pseudozonaria spurcoides (Gabb). Lorenz, 2017: p. 399.

Type material.—Lectotype ANSP 2999, designated by Pilsbry (1922: p. 365), length 32.8 mm, width 20.3 mm.

Paralectotype, also ANSP 2999, length 24.0 mm, width 15.7 mm (Richards, 1968: p. 190).

Type locality.—"Miocene," Santo Domingo, Gabb collection. The type locality here restricted to locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene.

Previously figured material.—Hypotypes (Maury, 1917a, pl. 19, fig. 7 (PRI 28778) and figs. 8, 9 (PRI 28779); refigured by Ingram, 1939b, pl. 22, fig. 4; 1947a, pl. 6, fig. 17).

Material.—1 lot, 2 specimens, ANSP coll.; 1 lot, USNM coll.; 11 lots, 11 specimens, NHMUK coll., NHMUK G11109, GG20405, 5368, GG20411 (collected by T. S. Heneken), G11104, G5368 (collected by Trechmann); 1 unnumbered lot, NMB collection; NHMW 2010/0036/0031 (1 specimen; locality NMB 17265); NHMW 2017/0124/0123–0128, 0133, 0134 (8 specimens; locality TU 1363/1364); NHMW 2010/0036/0032 (3 specimens; locality TU 1363/1364); NHMW 2017/0124/0261, 0262 (2 specimens; locality TU 1363/1364); NHMW 2017/0124/0135–0144 (10 specimens; locality TU 1215); NHMW 2017/0124/0145 (2 specimens; locality TU 1215); NHMW 2017/0124/0147 (1 specimen; locality TU 1354); NHMW 2017/0124/0148 (1 specimen; locality TU 1219); PRI 84445 (3 specimens + 1 fragment; locality TU 1215); PRI 84469 (1 specimen + 1 incomplete specimen; locality TU 1230); PRI 84472 (3 specimens; locality TU 1422); PRI 84473 (1 specimen; locality TU 1277); PRI 84474 (1 specimen; locality TU 1219); PRI 84476 (1 incomplete specimen; locality TU 1211); PRI 84488 (1 specimen + 1 incomplete specimen; locality TU 1293); PRI 84489 (1 specimen; locality TU 1278); PRI 84760 (1 specimen; locality TU 1447).

Measurements.—See Table 13.

Original description.—"Shell similar in form to *C. spurca* but somewhat broader and more narrowed in advance. Callus broad, convex below, slightly expanded laterally. Not crenulated above as in *C. spurca*. Crenulations of both lips well defined, more numerous on inner than outer lip. Color pattern mottled irregular. In color and size not unlike *C. bicallosa* but differs from it in its form and in the absence of the two callosities. It wants entirely the marginal pitting of *spurca*, which approaches nearest in form." (Gabb, 1872: p. 235).

Revised description.—Shell small to medium sized for genus, solid, ovate-pyriform, posteriorly swollen, in lateral profile dorsal curvature regularly attenuated abapically, spire marked

Text-fig. 15. *Zonaria spurcoides* (Gabb, 1872). 1–4, lectotype, ANSP 2999, length 32.5 mm, Sto. Domingo, 'Miocene'. 5–8, NHMW 2010/0036/0031, length 28.3 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene. 9–12, NHMW 2010/0036/0135, length 36.0 mm. 13–16, NHMW 2010/0036/0136, length 30.9 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

by dimple, covered by adapical callus; sides rounded, strongly callused; callus ascending above mid-height, its highest point at the dorsal hump; venter flattened, slightly convex in profile; aperture narrow, almost straight, adapically weakly curved to the left; siphonal canal long, abaxially asymmetrical, externally surrounded by relatively thick callus collar; exhalant channel produced, weakly bent adaxially, externally surrounded by thick adapical callus; terminal ridge well developed, tooth-like at its inner extremity; fossula much reduced, ridged; 17–24

columellar teeth; 4–5 anterior columellar teeth, most anterior thickest, adapically narrow, sharply cut, not extending onto venter, but extending onto columella, weakening and disappearing about half columellar width; 18–25 narrow, sharp labral teeth at lip edge, extending short distance onto labrum; indication of spotted dorsal color pattern under UV light.

Table 13. Measurements of *Zonaria spurcoides* specimens in mm. LT = labial tooth count; CT = columellar tooth count; ; n/c = not countable.

Specimen	Length	Width	Height	LT	CT	Locality
ANSP 2999 (lectotype)	32.5	20.5	16.5	22	>14	Sto. Domingo
ANSP 2999 (paralectotype)	24	16	13	18	20	Sto. Domingo
USNM 438610	39	26	20	25	19	Sto. Domingo
NHMW 2010/0036/0031	28.3	19.1	15.0	19	18	TU 1363/1364
NHMW 2017/0124/0123	31.7	19.9	16.2	21	24	TU 1363/1364
NHMW 2017/0124/0124	28.3	18.6	14.7	21	22	TU 1363/1364
NHMW 2017/0124/0125	29.0	18.3	14.9	20	19	TU 1363/1364
NHMW 2017/0124/0126	31.0	21.0	16.4	20	n/c	TU 1363/1364
NHMW 2017/0124/0127	24.2	15.5	12.6	20	19	TU 1363/1364
NHMW 2017/0124/0128	31.2	20.0	15.5	n/c	n/c	TU 1363/1364
NHMW 2017/0124/0133	27.6	17.7	13.6	21	22	TU 1363/1364
NHMW 2017/0124/0134	25.0	15.0	12.3	19	21	TU 1363/1364
NHMW 2017/0124/0261	25.4	17.1	13.2	19	20	TU 1363/1364
NHMW 2017/0124/0262	25.5	16.3	12.8	22	20	TU 1363/1364
NHMW 2017/0124/0135	36.0	21.6	17.3	22	22	TU 1215
NHMW 2017/0124/0136	30.9	17.6	14.0	24	20	TU 1215
NHMW 2017/0124/0137	27.7	17.0	13.8	23	21	TU 1215
NHMW 2017/0124/0138	31.3	17.8	15.2	n/c	n/c	TU 1215
NHMW 2017/0124/0139	27.1	15.4	12.5	21	21	TU 1215
NHMW 2017/0124/0140	29.4	17.7	14.8	23	21	TU 1215
NHMW 2017/0124/0141	24.4	15.3	11.9	18	22	TU 1215
NHMW 2017/0124/0142	29.3	16.7	13.5	n/c	n/c	TU 1215
NHMW 2017/0124/0143	26.7	15.0	12.4	n/c	n/c	TU 1215
NHMW 2017/0124/0144	27.8	16.1	12.8	22	23	TU 1215
NHMW 2017/0124/0147	30.1	19.1	15.4	22	17	TU 1354
NHMW 2017/0124/0148	30.2	17.9	14.6	20	18	TU 1219

Remarks.—Maury (1917a: p. 115) wrote that Gabb remarked the crenulations are more numerous on the inner than the outer lip of *Zonaria spurcoides*, but, from the larger series at hand, either the inner or outer lip can have more numerous teeth.

Comparison.—*Zonaria pseudotumulus* from the lower to middle Miocene Cantaure Formation of Venezuela differs from *Zonaria spurcoides* in having the anterior portion of the angulation markedly swollen and overhanging the fossula. *Zonaria pseudotumulus* also has strong anterior teeth that extend a short distance over the fossula and are obsolete mid-fossula in the paratypes; in the holotype, two anterior ridges run across the fossula, although these ridges are weakened. In *Z. spurcoides*, the anterior portion of the angulation is not as swollen as in *Z. pseudotumulus*. The columellar teeth are more widely spaced and continuous across the fossula as narrow

ridges; the ridges join the columellar teeth at the angulation between the teeth and the inner edge of the fossula. In *Z. pseudotumulus*, the anterior left terminal has a pinched and somewhat twisted appearance, constricted between the groove between the anterior terminal and first columellar tooth on the ventral side and the indented margination on the dorsum. This feature is not seen in *Z. spurcoides*. The fossula is also flatter in *Z. pseudotumulus*.

Dolin (1991, p. 36) compared specimens of *Zonaria spurcoides* from the Chipola Formation of Florida with those of the living *Erronea (Adusta) hungerfordi* (G. B. Sowerby III, 1888) [= *Paradusta hungerfordi*] from the western Pacific “as the most closely related species and it displays sharp and serrate columellar teeth essentially limited to the columellar area. [*Paradusta hungerfordi*] is, however, more globose and if the lateral margin calluses are equally enlarged, they develop curious glazed nodules.” This is a curious but incorrect

comparison, as *Z. spurcoides* only superficially resembles *P. hungerfordi* in overall shape and dentition.

Zonaria pittorum Groves, 1997 [= *Pseudozonaria pittorum*], from the lower Pliocene Esmeraldas beds of the Onzole Formation of Ecuador, was likened to *Zonaria porcellus* in the original discussion (Groves, 1997). The Ecuadorian species is closer to some of the more inflated forms of *Z. spurcoides* but is considered a valid species herein.

Occurrence.—Río Yaque del Norte (localities TU 1363/1364, TU 1447, NMB 17265); Río Gurabo (locality TU 1211, TU 1215, TU 1277, TU 1278); Cañada de Zamba (locality TU 1354); Río Amina (locality TU 1219), Río Cana (locality TU 1230), Arroyo Bellaco (locality TU 1422); Río Mao (locality TU 1293).

Distribution.—Miocene (indeterminate): Dominican Republic (Gabb, 1872; Pilsbry, 1922; Ingram, 1939a, 1947c; Weisbord, 1962; Richards, 1968; Fast, 1978); Trinidad (Weisbord, 1962). Lower Miocene: Chipola Formation, Florida, USA (Dolin, 1991). Lower–middle Miocene: Baitoa Formation, Dominican Republic (this paper); Machapure Member, Brasso Formation, Trinidad (Kugler, 2001). Middle Miocene: Tamana Formation, Trinidad (F. A. Schilder, 1939a). Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b). Miocene–Pliocene: Quebradillas Formation, Puerto Rico (Hubbard, 1920; Meyerhoff, 1931; Mitchell, 1954). Lower Pliocene: Gurabo Formation, Dominican Republic (Maury, 1917a; Vaughan and Woodring, 1921; Dolin, 1991).

Zonaria* cf. *pseudotumulus Landau and Groves, 2011
Text-figs. 16.1–16.5

cf. *Zonaria pseudotumulus* Landau and Groves, 2011: p. 25, text-fig. 9, figs. 132–139.

cf. *Zonaria pseudotumulus* Landau and Groves. Landau et al., 2016: p. 65, pl. 12, fig. 2.

Material.—NHMW 2017/0124/0129 (1 specimen; locality TU 1363/1364).

Measurements.—See Table 14.

Description.—Shell small, solid, inflated, pyriform; dorsum evenly rounded, with maximum diameter just posterior to mid-height, spire involute, covered by adapical callus; sides rounded, moderately callused, callus ascending to $\frac{1}{3}$ shell height; venter flattened, weakly convex in profile; aperture narrow, weakly sinuous, posteriorly curving to left, anterior portion very slightly wider; siphonal canal relatively short, narrow, abaxially asymmetrical; exhalant channel moderately

short, limited by parallel lips; columella denticulate along entire length, bearing 21 short denticles, three anterior columellar denticles coarser, posterior denticles not extending onto columellar peristome, delimited laterally by angulation, not extending onto venter; terminal fold damaged (incomplete), separated from the anterior columellar tooth by a broad, deep groove, bordering the siphonal canal groove; fossula poorly delimited, weakly concave, very steep, ridges originating from the anterior columellar teeth run weakly onto fossula, obsolete mid-fossula (which is smooth), inner edge bearing seven coarse denticles; outer lip flattened ventrally, broadened just above mid-height, edge slightly sinuous, 25 short labral teeth developed at lip edge, hardly running onto labrum. No color pattern preserved.

Remarks.—A single moderately well-preserved specimen from the lower to middle Miocene Baitoa Formation of Río Yaque del Norte (locality TU 1363/1364) might represent *Zonaria pseudotumulus* Landau and Groves, 2011. With only one specimen at hand, and in view of the small differences outlined below, the authors hesitate to synonymize them. The specimen may appear a little higher and narrower due to slight lateral compression. The inner edge of the fossula is difficult to photograph, as it is very deep, but it bears seven coarse denticles at its inner edge. The surface is somewhat eroded, and the callus margins are not clearly seen.

Comparison.—All three *Zonaria* species found in the Dominican assemblages co-occur in the Baitoa-age beds of locality TU 1363/1364. This specimen (NHMW 2017/0124/0129) is very similar to, and possibly conspecific with, *Zonaria pseudotumulus* from the contemporaneous Cantaure Formation of Venezuela. It is slightly larger than the Venezuelan specimens (length 30.3 mm vs 22.2–27.2 mm; see Landau and Groves, 2011, table 10). They share a similar evenly globose shape, although the terminals in the Venezuelan species are slightly more produced. The number of columellar and labial denticles is similar, as is the fossula with the smooth central portion and coarsely denticulate inner edge; however, *Zonaria pseudotumulus* seems to have more anterior teeth. More material would be required to synonymize the two populations.

Zonaria spurcoides is similar in size but is immediately separated by its more elongated shape and especially the anterior terminal, which is more produced; it also has a wider aperture and coarser dentition, especially on the columella. *Zonaria vokesae* is larger and more pyriform in shape; it has a more produced anterior terminal and coarser columellar denticles that extend onto the columellar peristome. *Zonaria pingata* Landau and Groves, 2011, from the Cantaure Formation, is a larger shell that is more pyriform in shape;

Text-figs. 16.1–16.5. *Zonaria* cf. *pseudotumulus* Landau and Groves, 2011. NHMW 2017/0124/0129, length 30.3 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene.

Table 14. Measurements of *Zonaria* cf. *pseudotumulus* specimens in mm. LT = labial tooth count; CT = columellar tooth count.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0129	30.3	20.2	15.6	25	21	TU 1363/1364

it has a wider aperture and fewer, coarser denticles. Lorenz (2017, 2018) reassigned *Z. pingata* to the genus *Cypraeorbis* based on “similar shell morphology” and because “the shape and dentition resembles the European branch of *Cypraeorbis*” (Lorenz, 2018, pl. 330 caption, p. 668). The authors do not concur.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364).

Distribution.—Lower–middle Miocene: Baitoa Formation, Dominican Republic (this paper).

Zonaria vokesae n. sp.
Text-figs. 17.1–17.5

Type material.—Holotype NHMW 2017/0124/0146.

Type locality.—Locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene.

ZooBank LSID.—urn:lsid:zoobank.org:act:A78669A4-0676-4D6B-8045-D33BA18ABA88

Material.—Known only from holotype.

Measurements.—See Table 15.

Diagnosis.—*Zonaria* species of medium to large size, relatively low dorsum, 17 columellar teeth, 3 anterior teeth running halfway across fossula, posterior teeth elongated, running over columellar peristome, not over venter, broad labrum, 24 labral teeth almost restricted to inner edge.

Description.—Shell medium sized, solid, inflated, pyriform, posteriorly swollen; dorsum relatively low (accentuated by surface abrasion), in lateral profile dorsal curvature regularly attenuated abapically, spire involute, covered by adapical callus; sides rounded, moderately callused, callus ascending to 1/3–1/2 shell height; venter flattened, weakly convex in profile; aperture of medium width, anterior portion almost straight, posteriorly curving to the left, anterior portion slightly wider; siphonal canal relatively long, narrow, abaxially asymmetrical; exhalant channel moderately produced, limited by parallel lips; columella denticulate along entire length, bearing 17 elongated denticles, three anterior columellar denticles coarser, elevated, posterior denticles extending deeply onto columellar peristome, delimited laterally by angulation, not extending onto venter; terminal fold separated from the anterior columellar tooth by a broad, deep groove, fold elevated, bordering the siphonal canal, splitting abaperturally and bifid over venter; fossula poorly delimited, weakly concave, very steep, ridges originating from the anterior columellar teeth run onto fossula becoming obsolete mid-fossula (which is smooth), inner edge smooth; outer lip broadened just above mid-height, edge slightly sinuous, 24 short labral teeth developed at lip edge, hardly running onto labrum. No color pattern preserved.

Remarks.—Despite being represented by a single imperfect specimen, this species is so distinctive that it merits formal description. *Zonaria vokesae* is far more similar to the Pliocene Mediterranean species *Zonaria porcellus* (Brocchi, 1814) than it is to any of its Caribbean congeners. There is no record of *Z. porcellus* in the Mediterranean before the early Pliocene, and it is possible that it evolved from a Caribbean predecessor. In

Text-figs. 17.1–17.5. *Zonaria vokesae* n. sp., NHMW 2017/0124/0146, length 52.0 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Baitoa Formation, lower–middle Miocene.

Table 15. Measurements of *Zonaria vokesae* holotype in mm. LT = labial tooth count; CT = columellar tooth count.

Specimen	Length	Width	Height	LT	CT	Locality
NHMW 2017/0124/0146 (holotype)	52.0	28.9	20.5	24	17	TU 1363/1364

fact, Vermeij and Rosenberg (1993: p. 187) estimated that at least 28 species have dispersed eastward across the Atlantic, but no cypraeoideans were noted. *Naria spurca* (see above) is another species that may have also migrated from the western to the eastern Atlantic.

Comparison.—*Zonaria vokesae* is remarkably similar in shape and size to *Zonaria porcellus* (Brocchi, 1814) from the Mediterranean Pliocene. It differs from that species in having a lower dorsum; however, the low dorsum is accentuated by decortication and, when complete, may have been equal in height to that of *Z. porcellus*. The anterior terminal is almost identical in the two species. The posterior terminal is more swollen on the labial side and the lips delimiting the exhalant channel stockier in *Z. porcellus*. The anterior portion of the aperture does not widen in *Z. porcellus* and the teeth on both lips are finer than in *Z. vokesae*. Nevertheless, their resemblance is striking and indicates a closer affinity than with any of the small number of Caribbean congeners.

Zonaria pittorum Groves, 1997 [= *Pseudozonaria pittorum*], from the lower Pliocene Esmeraldas beds of the Onzole Formation of Ecuador, was also likened to *Zonaria porcellus* in the original discussion in Groves (1997). It differs from *Zonaria vokesae* in being smaller shelled; it also has a shorter anterior terminal that is less constricted and fewer labial teeth that extend half way across the outer lip. The Ecuadorian species is closer to some of the more inflated forms of *Zonaria spurcoides* (Text-figs. 15.5–15.8). *Zonaria*

pseudotumulus, from the lower to middle Miocene Cantaure Formation of Venezuela, has a less pyriform shell shape and terminals that are broader and less produced. Furthermore, its aperture is more sinuous and its columellar teeth are smaller and restricted to the angulation.

Etymology.—Named after Emily H. Vokes of Tulane University (retired), valued friend to both authors, in recognition of her enormous contributions to Caribbean Neogene paleontology. *Zonaria* gender feminine.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364).

Distribution.—Lower–middle Miocene: Baitoa Formation, Dominican Republic (this paper).

Family **OVULIDAE** Fleming, 1822

Ovulidae Fleming, 1822: p. 490 (as Ovuladae).

Description.—Shell mostly striate, with elongate terminals. Protoconch not visible in the adult shell. Columella and labrum mostly without dentition. Aperture narrow. A characteristic radula separates the Ovulidae from the Cypraeidae and other allied groups (Lorenz and Fehse, 2009: p. 32).

Table 16. Ovulidae described and/or recorded from the Dominican Republic. Numbers of specimens of nine taxa of ovulid gastropods collected in the Cibao Valley for this study.

Taxon	Current Genus	No. of Specimens
<i>Cyphoma guraboensis</i> n. sp.		3
<i>Ovulum intermedium</i> G. B. Sowerby I, 1828	<i>Cyphoma</i>	30
<i>Cyphoma</i> sp.		2
<i>Ovula</i> (<i>Neosimnia</i>) <i>wisewoodae</i> Maury, 1917a	<i>Neosimnia</i>	33
<i>Neosimnia</i> sp.		12
<i>Ovulum uniplicatum</i> G. B. Sowerby II, 1849a	<i>Simnialena</i>	17
<i>Jenneria dominicensis</i> Olsson, 1967		2
<i>Jenneria gabbiana</i> (Guppy, 1876)		59
<i>Jenneria pilsbryi</i> Olsson, 1967		7

Remarks.—These are the egg or spindle cowries. Because of their minute and fragile shells, the early fossil record of the Ovulidae is poorly known (Lorenz and Fehse, 2009). The earliest ovulids are *Eocypraea pilulosa* (Stoliczka, 1867) and *Eocypraea abbassi* (Abbass, 1963), both of which appeared in the Late Cretaceous (Cenomanian) of India (M. Schilder and F. A. Schilder, 1971; Tracey et al., 1993: p. 148) and Egypt (Abbass, 1963: p. 87, 88). By the Eocene the family had attained a worldwide distribution.

Early classification schemes were based on shell morphology alone. The comprehensive treatment of the family by Cate (1973) also relied heavily on external morphology with little mention of the animal or host habitat. In addition to shell characters, Simone (2004) used anatomy as the basis of his analysis of the entire superfamily Cypraeoidea. Unfortunately, little information as to the classification of the ovulids at the family level resulted. Fehse (2001b) produced a highly useful catalog of the Ovulidae. Lorenz and Fehse (2009) provided the most comprehensive treatment of the Ovulidae thus far; they provided much-needed additional information pertaining to shell morphology, patterns of distribution, cryptic morphology, biology, and paleontology. The molecular analysis of Schiaparelli et al. (2005) has been helpful in the higher levels of ovulid systematics. However, they also noted that ovulid taxonomy is still far from being settled, having often been based on trivial and inconsistent morphological characters. Herein, the higher-level systematics (above superfamily) follow those of Bouchet et al. (2017). Lorenz and Fehse (2009) are followed for lower-level systematics. Nine species of ovulids were recognized in the Dominican Neogene assemblages (Table 16).

Subfamily **SIMNIINAE** F. A. Schilder, 1927

Simniinae F. A. Schilder, 1927: p. 76 (as tribe Simniini)

Description.—“Shells rhomboidal, slightly rhomboidal or lanceolate with a distinct, prominent transverse cord-like funiculum” (Lorenz and Fehse, 2009: p. 90).

Remarks.—The earliest Simniinae species are *Neosimnia vibrayana* (de Raincourt, 1870), *Neosimnia cossmanni* Schilder, 1927, and *Simnia lhommei* (Cossmann, 1907) from lower Eocene (Ypresian) strata of France.

Genus **CYPHOMA** Röding, 1798

Cyphoma, Röding, 1798: p. 21. Type species (by subsequent designation, Herrmannsen, 1847a: p. 355): *Bulla gibbosa* Linnaeus, 1758, Recent, Caribbean Sea.

Ulitmus de Montfort, 1810: pp. 642, 643. Type species (by original designation): *Bulla gibbosa* Linnaeus, 1758, Recent, Caribbean Sea.

Binvoluta Schlüter, 1838: p. 24. Type species (by original monotypy): *Bulla gibbosa* Linnaeus, 1758, Recent, Caribbean Sea.

Carinea Swainson, 1840: p. 326. Type species (by original monotypy): *Bulla gibbosa* Linnaeus, 1758, Recent, Caribbean Sea.

Cyphonia Gray, 1847: p. 143. Misspelling of *Cyphoma*.

Pseudocyphoma Cate, 1973: p. 69. Type species (by original designation): *Ovulum intermedium* G. B. Sowerby I, 1828, Recent, Caribbean Sea.

Original description.—No description was provided by Röding (1798: p. 21), but he does refer to *Cyphoma gibbosa* being cited in Gmelin (1791) and figured in Martini [and Chemnitz] (1776).

Revised description.—“Shells cylindrical, spindle-shaped or rhomboidal, often heavily calloused, with broad terminals and a transverse cord-like funiculum that is often covered by a callosity” (Lorenz and Fehse, 2009: p. 90).

Remarks.—Reijnen et al. (2017) showed that several well-known Caribbean *Cyphoma* species—*Cyphoma gibbosum* (Linnaeus, 1758), *Cyphoma mcgintyi* Pilsbry, 1939, and *Cyphoma signatum* Pilsbry and McGinty, 1939—that had been traditionally distinguished based on shell character and mantle color were all conspecific based on genetic analysis. Therefore, a rather conservative approach to the classification of fossil ovulids is taken, with ever-increasing trepidation.

Geographic distribution.—Bermuda (Jensen and Pearce, 2009), southern Florida, Gulf of Mexico, and Caribbean to Brazil, the entire Panamic Province.

Stratigraphic distribution.—Miocene to Recent.

***Cyphoma guraboensis* n. sp.**

Text-figs. 18.1–18.6

Cymbula acicularis (Lamarck). H. E. Vokes and E. H. Vokes, 1983: pl. 8, fig. 6 [not *Cymbovula acicularis* (Lamarck, 1810)].

Type material.—Holotype NHMW 2017/0124/0239; paratype 1 NHMW 2017/0124/0245; paratype 2 PRI 84864 (ex Tulane coll.), specimen illustrated by H. E. Vokes and E. H. Vokes (1983: pl. 8, fig. 6). The specimen illustrated by H. E. Vokes and E. H. Vokes (1983) is not Recent, but fossil, from locality TU 1215, Río Gurabo, Dominican Republic (E. H. Vokes personal communication BL; 06/07/2020).

Type locality.—TU locality 1227: Arroyo Zalaya, which crosses the road to Jánico from Santiago de los Caballeros, Dominican Republic (see Saunders et al., 1986: fig. 36), Gurabo Formation, lower Pliocene.

ZooBank LSID.—[urn:lsid:zoobank.org:act:01A49F06-59D4-418E-B54B-9599725060D4](https://zoobank.org/act:01A49F06-59D4-418E-B54B-9599725060D4)

Material.—Known from type series only.

Measurements.—See Table 17.

Diagnosis.—*Cyphoma* species of large size, slender spindle shape, dorsally arched in profile, with elongated slender terminals, dorsum bearing moderately well-developed saddle hump, funiculum transverse, moderately developed.

Description.—Shell of medium size and thickness, slender and spindle shaped with elongated narrow terminals, dorsally arched in profile. Dorsum moderately inflated, bearing slight to well-developed transverse saddle hump at mid-shell length; sculpture absent. Aperture elongated, slender, very narrow, widening slightly abapically. Outer lip moderately thickened

by labial varix, gently convex in lateral profile; posterior terminal slender, elongated, ending in rounded point; outer lip weakly flared abapically; anterior terminal long. Columellar callus weakly to moderately developed, forming callus wash over venter to slightly thickened columellar pad; moderately developed, adapically strongly oblique transverse funiculum.

Remarks.—The elongated spindle shape is a shell form common to several ovulid genera, and is more extreme in *Cyphoma guraboensis* than any other known *Cyphoma* species. The new species has been placed in *Cyphoma* based on the relatively solid shell, sometimes well-developed dorsal saddle, transverse funiculum, and lack of spiral sculpture. Placement in the genus *Neosimnia* Fischer, 1884, could also be argued; shells in that genus are spindle shaped like the new species, but they do not form a distinct dorsal saddle. Additionally, in most species of *Neosimnia* some spiral sculpture is present on the dorsum towards the terminals.

There are some differences in shell form between the holotype and the paratypes. The paratypes do not have the dorsal saddle as strongly developed, the labial callus is thinner, and the columellar callus is reduced to a thin wash. These are all characters that indicate that paratype 1 is not fully adult, despite being larger. Large variations in full adult height are not uncommon amongst ovulids; for example, in living specimens of *Cyphoma gibbosum*, a size range of 20–39 mm is recorded (Lorenz and Fehse, 2009: p. 90). No more can be said based on the small numbers of specimens available.

Comparisons.—*Cyphoma guraboensis* differs from all known *Cyphoma* species in being more strongly spindle shaped, with more produced and slenderer terminals. The most similar species is *Cyphoma intermedium* (G. B. Sowerby I, 1828), with which *C. guraboensis* co-occurs in the lower Pliocene Gurabo assemblages; however, *C. intermedium* has shorter terminals (see below). *Cyphoma christahemmenae* (Fehse, 1997), from the coasts of the southern Caribbean and Brazil, is also spindle shaped; however, it is more inflated and thinner shelled with the adapical portion strongly twisted at the funiculus.

Etymology.—Named after the Gurabo Formation. *Cyphoma* gender neuter.

Occurrence.—Río Gurabo (locality TU 1215); Arroyo Zalaya (locality TU 1227).

Distribution.—Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Text-fig. 18. *Cyphoma guraboensis* n. sp. 1–3, holotype, NHMW 2017/0124/0239, length 25.5 mm, width 7.2 mm; locality TU 1227, Arroyo Zalaya, Dominican Republic, Gurabo Formation, lower Pliocene. 4–6, paratype 1, NHMW 2017/0124/0245, length 32.5 mm, width 9.5 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Table 17. Measurements of *Cyphoma guraboensis* specimens in mm.

Specimen	Length	Width	Height	Locality
Holotype NHMW 2017/0124/0239	25.5	7.2	6.2	TU 1227
Paratype 1 NHMW 2017/0124/0245	32.5	9.5	7.0	TU 1215
Paratype 2 PRI 84864	21.0	5.9	4.6	TU 1215

Cyphoma intermedium (G. B. Sowerby I, 1828)
Text-figs. 19.1–19.9

Ovulum intermedium G. B. Sowerby I, 1828: p. 158.
Ovula intermedia (G. B. Sowerby I). Kiener, 1843: p. 23, pl. 4, fig. 2.
Ovulum intermedium G. B. Sowerby I. G. B. Sowerby II, 1849b: p. 479, pl. 100, figs. 61, 62.
Ovulum immunitum Guppy, 1873: pp. 78, 79, pl. 1, fig. 7.
Ovulum immunitum Guppy. Guppy, 1874: pp. 409, 440, pl. 16, fig. 7.
Ovula intermedia (G. B. Sowerby I). Weinkauff, 1881b: p. 195, pl. 49, figs. 10, 11.
Cyphoma intermedia (G. B. Sowerby I). Paetel, 1887: p. 326, pl. 4, fig. 2.
Ovula (*Simnia*) *immunita* (Guppy). Dall, 1903: p. 1584.
Simnia (*Neosimnia*) *intermedia* (G. B. Sowerby I). Maury, 1925: p. 112.
Simnia (*Calpurna*) *immunita* Woodring (*partim*), 1928: p. 315, pl. 21, figs. 3, 4 only (not figs. 5–8).
Ovula (*Neosimnia*) *puana* Anderson, 1929: p. 140, pl. 9, figs. 9, 10.
Neosimnia (*Neosimnia*) *immunita* (Guppy). F. A. Schilder, 1932a: p. 236.
Cyphoma intermedia (G. B. Sowerby I). F. A. Schilder, 1932a: p. 238.
Cyphoma puana (Anderson). F. A. Schilder, 1932a: p. 238.
Cyphoma intermedia (G. B. Sowerby I). F. A. Schilder, 1932b: p. 55, pl. 5, fig. 69.

Simnia (*Neosimnia*) *intermedia* (G. B. Sowerby I). Johnson, 1934: p. 111.
Cyphoma puana bowdenensis F. A. Schilder, 1939a: pp. 7, 9, 14, fig. 9.
Neosimnia (*Neosimnia*) *immunita* (Guppy). F. A. Schilder, 1939a: pp. 9, 14.
Cyphoma bowdenensis Schilder. F. A. Schilder, 1941: p. 109.
Cyphoma puana (Anderson). F. A. Schilder, 1941: p. 109.
Simnia immunita (Guppy). F. A. Schilder, 1941: p. 109.
Cyphoma intermedia (G. B. Sowerby I). Allan, 1956: p. 132, pl. 13, fig. 11.
Cyphoma intermedium (G. B. Sowerby I). Warmke and Abbott, 1961: p. 93, pl. 16, fig. j.
Cyphoma intermedia [*sic*] (G. B. Sowerby I). Cate, 1969: p. 101, pl. 8, fig. 11.
Cyphoma intermedium (G. B. Sowerby I). McGinty, 1970: p. 55.
Cyphoma intermedium (G. B. Sowerby I). Hoerle, 1970: p. 63.
Cyphoma intermedium (G. B. Sowerby I). Andrews, 1971: p. 99, unnumbered fig.
Simnia rufa immunita (Guppy). M. Schilder and F. A. Schilder, 1971: pp. 75, 122.
Cyphoma intermedia intermedia (G. B. Sowerby I). M. Schilder and F. A. Schilder, 1971: pp. 76, 123.
Cyphoma intermedia puana (Anderson). M. Schilder and F. A. Schilder, 1971: pp. 76, 147.
Cyphoma intermedia bowdenensis (Schilder). M. Schilder and F. A. Schilder, 1971: pp. 76, 100.
Aperiovula abbotti Cate, 1973: p. 39, fig. 78.

Text-fig. 19. *Cyphoma intermedium* (G. B. Sowerby I, 1828). 1–3, NHMW 2017/0124/0240, length 18.7 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 4–6, NHMW 2017/0124/0241, length 18.3 mm; locality NMB 16844. 7–9, NHMW 2017/0124/0246, length 22.3 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Pseudocyphoma intermedium (G. B. Sowerby I). Cate, 1973: p. 69, figs. 155, 156.

Pseudocyphoma kathiewayae Cate, 1973: p. 70, fig. 45a.

Cyphoma (*Pseudocyphoma*) *intermedium* (G. B. Sowerby I). Abbott, 1974: p. 153, fig. 1669, pl. 3, fig. 1669.

Cyphoma (*Cyphoma*) *intermedium* (G. B. Sowerby I). Rios, 1975: p. 73, pl. 20, fig. 297.

Simnia (*Neosimnia*) *intermedia* (G. B. Sowerby I). Regteren Altena, 1975: p. 35.

Cyphoma intermedium (G. B. Sowerby I). Abbott and Dance, 1982: p. 99, unnumbered fig.

Cyphoma (*Pseudocyphoma*) *intermedium* (G. B. Sowerby I). Rios, 1985: p. 66, pl. 23, fig. 293.

Pseudocyphoma gibsonsmithorum Petuch, 1987: p. 94, pl. 26, figs. 6, 7.

Phenacovolva (*Turbovula*) *lindae* Petuch, 1987: pp. 94, 95, pl. 26, figs. 8, 9 [not *Cyphoma lindae* Petuch, 1987 = *C. gibbosum* (Linnaeus, 1758)].

Cyphoma sp. Petuch, 1988: pl. 17, figs. 9, 10.

Pseudocyphoma intermedium (G. B. Sowerby I). Robinson, 1991: p. 263, pl. 11, figs. 4, 4a.

Pseudocyphoma intermedia (G. B. Sowerby I). Petuch, 1994: p. 108, pl. 33, fig. K.

Pseudocyphoma immunita (Guppy). Petuch, 1994: p. 108, pl. 33, figs. N, O.

Pseudocyphoma intermedium (G. B. Sowerby I). Fehse, 1997: p. 35, fig. 5.

Pseudocyphoma intermedium (G. B. Sowerby I). Carlos and Joaquín, 1998: p. 127.

Pseudocyphoma kathiewayae Cate. Fehse 2000: p. 52, figs. 1, 2, 2a, b, 4, 4a, b, 5, 5a, b, 6, 6a, b, 13, 13a, b.

Pseudocyphoma rosenbergi Fehse, 2001a: p. 39, fig. 3.

Pseudocyphoma intermedium (G. B. Sowerby I). Fehse, 2003b: p. 19, pl. 9, figs. 53, 53a, pl. 16, fig. 1.

"*Pseudocyphoma*" *immunita* (Guppy). Fehse, 2003b: p. 21, pl. 16, fig. 2.

Pseudocyphoma bowdenensis (Schilder). Fehse, 2003b: p. 22, pl. 16, fig. 3.

Pseudocyphoma kathiewayae Cate. Fehse, 2003b: p. 23, pl. 10, figs. 59–62, pl. 16, fig. 4.

Pseudocyphoma gibsonsmithorum Petuch. Fehse, 2003b: p. 26, pl. 9, figs. 50–52, pl. 16, fig. 6.

Pseudocyphoma rosenbergi Fehse. Fehse, 2003b: p. 28, pl. 11, figs. 63–69, pl. 13, figs. 85, 86.

Pseudocyphoma intermedium (G. B. Sowerby I). Jensen and Pearce, 2009: pp. 65, 66.

Cyphoma intermedia [sic] (G. B. Sowerby I). Lorenz and Fehse, 2009: p. 94, pl. 118, figs. 1–9, 13, 14 (holotype of *Pseudocyphoma kathiewayae* Cate, 1973).

Pseudocyphoma kathiewayae Cate. Lorenz and Fehse, 2009: p. 94.

Pseudocyphoma intermedium (G. B. Sowerby I). Massemin et al., 2009: p. 102, 2 unnumbered figs.

Cyphoma (*Pseudocyphoma*) *intermedium* (G. B. Sowerby I). Rios, 2009: p. 135, fig. 320.

Cyphoma cf. *intermedia* (G. B. Sowerby, I). Lorenz and Fehse, 2009: p. 94, pl. 117, figs. 4, 5, 8, 9, 11, 12, pl. 118, figs. 10–12, A209, A210.

Pseudocyphoma intermedium (G. B. Sowerby I). Tunnell et al., 2010: p. 174, unnumbered fig.

Pseudocyphoma intermedium (G. B. Sowerby I). Petuch and Sargent, 2011: pp. 49, 80, 136, fig. 3.4D.

Pseudocyphoma intermedium (G. B. Sowerby I). Simone, 2011: pp. 167, 215.

Pseudocyphoma rosenbergi Fehse. Petuch, 2013: p. 166.

Pseudocyphoma intermedium (G. B. Sowerby I). Petuch and Myers, 2014: pp. 97, 98, 255, fig. 5.6K.

Cyphoma intermedium (G. B. Sowerby I). Lamy and Pointier, 2017: p. 173, pl. 49, figs. 8a–d, pl. 50, fig. 7.

Type material.—*Ovulum intermedium*, neotype (Lorenz and Fehse, 2009: p. 94) ZSM 20070694; *Ovulum immunitum*, current whereabouts unknown; *Ovula* (*Neosimnia*) *puana*, holotype CAS 4626 (= CASG 351.01); *Cyphoma puana bowdenensis*, holotype in NMB; *Aperiovula abbotti*, holotype ANSP 301668; *Pseudocyphoma kathiewayae*, holotype FMNH 161588; *Pseudocyphoma gibsonsmithorum*, holotype USNM 859829; *Phenacovolva* (*Turbovula*) *lindae*, holotype USNM 859828; *Pseudocyphoma rosenbergi*, holotype HNC 57353, 3 paratypes HNC 57354–57356.

Type locality.—*Ovulum intermedium*, Monte Cristi Beach, northwest Dominican Republic, Recent (designated by Cate,

1973: p. 70 for *Pseudocyphoma intermedium*); Icacos Island, northeast of Puerto Rico, Recent (designated by Fehse, 2000: p. 55 for *Pseudocyphoma kathywayae*); Meiaipe, Guarapi, Espirito Santo State, Brazil, Recent (according to Lorenz and Fehse, 2009: p. 94 for *Cyphoma intermedium*); *Ovulum immunitum*, Jamaica(?), Pliocene, Bowden Member of the Layton Formation; *Ovula (Neosimnia) puana*, near Punta Pua, Bolivar Province, Colombia, Tuberá Group, Miocene, CASG loc. 351; *Cyphoma puana bowdenensis*, Bowden, Jamaica, Miocene; *Aperiovula abbotti*, South Padre Island, Texas, USA; *Pseudocyphoma kathywayae* (see Lorenz and Fehse, 2009: p. 94 for details); *Pseudocyphoma gibsonsmithorum*, Borboruta, Carabobo State, Venezuela, Recent; *Phenacovolva (Turbovula) lindae*, off Cabo La Vela, Goajira Peninsula, Colombia, Recent; *Pseudocyphoma rosenbergi*, Meaipe, Guarapari, Espirito State, Brazil, Recent.

Material.—NHMW 2017/0124/0240-0241 (2 specimens; locality NMB 16844); NHMW 2017/0124/0246 (5 specimens; locality NMB 16844); NHMW 2017/0124/0246 (1 specimen; locality TU 1215); NHMW 2017/0124/0247 (1 specimen; locality TU 1215); NHMW 2017/0124/0248 (13 specimens; locality TU 1215); NHMW 2017/0124/0255 (2 specimens; locality TU 1358); PRI 84774 (1 specimen; locality TU 1227A); PRI 84872 (2 specimens; locality TU 1250); PRI 84860 (3 specimens; locality TU 1215).

Measurements.—Maximum length 22.3 mm, width 7.7 mm, height 7.1 mm.

Original description.—"O. testa ovato-oblonga, utrinque subacuminata; dorso supra medium transversim subangulato, labio columellari prope extremitatem superiorem oblique uniplicato; labii extreni margine interno edentulo" (G. B. Sowerby I, 1828: p. 158).

Revised description.—Shell of medium size and thickness, moderately broad, spindle shaped, with produced, rounded terminals. Dorsum moderately inflated, bearing well-developed narrow transverse saddle hump at mid-shell length; sculpture absent. Aperture elongated, slender, very narrow, widening slightly abapically. Outer lip thickened by prominent, rounded labial varix, weakly convex in lateral profile; posterior terminal slender, produced, rounded at tip; outer lip somewhat flared abapically; anterior terminal moderately long. Columellar callus weakly to moderately developed; adapically well-developed transverse funiculum.

Remarks.—*Cyphoma intermedium* is characterized by its relatively broad, spindle-shaped shell and well-developed but narrow dorsal saddle. In view of the finding of Reijnen et al.

(2017) concerning *Cyphoma gibbosum* (discussed under the generic note), it is likely that present-day Caribbean *Cyphoma* species with slender shells will be synonymized, but revision of these species is beyond the scope of this work. Therefore, a broad approach is taken to *C. intermedium* in the fossil faunas. The hypotype of *Simnia (Calpurna) immunita* Woodring, 1928, from the Pliocene Bowden Member of the Layton Formation of Jamaica falls within the range of variability of *C. intermedium*. The smaller specimens illustrated by Woodring (1928) probably represent a *Simnialena* Cate, 1973, species (Woodring, 1928: pl. 21, figs. 5, 6) and a *Neosimnia* Fischer, 1884 species (Woodring, 1928: pl. 21, figs. 7, 8).

Ovula (Neosimnia) puana Anderson, 1929, from the lower Pliocene Tubará Formation of Colombia, is based on an incomplete specimen showing a clear dorsal saddle. It is likely to represent *C. intermedium*. The present authors agree with Fehse (2003b: p. 22) that the specimen is far from perfect, but the species is described and illustrated adequately and, therefore, cannot be considered a *nomen nudum*.

Living specimens can be found from the intertidal to 300 m on a variety of hosts (Lorenz and Fehse, 2009).

Comparisons.—It is difficult to offer a comparison with related species following Reijnen et al. (2017), who showed shell morphology may not be useful in separating the more rounded *Cyphoma* species (*C. gibbosum* and *C. mcgintyi*, and *C. signatum*). In the past, great efforts have been made to recognize species within what Fehse called the "*Cyphoma-Pseudocyphoma* complex" (Fehse, 2001a, 2003a, b), but it is likely that most if not all these taxa represent a single species. *Cyphoma guerrinii* Fehse, 2001a, may be a geographically isolated species or variety; it is separated by its faintly transversely striated dorsum. The present authors conclude that the Caribbean fossil taxa described as *Ovulum immunitum* and *Cyphoma puana bowdenensis* from the Bowden Member of the Layton Formation of Jamaica, and *Ovula (Neosimnia) puana* from the Tubará Formation of Colombia all fit within the variability of *Cyphoma intermedium*.

Occurrence.—Río Cana (locality NMB 16844); Río Gurabo (localities TU 1215, TU 1358); Arroyo Zalaya (locality TU 1227A); Río Verde (locality TU 1250).

Fossil distribution.—Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper); Tubará Formation, Colombia (Anderson, 1929); Pinecrest Beds, Florida (Petuch, 1994). Pliocene: Bowden Member of the Layton Formation, Jamaica (Guppy, 1873, 1874; Woodring, 1928; F. A. Schilder, 1932a, 1939a). Pleistocene (indeterminate): "Glades" Unit, Palm Beach County, Florida

Text-fig. 20. *Cyphoma* sp. 1–3, NHMW 2017/0124/0276, length 12.1 mm, width 6.0 mm, height 5.0 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 4–6, PRI 84870, length 13.0 mm, width 7.2 mm, height 5.0 mm; locality TU 1250, Río Verde, Dominican Republic, Gurabo Formation, lower Pliocene.

(Hoerle, 1970). Lower Pleistocene: Moin Formation, Costa Rica (Robinson, 1991). Upper Pleistocene: Bermont Formation, Florida (Petuch, 1994).

Recent distribution.—Central Caribbean, Venezuela to Brazil (Lorenz and Fehse, 2009).

***Cyphoma* sp.**

Text-figs. 20.1–20.6

Material.—NHMW 2017/0124/0276 (1 specimen; locality NMB 16844); PRI 84870 (1 specimen; locality TU 1250).

Measurements.—Maximum length 13.0 mm.

Description.—Shell of small to medium size, solid, broad, squat, and spindle shaped with short, pointed terminals. Dorsum relatively strongly inflated, moderately to weakly humped; weakly developed sculpture of fine incised spiral lines restricted to extremities. Aperture elongated, slender, narrow, widened abapically. Outer lip strongly thickened by rounded labial varix, almost straight in lateral profile; posterior terminal short, straight, pointed at tip; outer lip flared abapically; anterior terminal short. Columella slightly concave abapically. Columellar callus thin, sharply delimited, covering entire venter; adapically oblique spiral funiculum.

Remarks.—This unnamed species is placed in the genus *Cyphoma* based on its thick shell, short terminals, humped dorsum, thick outer lip, and columella callus that covers the entire venter. *Neosimnia* Fischer, 1884, species tend to be slenderer with longer terminals, although placement in *Neosimnia* is also possible. Unfortunately, this species is represented by only two specimens; the shell thickness and broad labial callus indicate they are fully adult. There is some variability as to the sharpness of the dorsal hump in the

two specimens at hand, which is not unusual in the genus. Additional material is required to further characterize this species.

Comparisons.—*Cyphoma* sp. is immediately separated from its Dominican congeners *Cyphoma guraboensis* and *Cyphoma intermedium* in having a smaller, squatter shell with less produced terminals. Some of the shells identified as *Cyphoma versicolor* Fehse, 2003b, by Lorenz and Fehse (2009: pl. 116, fig. 10, pl. 117, fig. 2) from Brazil seem similar in shape, and *C. versicolor* is characterized by its lack of spiral surface sculpture. In view of the problems discussed in the generic remarks, it will be interesting to see how many of these tropical Western Atlantic nominal taxa will survive the test of time.

Occurrence.—Río Cana (locality NMB 16844); Río Verde (locality TU 1250).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Genus *NEOSIMNIA* Fischer, 1884

Calpurna Fleming, 1828: pp. 328, 331. Type species (by original monotypy): *Ovula leathsii* J. de C. Sowerby, 1825 (*sensu* Tryon, 1885: p. 254), Pliocene, England (suspected misspelling of *Calpurnus*).

Velox Monterosato, 1878: p. 319. Type species (by original monotypy): *Bulla spelta* Linnaeus, 1758, Recent, Mediterranean Sea (suspected error for of *Volva*).

Neosimnia Fischer, 1884: p. 664. Type species (by original monotypy): *Bulla spelta* Linnaeus, 1758, Recent, Mediterranean Sea.

Spiculata Cate, 1973: p. 82. Type species (by original description): *Ovula loebbeckeana* Weinkauff, 1881b, Recent, southern California to Baja California Sur, México.

Original description.—"Coquille ovale ou étroite, subfusiforme, à extrémités peu prolongées; labre épais; columelle munie en arrière d'un pli calleux, oblique" (Fischer, 1884: p. 664).

Revised description.—"Shells ovate, broad centrally, with a curling posterior. Funiculum spiral cord like" (Lorenz and Fehse, 2009: p. 97).

Remarks.—Dolin and Ledon (2002) considered *Neosimnia* as a synonym of *Simnia* Risso, 1826. Lorenz and Fehse (2009: pp. 95–102, pl. 122–132) considered the two genera distinct and figured many species of each genus; their interpretation was confirmed by Fehse (2016b: p. 40; 2018: pp. 3, 4). Based on the generic attributions of Lorenz and Fehse (2009) and Fehse (2016b, 2018), there seem to be clear differences in shell morphology between *Neosimnia* and *Simnia* species; *Neosimnia* species are thicker shelled with a thickened outer lip, whereas *Simnia* species have a wider aperture abapically and an outer lip devoid of varix. As previously mentioned, however, Schiparelli et al. (2005) noted that ovulid taxonomy is still far from being settled, having often been based on trivial and inconsistent morphological characters.

Geographic range.—Mediterranean and West Africa, Caribbean and Panamic Province to northern California.

Stratigraphic range.—Eocene (?), Miocene to Recent

***Neosimnia wisewoodae* (Maury, 1917a)**

Text-figs. 21.1–21.17

Ovula (Neosimnia) wisewoodae Maury, 1917a: pp. 113, 114, pl. 48, fig. 17.

Ovula (Neosimnia) wisewoodae Maury. Maury, 1917b: p. 13.

Ovula (Radius) wisewoodae Maury. Vaughan and Woodring, 1921: p. 120.

Neosimnia (Neosimnia) wisewoodae (Maury). F. A. Schilder, 1932a: p. 236.

Simnia inflexa wisewoodae (Maury). M. Schilder and F. A. Schilder, 1971: pp. 76, 168.

Ovula (Neosimnia) wisewoodae Maury. Fast, 1978: p. 170.

Type material.—Holotype PRI 28823; length 13.5 mm, width 5.4 mm; Fast (1978: p. 170) provided the previously unpublished type number.

Type locality.—Bluff 3, Cercado de Mao, Dominican Republic (= locality TU 1294), Cercado Formation, upper Miocene.

Material.—NHMW 2017/0124/0240-0251 (1 specimen; locality TU 1449); NHMW 2017/0124/0252, 0253 (2 specimens; TU 1358); NHMW 2017/0124/0254 (13 incomplete and juvenile specimens; locality TU 1358);

NHMW 2017/0124/0256 (4 incomplete specimens; locality TU 1215); NHMW 2017/0124/0273-0274 (2 specimens; locality NMB 15907); PRI 84861 (1 specimen; locality TU 1215).

Measurements.—Maximum length 22.0 mm, width 7.7 mm, height 5.4 mm.

Original description.—"Shell resembling *O. spelta* in outline, smooth except for fine, wavy spirals near the extremities and delicate longitudinal growth-lines; outer lip markedly arcuate, bordered by a callus band; dorsal surface convex, with a slight but obvious hump most apparent on the latter half of the body whorl; columella with one very strong posterior plication; posterior canal sharply reflexed" (Maury, 1917a: p. 113).

Revised description.—Shell of medium size, relatively thin, slender, spindle shaped, with elongated, narrow, recurved terminals. Dorsum moderately inflated, obsoletely and widely humped mid-shell length; sculpture of fine incised spiral lines towards extremities weakly developed. Aperture elongated, slender, narrow, widening abapically. Outer lip slightly thickened by narrow labial varix, convex in lateral profile; posterior terminal slender, elongated, recurved, pointed; outer lip abapically flared; anterior terminal moderately long. Columellar callus weakly to moderately developed, forming callus wash over venter to slightly thickened columellar pad; strongly developed, oblique spiral funiculum adapically.

Remarks.—The series illustrated shows some variability in the inflation of the last whorl and the prominence of the dorsal hump. The curved outer lip on profile view described by Maury (1917a: p. 113) is clearly seen (Text-figs. 21.4, 21.7, 21.10).

Comparisons.—According to Lorenz and Fehse (2009), two *Neosimnia* species occur in the present-day western Atlantic: *Neosimnia bijuri* (Cate, 1976) and *Neosimnia bartschi* (Cate, 1973). Both are smaller-shelled, squatter, and more inflated mid-whorl than *Neosimnia wisewoodae* (Maury, 1917a); furthermore, their inflation is smoother and less humped. *Neosimnia bartschi* has a recurved, pointed posterior terminal similar to that of *N. wisewoodae*, whereas the posterior terminal in *N. bijuri* is straight and blunter. *Neosimnia loebbeckeana* (Weinkauff, 1881b), from the present-day eastern Pacific from Monterey, California to Bahía Magdalena, Baja California Sur, México, is more similar in shape to *N. wisewoodae* than any of the extant Caribbean species, and some specimens of *N. loebbeckeana* show a similarly recurved posterior terminal. *Neosimnia loebbeckeana* differs from *N. wisewoodae* in having the dorsal hump narrower but more accentuated mid-whorl.

Text-fig. 21. *Neosimnia wisewoodae* (Maury, 1917a). 1, 2, holotype, PRI 28823, length 13.5 mm; Bluff 3 (= TU 1294), Cercado de Mao, Río Mao, Dominican Republic, probably Cercado Formation, upper Miocene. 3–5, NHMW 2017/0124/0273, length 18.0 mm; locality NMB 15907, Río Gurabo, Dominican Republic, Cercado Formation, upper Miocene. 6–8, NHMW 2017/0124/0274, length 16.9 mm, locality NMB 15907. 9–11, NHMW 2017/0124/0251, length 22.0 mm; locality TU 1449, La Barranca, Río Yaque del Norte, Dominican Republic, Gurabo Formation, lower Pliocene. 12–14, NHMW 2017/0124/0252, length 19.0 mm; locality TU 1358, Río Gurabo, Dominican Republic, Cercado Formation, upper Miocene. 15–17, NHMW 2017/0124/0253, length 16.5 mm; locality TU 1358.

Occurrence.—Río Yaque del Norte (locality TU 1449); Río Gurabo (localities TU 1215, TU 1358, NMB 15907).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; F. A. Schilder, 1932a). Lower Pliocene: Gurabo Formation (this paper).

***Neosimnia* sp.**

Text-figs. 22.1–22.12

Simnia (*Calpurna*) *immunita* Woodring (*partim*), 1928: p. 315, pl. 21, figs. 7, 8 only [not figs. 3, 4 = *Cyphoma intermedium* (G. B. Sowerby I, 1828); not figs. 5, 6 = ?*Simnialena* sp.].

Material.—NHMW 2017/0124/0257, 0258 (2 specimens; locality TU 1215); NHMW 2017/0124/0259 (1 specimen; locality TU 1210); NHMW 2017/0124/0242 (1 specimen; locality TU 1449); NHMW 2017/0124/0275 (1 specimen; locality NMB 15907); PRI 84771 (1 adult + 3 juvenile specimens; locality TU 1294); PRI 84772 (1 adult + 2 juvenile specimens; locality TU 1419).

Measurements.—Maximum length 15.8 mm, width 4.9 mm, height 4.0 mm.

Description.—Shell of small to medium size, relatively solid, slender, spindle shaped, with short, rounded terminals. Dorsum hardly inflated, not humped; sculpture of fine incised spiral lines towards extremities weakly developed. Aperture elongated, slender, narrow, hardly widened abapically. Outer lip thickened by rounded labial varix, gently and evenly convex in lateral profile; posterior terminal short, straight, rounded at tip; outer lip hardly flared abapically; anterior terminal moderately short. Columellar callus moderately developed, forming thickened columellar pad; moderately to strongly developed, oblique spiral funiculum adapically.

Remarks.—One of the smaller specimens from the Pliocene Bowden Member of the Layton Formation of Jamaica illustrated by Woodring (1928: pl. 21, figs. 7, 8) as *Simnia* (*Calpurna*) *immunita* may represent this species.

Text-fig. 22. *Neosimnia* sp. 1–3, NHMW 2017/0124/0257, length 15.4 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 4–6, NHMW 2017/0124/0258, length 15.8 mm; locality TU 1215. 7–9, NHMW 2017/0124/0259, length 11.6 mm; locality TU 1210, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 10–12, NHMW 2017/0124/0242, length 10.1 mm; locality TU 1449, La Barranca, Río Yaque del Norte, Dominican Republic, Gurabo Formation, lower Pliocene.

Comparisons.—*Neosimnia* sp. differs from *N. wisewoodae*, with which it co-occurs in the Dominican assemblages of Gurabo age, in being smaller shelled and having terminals that are less elongated and rounded at the tips. Its dorsum is hardly inflated mid-whorl, and it has a narrower aperture that hardly widens abapically. Additionally, the outer lip is less convex in profile and less flared abapically.

Neosimnia sp. is more slender than the extant Caribbean *Neosimnia* species *Neosimnia bijuri* and *Neosimnia barschi*, with a narrower aperture and shorter terminals. It is most similar to the eastern Pacific species *Neosimnia arcuata* (Reeve, 1865), although the anterior terminal in the *N. arcuata* series illustrated by Lorenz and Fehse (2009: pl. 128) seems to be sharper and the aperture slightly wider abapically. In view of the difficulties and controversies surrounding ovulid systematics, at present it is not helpful to erect yet another species.

Occurrence.—Río Gurabo (localities TU 1210, TU 1215, TU 1419, NMB 15907); La Barranca, Río Yaque del Norte (locality TU 1449); Río Mao (locality TU 1294).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper). Pliocene (indeterminate): Bowden Member of the Layton Formation, Jamaica (Woodring, 1928).

Genus **SIMNIALENA** Cate, 1973

Simnialena Cate, 1973: p. 75. Type species (by original description): *Simnialena marferula* Cate, 1973, Recent, southwestern Texas, USA.

Original description.—“Shells of this genus are of medium size, oblong-ovate, usually thinly formed, with thinly-rolled outer lip edges; they possess a peculiar flatly-inflected, spiraling funicular cord, which distorts the adapical base, causing a suboblique angular ridge above the adapical terminal collar” (Cate, 1973: p. 75).

Revised description.—“Spindle-shaped, thin-shelled, with thinly enrolled labral edges. Funiculum peculiar, spiral, cord-like, forming an angular ridge above the posterior terminal collar. Posterior spatulate” (Lorenz and Fehse, 2009: p. 105).

Geographic distribution.—Caribbean and adjacent Atlantic and eastern Pacific (Lorenz and Fehse, 2009: p. 105).

Stratigraphic distribution.—Miocene to Recent.

Simnialena uniplicata (G. B. Sowerby II, 1849a)

Text-figs. 23.1–23.9

Ovulum acicularis var. G. B. Sowerby I, 1830: p. 10, pl. 6, fig. 6 [not *Cymbovula acicularis* (Lamarck, 1811)].

Ovulum uniplicatum G. B. Sowerby II, 1849a: p. 135.

Ovulum subrostratum G. B. Sowerby II, 1849a: p. 136.

Ovulum uniplicatum G. B. Sowerby II. G. B. Sowerby II, 1849b: pl. 100, figs. 30–32.

Simnia uniplicata (G. B. Sowerby II). Troschel, 1863: p. 219, pl. 18, figs. 8a–c (radula).

Ovulum antillarum Reeve, 1865: pl. 14, figs. 64a, b.

Ovula carolinensis Mörch, 1877: p. 54.

Ovula uniplicata (G. B. Sowerby II). Weinkauff, 1881b: pp. 205, 206, pl. 52, figs. 2, 8.

Ovula subrostrata (G. B. Sowerby II). Weinkauff, 1881b: p. 212, pl. 53, figs. 14, 15.

Ovula antillarum (Reeve). Weinkauff, 1881b: pp. 212, 213, pl. 53, figs. 10, 11.

Text-fig. 23. *Simnialena uniplicata* (G. B. Sowerby II, 1849a). 1–3, NHMW 2017/0124/0243, length 12.3 mm. 4–6, NHMW 2017/0124/0244, length 17.2 mm. 7–9, NHMW 2017/0124/0249, length 17.2 mm. All specimens from locality TU 1358, Río Gurabo, Dominican Republic, Cercado Formation, upper Miocene.

Ovula uniplicata (G. B. Sowerby II). Tryon, 1885: pp. 254, 255, pl. 5, figs. 39–50.

Ovula canadiensis [sic] Tryon, 1885: p. 255 [error pro *canadinensis* Weinkauff, 1882: p. 178].

Ovula carolinensis Mörch. Tryon, 1885: p. 255.

Simnia (*Neosimnia*) *uniplicata* (G. B. Sowerby II). Maury, 1925: p. 112.

Simnia (*Neosimnia*) *uniplicata* (G. B. Sowerby II). Johnson, 1934: p. 111.

Simnia uniplicata (G. B. Sowerby II). F. A. Schilder, 1941: p. 109.

Neosimnia uniplicata (G. B. Sowerby II). Abbott, 1954: p. 182, pl. 7, fig. E.

Neosimnia uniplicata (G. B. Sowerby II). Allan, 1956: p. 129.

Neosimnia uniplicata (G. B. Sowerby II). Olsson and McGinty, 1958: p. 15.

Neosimnia uniplicata (G. B. Sowerby II). Warmke and Abbott, 1961: pp. 92, 93, pl. 16, fig. m.

Neosimnia cf. *uniplicata* (G. B. Sowerby II). Jung, 1969: p. 479, pl. 48, figs. 11, 12.

Neosimnia uniplicata (G. B. Sowerby II). Andrews, 1971: p. 98, unnumbered fig.

Simnia inflexa uniplicata (G. B. Sowerby II). M. Schilder and F. A. Schilder, 1971: pp. 76, 165.

Simnia inflexa antillarum (Reeve). M. Schilder and F. A. Schilder, 1971: pp. 76, 95.

Simnia inflexa carolinensis (Möorch). M. Schilder and F. A. Schilder, 1971: pp. 76, 103.

Simnia inflexa canadinensis (Weinkauff). M. Schilder and F. A. Schilder, 1971: pp. 76, 102.

Simnialena marferula Cate, 1973: p. 75, fig. 165.

Simnialena uniplicata (G. B. Sowerby II). Cate, 1973: pp. 76, 77, fig. 168.

Simnia uniplicata (G. B. Sowerby II). Abbott, 1974: p. 152, fig. 1657.

Simnia uniplicata (G. B. Sowerby II). Rios, 1975: p. 73, pl. 20, fig. 300.

Neosimnia uniplicata (G. B. Sowerby II). Neck, 1977: p. 367.

Simnia uniplicata (G. B. Sowerby II). Lozet and Pétron, 1977: p. 54, fig. 42.

?*Simnia* (*Simnialena*) *oryzagrana* Dolin, 1991: p. 45, figs. 52a–c.

Simnia uniplicata (G. B. Sowerby II). Díaz and Puyana, 1994: p. 168, fig. 624.

Simnia uniplicata (G. B. Sowerby II). Espinosa et al., 1988: p. 21.

Simnia uniplicata (G. B. Sowerby II). Carlos and Joaquín, 1998: p. 126.

Simnialena uniplicata (G. B. Sowerby II). Lorenz and Fehse, 2009: p. 105, pl. 137, figs. 7–12, A223, A224.

Simnialena uniplicata (G. B. Sowerby II). Rios, 2009: p. 136, fig. 322.

Simnialena uniplicata (G. B. Sowerby II). Jensen and Pearce, 2009: p. 66.

Simnialena uniplicata (G. B. Sowerby II). Lee, 2009: p. 78.

Simnialena uniplicata (G. B. Sowerby II). Reijnen et al., 2010: pp. 70–76, figs. 1e, 2f, g, 3, 4d.

Simnialena uniplicata (G. B. Sowerby II). Tunnell et al., 2010: p. 174, unnumbered fig.

Simnialena uniplicata (G. B. Sowerby II). Brunner and Brunner, 2011: p. 8, unnumbered fig.

Simnialena uniplicata (G. B. Sowerby II). Daccarett and Bossio, 2011: p. 66.

Simnialena uniplicata (G. B. Sowerby II). Simone, 2011: pp. 167, 215.

Simnialena uniplicata (G. B. Sowerby II). Petuch and Myers, 2014: pp. 97, 255.

Simnialena uniplicata (G. B. Sowerby II). Lamy and Pointier, 2017: p. 174, pl. 50.

Type material.—*Ovulum uniplicatum*, whereabouts presently unknown, possibly at NHMUK (Cate, 1973: p. 77) [No type recorded on NHMUK website]; *Ovulum subrostratum*, Mr. Cuming's collection; *Ovulum antillarum*, Mus. Cuming; *Ovula carolinensis*, unknown; *Ovula canadinensis*, unknown; *Simnialena marferula*, holotype LACM 1293; *Simnia* (*Simnialena*) *oryzagrana*, holotype USNM 442671.

Type locality.—*Ovum uniplicatum*, near Charleston, South Carolina, USA; *Ovulum subrostratum*, Honduras Bay; *Ovulum antillarum*, West Indies; *Ovula carolinensis*, Charleston, South

Carolina, USA; *Ovula canadensis*, unknown; *Simnialena marferula*, Port Aransas, Texas, USA; *Simnia* (*Simnialena*) *oryzagrana*, TU locality 458, Chipola River, east bank, about 1/3 mile above mouth of Farley Creek (SW 1/4 sec. 20, T1N, R9W), Calhoun Co., Florida, Chipola Formation.

Material.—NHMW 2017/0124/0244-0245 (2 specimens; locality TU 1358); NHMW 2017/0124/0249 (1 specimen; locality TU 1358); NHMW 2017/0124/0250 (14 specimens; locality TU 1358).

Measurements.—Maximum length 17.2 mm, width 5.9 mm, height 4.8 mm.

Original description.—"Ovulum uniplicatum—Ovul. testa elongata, subcylindrica, pellucida, minutissime striata, aurantia, seu violacea, antice subacuminata, postice subrotundata; dorso margine distincto; apertura subaperta; labio externo paululum incrassato, ad extremitates recedente, antice subangulato, ad canalem emarginato; labio interne intus subdepresso, postice spiraliter uniplicato, ad canal tortuo, versus externum deflecto, antice subtortuo acuminato" (G. B. Sowerby II, 1849a: p. 135).

Revised description.—Shell of small to medium size, thin, slender, spindle shaped, with moderately produced terminals. Dorsum hardly inflated, not humped; sculpture of fine incised spiral lines towards extremities weakly developed. Aperture elongated, slender, narrow, widening abapically. Outer lip thickened by narrow labial varix, gently and evenly convex in lateral profile; posterior terminal moderately produced, forming an auriculiform adapical process; outer lip moderately flared abapically; anterior terminal moderately long. Columellar callus hardly developed, reduced to callus wash or at most slight columellar thickening, oblique spiral funiculum truncating apex.

Remarks.—The genus *Simnialena* is characterized by spindle-shaped ovulid shells in which the funiculum truncates the posterior end and the posterior process is produced, forming a small open adapical auricular process to the outer lip.

It is unclear how many species occur in the western Atlantic. Lorenz and Fehse (2009) recognized three species: *Simnialena marferula* Cate, 1973, *S. uniplicata* (G. B. Sowerby II, 1849a), and *S. ilhabelaensis* Fehse, 2001a. *Simnialena marferula* is considered a synonym of *S. uniplicata* herein.

Living specimens are common from 15 to 30m on various *Leptogorgia* and *Lophogorgia* soft coral species (Lorenz and Fehse, 2009), *Gorgonia flabellum* (Linnaeus, 1758), and *Gorgonia ventalina* (Linnaeus, 1758) (Reijnen et al., 2010); all three genera are in the family Gorgoniidae.

Comparisons.—The only distinguishing character given by Lorenz and Fehse (2009: p. 105) between *Simnialena marferula* and *Simnialena uniplicata* is a wider aperture in the former. Their figure of *S. marferula* (Lorenz and Fehse, 2009: pl. 137, fig. 4) is nearly identical to their figure of *S. uniplicata* (Lorenz and Fehse, 2009: fig. 7). In view of the problems surrounding ovulid systematics discussed above, these two species are considered synonyms. *Simnialena ilhabelaensis* from the present-day of Ilhabela Island, Brazil, differs in having a more solid shell; additionally, its entire dorsum is spirally striate. This form seems to be geographically restricted to its type locality.

Dolin (1991: p. 45) described *Simnia* (*Simnialena*) *oryzagrana* based on a single specimen from the lower Miocene Chipola Formation of Florida. Based on Dolin's figures (figs. 52a–c), it fits within the variability of *Simnialena uniplicata*, differing only in its smaller dimensions. Similarly, Jung (1969, pl. 48, figs. 11, 12) illustrated a specimen as *Neosimnia* cf. *uniplicata* from the lower Pleistocene Matura Beds, Talparo Formation of Trinidad; it also differs from *S. uniplicata* only in its smaller dimensions.

One of the smaller specimens from the Pliocene Bowden Member of the Layton Formation of Jamaica illustrated by Woodring (1928: pl. 21, figs. 6, 7) as *Simnia* (*Calpurna*) *immunita* has an odd funiculus and posterior terminal; it might represent a *Simnialena* species, although more material would be required to confirm this. This specimen was renamed *Neosimnia* (*Neosimnia*) *woodringi* by (F. A. Schilder, 1932a: p. 237).

Occurrence.—Río Gurabo (locality TU 1358).

Fossil distribution.—Lower Miocene: Chipola Formation, Florida (Dolin, 1991). Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pleistocene: Matura Beds, Trinidad (Jung, 1969).

Recent distribution.—Bermuda (Jensen and Pearce, 2009), Caribbean Sea and Gulf of Mexico (Lorenz and Fehse, 2009).

Subfamily **PEDICULARIINAE** Gray, 1853

Pediculariinae Gray, 1853: p. 41 (as family Pediculariidae).

Remarks.—The earliest pediculariid, *Cypraedia orglandensis* Schilder, 1941, appeared in the latest Cretaceous (Maastrichtian) of Cotentin, Manche Department, France (F. A. Schilder, 1941: p. 101; Groves, 1994: p. 39).

Tribe **CYPRÆDIINI** F. A. Schilder, 1927

Cypraediini F. A. Schilder, 1927: p. 67 (as subfamily Cypraediinae).

Remarks.—Reassigned to tribe from subfamily level by Bouchet et al. (2017: p. 347).

Genus **JENNERIA** Jousseume, 1884a

Jenneria Jousseume, 1884b: p. 415. Type species (by original description): *Cypraea pustulata* Lightfoot, 1786, Pleistocene to Recent, Golfo de California, México to Ecuador

Original description.—“Coquille semi-ovale, déprimée, presque plane et costulée transversalement en dessous, convexe, arrondie et recouverte de pustules isolées et saillantes à la face supérieure; un sillon dorsal la sépare en deux parties à peu près égales; extrémités peu saillantes, arrondies; ouverture un peu sinueuse, subcentrale, étroite et dilatée en avant; bord denté; sillon columellaire assez étroit, s’élargissant en avant, limité eu dedans et antérieurement par un bourrelet lisse et saillant” (Jousseume, 1884a: pp. 98, 99).

Revised description.—“Small to medium-sized, *Cypraea*-like shells with ovate to elliptical form, rounded dorsum, covered with solid, wart-like pustules on a transversely threaded surface, the base *Trivia*-like, flattened or a little arched and sculptured with strong cross-ribs terminating in teeth along the aperture and in pustules along the outer edge. The dorsal furrow is generally weak. The pustules are generally arranged more or less in line, each line connected by a thread, like pearls on a string, except those in the middle of the dorsum, which may stand free. Immature specimens, even with a rounded lip, have no pustules and the sculpture consists only of fine, transverse threads on the upper surface, and partly developed, stronger cross-ribs on the base. The fossula is a large, smooth, excavated pit bounded within by a sharp ridge” (Olsson, 1967: pp. 4, 5).

Remarks.—The genus *Jenneria* Jousseume comprises a group of beautiful medium to small *Cypraea*-like shells; they are covered with wart-like pustules on the dorsum and have teeth that extend across the venter. The zoological position of this group is not yet settled. They were placed in the Eocypraeidae Schilder, 1924, by Fehse (2001b); in the Ovulidae, subfamily Jenneriinae Thiele, 1929, by Bouchet and Rocroi (2005); and more recently transferred to the Pediculariidae H. Adams and A. Adams, 1855, subfamily Cypraediinae Schilder, 1927, by Lorenz and Fehse (2009). Most recently, Bouchet et al. (2017) re-assigned the group to the family Ovulidae, subfamily Pediculariinae, tribe Cypraediini (= Jenneriinae of Thiele,

1929). Preliminary DNA results support a separation from the Cypraeidae and Ovulidae and possibly a closer relationship to the Triviidae Troschel, 1863 (Simone, 2004). A maximum parsimony tree produced by Schiparelli et al. (2005) using 16S rRNA gene sequences indicated that *Jenneria* is closely related to *Pseudocypraea* and *Pedicularia*.

The genus *Jenneria* in the tropical American Neogene was reviewed by Olsson (1967). His descriptions of the Dominican Republic fossil species are adequate, making a revised description unnecessary. Petuch (1988, 1991) described further species from the Floridian Plio-Pleistocene; most, if not all, are synonyms of previously described Floridian taxa (see Landau and Silva, 2010: p. 41). Gibson-Smith (1974) described a species from the Cantaure Formation of Venezuela; further extensive discussion on the Venezuelan Miocene to Pliocene species is given by Landau and Silva (2010) and Landau et al. (2016).

Jenneria is a paciphile genus. Its Gatunian fossil record starts in the late early to early middle Miocene Caribbean and it disappears at the end of the early Pleistocene. It is therefore part of the small stock of Gatunian Neogene Paciphilic Molluscan Unit 2 (GNPMU2) paciphiles (Landau et al., 2009). In the eastern Pacific fossil record, it first appears later, in the lower Pliocene Esmeraldas beds of the Onozole Formation of Ecuador as *Jenneria panamaensis* (Olsson, 1967) (Groves, 1997) and the upper Pliocene to lower Pleistocene Charco Azul Group of Costa Rica (Olsson, 1967). It is represented today in the Panamic Province by a single species, *Jenneria pustulata* (Lightfoot, 1786) (Keen, 1971; Lorenz and Fehse, 2009).

In the Dominican assemblages the genus is represented by three species. *Jenneria dominicensis* Olsson, 1967, is restricted to the lower to middle Miocene Baitoa Formation; *Jenneria gabbiana* (Guppy, 1876) and *Jenneria pilsbryi* Olsson, 1967, co-occur in beds of lower Pliocene Gurabo age. *Jenneria* has not been collected in the Cercado Formation. Specimens are usually found in coral facies, preserved in mudstone, lodged in holes or gaps between the corals. At all localities they are uncommon.

In his original introduction and description of *Jenneria*, Jousseume (1884a: p. 99; 1884b: p. 415) assigned *Jenneria duclosiana* (Basterot, 1825) of the Miocene of France to *Jenneria*. This assignment was also noted by Dolin and Lozouet (2004), who described *Jenneria nodulosa* from the Aquitanian of southwestern France.

Geographic distribution.—Fossil: Florida and the Dominican Republic to Venezuela, Costa Rica, Panama, and Ecuador; eastern Atlantic, Paratethys, Indo-Pacific. Recent: the entire Panamic Province of the eastern Pacific.

Text-figs. 24.1–24.4. *Jenneria dominicensis* Olsson, 1967. NHMW 2017/0124/0225, length 20.2 mm; locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Baitoa Formation, lower–middle Miocene.

Statigraphic distribution.—Early Miocene (Aquitanian) to Recent.

***Jenneria dominicensis* Olsson, 1967**

Text-figs. 24.1–24.4

Pustularia nucleus (Linnaeus). Gabb (in part), 1872: p. 236 [not *Nucleolaria nucleus* (Linnaeus, 1758)].

Jenneria dominicensis Olsson, 1967: p. 6, pl. 2, figs. 5, 5a–5d.

Cypropterina (Jenneria) dominicensis (Olsson). M. Schilder and F. A. Schilder, 1971: pp. 71, 111.

Jenneria dominicensis Olsson. Landau and Silva, 2010: p. 40.

Jenneria dominicensis Olsson. Landau et al., 2016: p. 68.

Type material.—Holotype ANSP 3004, length 20.2, width 13.0 mm, height 10.3 mm; paratype ANSP 3004a, length 20.2, width 12.8 mm, height 9.8 mm.

Type locality.—Santo Domingo, exact locality unknown. Although the locality is uncertain, it is almost certainly Arroyo Hondo, as Olsson and Dohm collected there (see E. H. Vokes, 1998: p. 12). The type locality here restricted to locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte.

Material.—NHMW 2017/0124/0225, 0226 (2 specimens; locality TU 1363/1364).

Measurements.—Maximum length 20.2 mm, width 12.9 mm, height 10.0 mm.

Original description.—“Shell of medium size, ovate, with nearly equal sides that on the body [sic?] a little shorter and more rounded, the dorsum high and inflated, the two ends

somewhat narrowed and produced. Aperture narrow, the basal surface on both sides rounded and heavily sculptured. The dorsal furrow is distinct and extends the full length of the dorsum and shows as a narrow, indented line which scarcely interrupts the transverse sculpture, their ends touching if not directly continuous. The sculpture consists of numerous solid tubercles or pustules, larger on top, connected by a network of fine, interlaced, transverse threads, details best shown by the figures. The sculpture on the base is produced by strong, primary transverse riblets (about 20) with a smaller and generally shorter secondary thread in each interspace; on the body side, the transverse, basal riblets become slightly enlarged or elongated into teeth along the aperture or extend a short distance within; on the outer lip side, the riblets curve around in sharp, ringlike teeth. Fossula is a narrow, excavated zone, smooth or marked in spots with fine, thread-like spirals” (Olsson, 1967: p. 6).

Remarks.—*Jenneria dominicensis* is characterized by its elongated terminals; large, coarse tubercles that are rather pointed; delicate, interlacing dorsal ribs that cover the entire surface; and coarse ribs and teeth on the venter. This species is also relatively constant in size; both specimens illustrated by Olsson (1967: pl. 2, figs. 5, 5a–d) and the two specimens at hand are 20.2 mm in length and have almost the same width/height proportions. The sculpture is also constant.

Gabb listed *Pustularia nucleus* from the DR, which is this species in part. The types for *Jenneria dominicensis* were selected by Olsson (1967, p. 7) and are the two larger specimens of the lot of four specimens called *P. nucleus* by Gabb. Their exact locality in the DR is not known, but *J. dominicensis* has only been found at Arroyo Hondo (= locality TU 1363/1364) on the Río Yaque del Norte in beds of the Baitoa Formation,

lower to middle Miocene. This species is extremely rare, with only two specimens found in over ten collecting trips to the Dominican Republic.

Comparisons.—In the Dominican assemblages *Jenneria pilsbryi* Olsson, 1967, is most similar to *Jenneria dominicensis*. It differs in having smaller tubercles; furthermore, the dorsal riblets do not extend onto the apex of the dorsum, and the ventral ribs and apertural teeth are finer. *Jenneria venezuelana* Gibson-Smith, 1974, from the lower to middle Miocene Cantaure Formation, has shorter terminals and smaller tubercles; also, the dorsal riblets are less interlacing and do not extend along the entire dorsum.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364).

Distribution.—Miocene (indeterminate): Dominican Republic (Olsson, 1967; Richards, 1968).] Lower-middle Miocene: Baitoa Formation, Dominican Republic (this paper).

***Jenneria gabbiana* (Guppy, 1876)**

Text-figs. 25.1–25.19

- Cypraea pustulata* Lamarck. Guppy, 1867: p. 160 [not *Jenneria pustulata* (Lightfoot, 1786)].
Pustularia nucleus (Linnaeus). Gabb (in part), 1872: p. 236 [not *Nucleolaria nucleus* (Linnaeus, 1758)].
Cypraea pustulata Lamarck. Guppy, 1874: p. 440 [not *Jenneria pustulata* (Lightfoot, 1786)].
Cypraea gabbiana Guppy, 1876: pp. 528, 529, pl. 29, fig. 10.
Cypraea gabbiana Guppy. Dall, 1890: p. 165.
Cypraea (Pustularia) gabbiana Guppy. Maury, 1917a: p. 116, pl. 19, fig. 12.
Cypraea (Pustularia) gabbiana Guppy. Maury, 1917b: p. 21.
Cypraea (Erosaria) gabbiana Guppy. Vredenburg, 1920: p. 113.
Pustularia gabbiana (Guppy). Vaughan and Woodring, 1921: p. 141.
Pustularia gabbiana (Guppy). Pilsbry, 1922: p. 366.
Cypraea (Pustularia) gabbiana Guppy. Anderson, 1929: p. 97, 139, 140, pl. 15, figs. 4, 5.
Cypropterina (Jenneria) pustulata gabbiana (Guppy). F. A. Schilder, 1932a: p. 207.
Cypraea (Pustularia) gabbiana Guppy. Smith, 1936: p. 137.
Nuclearia gabbiana (Guppy). Ingram, 1939b: pp. 337, 338, pl. 22, fig. 1.
Jenneria gabbiana (Guppy). Olsson, 1967: p. 5, pl. 1, figs. 4, 4a, 4b.
Cypropterina (Jenneria) gabbiana (Guppy). M. Schilder and F. A. Schilder, 1971: pp. 71, 117.
Cypraea (Pustularia) gabbiana Guppy. Fast, 1978: p. 83.
Jenneria (Jenneria) gabbiana (Guppy). Dolin, 1996: p. 24, figs. 8a, b.
Jenneria gabbiana (Guppy). Landau and Silva, 2010: p. 40.
Jenneria gabbiana (Guppy). Groves and Squires, 2018: p. 124.

Type material.—Holotype NHMUK GG 20289 (*ex* Heneken collection).

Type locality.—Río Yaque area, Dominican Republic, Miocene. The type locality here restricted to locality TU 1215, Río Gurabo.

Previously figured material.—Hypotype (Maury, 1917a, pl. 19, fig. 12) PRI 28782, Fast (1978: p. 83) provided previously unpublished type number; hypotype (Anderson, 1929, pl. 15, figs. 4, 5), CAS 4653 [= CASG 351.02].

Material.—NHMW 2017/0124/0227, 0228 (2 specimens; locality TU 1219); NHMW 2017/0124/0229–0232 (4 specimens; locality TU 1215); NHMW 2017/0124/0233 (22 specimens; locality TU 1215); NHMW 2017/0124/0234 (20 specimens; locality TU 1293); PRI 84773 (1 specimen; locality TU 1453A); PRI 84768 (1 specimen; locality TU 1215); PRI 84868 (3 specimens; locality TU 1227A); PRI 84858 (3 specimens; locality TU 1422); PRI 84855 (2 specimens; locality TU 1230); PRI 84854 (1 specimen; locality TU 1354).

Measurements.—Maximum length 22.6 mm, width 13.8 mm, height 11.7 mm.

Original description.—“Oval-elongate, rostrated at both ends, superiorly covered with large shining tubercles, which are almost circular upon the back, but become elongate and have a tendency to run into ribs near the thickened and regularly grooved lip, whose dentations are continuous with the ribs on the outside. A dorsal groove separates the back into two nearly equal halves” (Guppy, 1876: p. 529).

Remarks.—*Jenneria gabbiana* is characterized by having the smallest and most numerous tubercles compared to its Dominican congeners; it also has the most numerous relatively straight dorsal riblets that extend across the entire dorsum. The shell shape is typically relatively elongated (Text-figs. 25.1–25.8), although, as seen in the series illustrated, more rounded forms occur (Text-figs. 25.9–25.12). The ribs on the venter are narrow and relatively closely spaced, forming drop-like teeth at the columellar angulation. This is the most abundant *Jenneria* in the Dominican assemblages, but it has not been found at the type locality of Río Yaque del Norte.

Comparison.—*Jenneria gabbiana* coexists in the Gurabo deposits with *Jenneria pilsbryi*; *J. pilsbryi* differs in being smaller and more rounded with fewer dorsal riblets that do not extend onto the apex.

Text-fig. 25. *Jenneria gabbiana* (Guppy, 1876). 1–4, NHMW 2017/0124/0227, length 23.0 mm, locality TU 1219, Río Amina, Dominican Republic, Gurabo Formation, lower Pliocene. 5–8, NHMW 2017/0124/0228, length 23.4 mm; locality TU 1219. 9–12, NHMW 2017/0124/0229, length 18.7 mm, locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 13–16, NHMW 2017/0124/0230, length 17.4 mm, locality TU 1215. 17, 18, NHMW 2017/0124/0231, length 16.9 mm, locality TU 1215. 19, NHMW 2017/0124/0232, length 13.9 mm, locality TU 1215.

Occurrence.—Río Amina (locality TU 1219); Río Gurabo (locality TU 1215); Río Mao (locality TU 1293); Arroyo Zalaya (localities TU 1227, TU 1453A); Arroyo Bellaco (locality TU 1422); Río Cana (locality TU 1230); Cañada de Zamba (locality TU 1354).

Distribution.—Miocene (indeterminate): Haiti (Gabb, 1872; Guppy, 1876; Pilsbry, 1922; Ingram, 1939b, 1947a, 1947c), Dominican Republic (Guppy, 1867; F. A. Schilder, 1932a). Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; Ingram, 1939b, 1947c; Olsson, 1967; Fast, 1978); Tubará Formation, Colombia (F. A. Schilder, 1932a).

***Jenneria pilsbryi* Olsson, 1967**

Text-figs. 26.1–26.8

Jenneria pilsbryi Olsson, 1967: p. 7, pl. 1, figs. 5, 5a, 5b.

Jenneria pilsbryi Olsson. Richards, 1968: p. 174.

Cypropterina (Jenneria) dominicensis pilsbryi (Olsson). M. Schilder and F. A. Schilder, 1971: pp. 71, 144.

Jenneria pilsbryi Olsson. Landau and Silva, 2010: p. 40.

Type material.—Holotype ANSP 31245, length 15.3, width 10.0 mm, height 7.6 mm.

Type locality.—Santo Domingo, exact locality unknown. The type locality here restricted to locality TU 1215, Río Gurabo.

Text-fig. 26. *Jenneria pilsbryi* Olsson, 1967. 1–4, NHMW 2017/0124/0235, length 19.2 mm; locality NMB 15889, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene. 5–8, NHMW 2017/0124/0236, length 17.3 mm; locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Material.—NHMW 2017/0124/0235 (1 specimen; locality NMB 15889); NHMW 2017/0124/0236 (1 specimen; locality TU 1422); NHMW 2017/0124/0237 (1 specimen; locality TU 1215); NHMW 2017/0124/0238 (2 specimens; locality TU 1215); PRI 84859 (1 specimen; locality TU 1422); PRI 84856 (1 specimen; locality TU 1215).

Measurements.—Maximum length 19.2 mm, width 12.8 mm, height 9.9 mm.

Original description.—“Shell small, the dorsal surface evenly rounded, sprinkled over rather thickly with tubercles, large on top and with some small ones on secondary threads, all connected by transverse or radial threads which are joined below with the strong transverse riblets on the base; for the most part, the connecting radials are simple, thread-like, only a few interlaced together. The dorsal furrow is fairly sharp and extends nearly the whole length of the dorsum, dislocating the transverse sculpture, its surface showing the primary sculpture of the shell itself. The sides at the base are rounded, except for a slight angulation produced by a line of large, peaked tubercles. The base is flattened, ornamented by large and small cross riblets, the primary ones sometimes keeled in the middle, the secondary ones often with small tubercles on the sides, their number shown in the figures. The aperture is relatively narrow, wider in the section above the fossula” (Olsson, 1967: p. 7).

Remarks.—*Jenneria pilsbryi* is characterized by its small size, rounded shell shape, small and numerous dorsal pustules, and relatively straight dorsal riblets that do not extend onto the

apex. This is the smallest *Jenneria* species in the Dominican assemblages and is found together with *Jenneria gabbiana*, but is even less plentiful. Judging from the few specimens available, there is little variation in shape and sculpture.

Comparisons.—In shape *Jenneria pilsbryi* is most like the stratigraphically older *Jenneria dominicensis*, but has smaller tubercles and finer ribs on the venter. For further comparisons, see above.

Occurrence.—Río Gurabo (localities TU 1215, NMB 15889); Arroyo Bellaco (locality TU 1422).

Distribution.—Miocene (indeterminate): Dominican Republic (Olsson, 1967; Richards, 1968). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Family TRIVIIDAE Troschel, 1863

Triviidae Troschel, 1863: p. 214 (as superfamily Triviacea).

Description.—Shell usually globose, prominently ribbed with a narrow, toothed aperture. Spire involute, notched anterior and posterior canals, axial dorsal sulcus in some genera. Living species possess taenioglossate radula.

Remarks.—The family Triviidae first appeared in the early Eocene (Ypresian) London Clay of Whetstone, England, with the occurrence of *Prototrivia wetherellii* (Edwards, 1854) (F. A. Schilder, 1933c; Fehse, 2002). By the late Eocene the family was widespread in Europe, New Zealand, and Australia

(M. Schilder and F. A. Schilder, 1971). Numerous Oligocene through Pliocene species are documented from western and southern Europe (Fehse and Landau, 2003; Fehse and Grego, 2012). M. Schilder and F. A. Schilder (1971) reported Miocene species from New Zealand, Australia, Japan, the Caribbean, Indonesia, the eastern United States, and Florida. Landau and Fehse (2004) documented Pliocene faunas from southern Spain, and Ladd (1977) described a new species from Pliocene of Fiji.

F. A. Schilder (1936) utilized the radula and osphradia in addition to shell morphology to develop his later classifications of the triviids. This classification was largely utilized by M. Schilder and F. A. Schilder (1971) as well. Cate (1979) produced the most complete monograph on living triviids and adopted the classification scheme of M. Schilder and F. A. Schilder (1971). Dolin (1991) included the family in his fossil documentation of the lower Miocene Chipola Formation of Florida. Most recently, Fehse and Landau (2001a, 2001b, 2003) and Landau and Fehse (2004) included triviids in their publications on western European species, and Landau et al. (2016) noted the presence of Triviidae in the Miocene Cantaure Formation of Venezuela. Higher-level systematics above superfamily follow that of Bouchet et al. (2017); M. Schilder and F. A. Schilder (1971) and Fehse (2002) are followed for lower-level systematics. These are the coffee-bean cowries.

Genus *DOLICHUPIS* Iredale, 1930

Dolichupis Iredale, 1930: p. 83. Type species (by original designation): *Cypraea producta* Gaskoin, 1836: Recent, southwest Pacific and the Philippines.

Trivellona Iredale, 1931: Type species (by original designation): *Trivella excelsa* Iredale, 1931: p. 221. Recent, New South Wales, Australia.

Decoriatrivia Cate, 1979: p. 95. Type species (by original designation): *Cypraea paucilirata* G. B. Sowerby II, 1870, Recent, Panama to Ecuador.

Circumscapula Cate, 1979: p. 109. Type species (by original designation): *Trivia* (*Pusula*) *myrae* Campbell, 1961, Recent, Golfo de California, México.

Original description.—"The small globular "Trivias", of which there is more than one species confused, ... the forms with produced extremities, following Schilder, are separated, and the new genus name *Dolichupis* proposed, *producta* Gaskoin being selected as type" (Iredale, 1930: p. 83).

Revised description.—"Shell evenly ovate, mostly with deep, acutely defined dorsal sulcus. Terminal beaks protrude, somewhat square. Surface ribbing numerous, continuous from outer apertural lip edge to inner columellar-fossular adaxial ridge" (Cate, 1979: p. 117).

Remarks.—Iredale (1930: p. 83) proposed *Dolichupis* as a full genus. F. A. Schilder (1939b: pp. 173, 174), Keen (1971: p. 486), M. Schilder and F. A. Schilder (1971: p. 21), Abbott (1974: p. 149), and Cate (1979: p. 107) all treat *Dolichupis* as a subgenus of *Pusula*, whereas Allan (1956: p. 156), Dolin (1991: p. 53), Fehse (2002: pp. 13, 14), and Fehse and Grego (2010: p. 4) retain *Dolichupis* as a full genus. According to Dolin (1991: p. 52), species of the genus *Dolichupis* differ from *Trivia* Broderip, 1837 (type species: *Cypraea europaea* Montagu, 1808) in having a non-projecting spire. *Trivia islahispaniolae* Maury, 1917a belongs within *Dolichupis*.

Geographic range.—Monterey Bay, Monterey County, central California, and the entire Pacific Panamic Province to the southwest Pacific, the Philippines, and Sri Lanka; southern Florida and the Gulf of Mexico to Panama, the Lesser Antilles, and Brazil.

Stratigraphic range.—Middle Oligocene (Rupelian) to Recent.

Dolichupis islahispaniolae (Maury, 1917a)

Text-figs. 27.1, 27.2, 27.5, 27.6; 28.1–28.10; 29.1–29.18

Trivia globosa (Gray in G. B. Sowerby I, 1832). Dall, 1889: p. 241 [not *Trivia globosa* (Gray in G. B. Sowerby I, 1832)].

Trivia globosa Gray in G. B. Sowerby I. Dall, 1890: p. 168 [not *Trivia globosa* (Gray in G. B. Sowerby I, 1832)].

Trivia globosa Gray in G. B. Sowerby I. Dall, 1903: p. 1854 [not *Trivia globosa* (Gray in G. B. Sowerby I, 1832)].

Trivia globosa Gray in G. B. Sowerby I. Maury, 1917a: p. 117, pl. 40, fig. 13 [not *Trivia globosa* (Gray in G. B. Sowerby I, 1832)].

Trivia islahispaniolae Maury, 1917a: p. 117, pl. 40, fig. 13.

Trivia islahispaniolae Maury. Maury, 1917b: p. 13.

Trivia islahispaniolae Maury. Vaughan and Woodring, 1921: p. 120.

Trivia globosa Gray in G. B. Sowerby I. Woodring, 1928: p. 319, pl. 22, figs. 4, 5 [not *Trivia globosa* (Gray in G. B. Sowerby I, 1832)].

Trivia islahispaniolae Maury. F. A. Schilder, 1932a: p. 108.

Trivia islahispaniolae Maury. Jung, 1971: pp. 180, 181, pl. 7, figs. 8–11.

Trivia (*Trivia*) *islahispaniolae islahispaniolae* Maury. M. Schilder and F. A. Schilder, 1971: pp. 17, 124.

Trivia islahispaniolae Maury. Fast, 1978: p. 233.

Dolichupis islahispaniolae (Maury). Dolin, 1991: pp. 52, 54.

Trivia islahispaniolae Maury. Fehse, 2002: p. 24.

Type material.—Holotype PRI 28784, length 7.6 mm, width 6.2 mm.

Type locality.—Bluff 3, Cercado de Mao, Dominican Republic (= locality TU 1294), Cercado Formation, upper Miocene.

Text-fig. 27. Triviid species in Maury (1917a). 1, 2, *Trivia islahispaniolae* Maury, 1917a, holotype, PRI 28784, length 7.6 mm; Bluff 3 (= locality TU 1294), Cercado de Mao, Dominican Republic, Cercado Formation, upper Miocene. 3, 4, *Trivia suffusa* var. *Sancti-Dominici* Maury, 1917a, holotype, PRI 28785, length 7.8 mm; Bluff 3 (= locality TU 1294), Cercado de Mao, Dominican Republic, Cercado Formation, upper Miocene. 5, 6, *Trivia globosa* Gray in G. B. Sowerby II, 1832, hypotype (of Maury, 1917a), PRI 28783, length 5.5 mm; Río Cana at Caimito, Cercado Formation, upper Miocene; probably a worn specimen of *Dolichupis islahispaniolae* (Maury, 1917a). Photos courtesy of PRI.

Text-fig. 28. *Dolichupis islahispaniolae* (Maury, 1917a). 1, 2, NHMW 2017/0124/0215, length 6.5 mm. 3, 4, NHMW 2017/0124/0216, length 6.6 mm. 5, 6, NHMW 2017/0124/0217, length 6.2 mm. 7, 8, NHMW 2017/0124/0218, length 5.1 mm. Figs. 9, 10. NHMW 2017/0124/0219, length 6.4 mm. All specimens from locality TU 1215, Río Gurabo, Dominican Republic, Gurabo Formation, lower Pliocene.

Material.—NHMW 2017/0124/0191–0197 (7 specimens; locality NMB 16844); NHMW 2017/0124/0198 (13 specimens; locality NMB 16844); NHMW 2017/0124/0215–0219 (5 specimens; locality TU 1215); NHMW 2017/0124/0220 (1 specimen; locality TU 1215); NHMW 2017/0124/0214 (1 specimen; locality TU 1219); NHMW 2017/0124/0221 (1 specimen; locality TU 1354); PRI 84865 (2 specimens; locality TU 1448).

Measurements.—Maximum length 7.4 mm, width 5.8 mm, height 4.8 mm.

Original description.—“Shell sub-pisiform, very ventricose, slightly produced and notched anteriorly and with the lips, especially the outer, flaring a trifle posteriorly, sharply sculptured with well-defined ribs of which there are about twenty-three on the outer and twenty on the inner lip; dorsal surface evenly convex with only the faintest suggestion of a sulcus over which the ribs continue without any interruption, aperture narrow” (Maury, 1917a: p. 117).

Revised description.—Shell small, solid, globose, ovate. Dorsum high, indistinctly humped in the posterior half; poorly defined sulcus present that interrupts, narrows, or

Text-fig. 29. *Dolichupis islahispaniolae* (Maury, 1917a). 1–4, NHMW 2017/0124/0191, length 5.7 mm. 5–8, NHMW 2017/0124/0192, length 6.7 mm. 9, 10, NHMW 2017/0124/0193, length 5.8 mm. 11, 12, NHMW 2017/0124/0194, length 5.9 mm. 13, 14, NHMW 2017/0124/0195, length 5.1 mm. 15, 16, NHMW 2017/0124/0196, length 6.1 mm. 17, 18, NHMW 2017/0124/0197, length 4.3 mm. All specimens from locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

distorts most ribs; ribs strong, variable in number, continuing uninterrupted onto venter. Margins callused, especially labial side. Venter rounded, ribs slightly swollen at columellar angulation forming small denticles; 14–18 columellar teeth, 18–24 labial teeth. Aperture narrow, linear, slightly curved, not widening anteriorly. Outer lip wide, rounded, obscuring inside of shell on apertural view. Fossula concave, poorly delimited, strongly ribbed; ribs forming teeth at inner edge. Terminals marginate, thickened, moderately short; anterior

terminal slightly reflected dorsally; posterior terminal curved adaxially.

Remarks.—Two series are illustrated separating the upper Miocene Cercado Formation specimens (Text-figs. 29.1–29.18) from those of the younger lower Pliocene Gurabo Formation (Text-figs. 28.1–28.10). Although the Cercado specimens are slightly more humped dorsally than the Gurabo specimens—which are more rounded—they are considered to

represent a single species. The dorsal sculpture and number of ribs is highly variable. The dorsal sulcus can be relatively neatly incised (Text-fig. 29.10) to hardly developed (Text-fig. 28.10); the sulcus may interrupt all of the ribs (Text-fig. 29.10), distorting them (Text-figs. 29.4, 29.12) or hardly affecting them (Text-fig. 29.8). This species is uncommon in the Dominican assemblages, except for in a coquina layer at locality NMB 16844 on the Río Cana.

Comparisons.—*Dolichupis clypeus* Dolin, 1991, recorded from the lower Miocene Chipola Formation of Florida and the lower to middle Miocene Cantaure Formation of Venezuela (Landau et al., 2016), is the earliest known Caribbean member of the genus. It differs from *Dolichupis islahispaniolae* in being less inflated, with the dorsum not humped and the terminals not recurved dorsally. The number of labial and columellar teeth overlap in the two species. The living Caribbean *Dolichupis leei* Fehse and Grego, 2010, differs from *D. islahispaniolae* in having fewer, coarser, and more widely spaced ribs; the dorsum does not bear a sulcus and the margins are more strongly callused. *Dolichupis virgo* Fehse and Grego, 2005, from the coasts of Espírito Santo State, Brazil, is more inflated with more strongly callused margins than *D. islahispaniolae*.

Trivia islahispaniolae petrela Olsson and Harbison, 1953, from the Pliocene of Florida was said to differ from *Dolichupis islahispaniolae* “.... in details of sculpture, the weaker development of the external rim of the outer lip, and in shape” (Olsson and Harbison, 1953: p. 264). Although Dolin (1991: p. 54) stated that the two taxa differed only in size, with the Floridian shells larger, the differences given by Olsson and Harbison and the absence of any dorsal sulcus indicate that the two should be separated at full species level.

Occurrence.—Río Gurabo (localities TU 1215, TU 1219); Río Cana (locality NMB 16844); Cañada de Zamba (locality TU 1354); Río Mao (locality TU 1294); Río Yaque del Norte (locality TU 1448).

Distribution.—Miocene (indeterminate): Dominican Republic (F. A. Schilder, 1932a). Middle Miocene: Belmont Formation and Grand Bay Formation, Carriacou, Grenada (Jung, 1971). Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; Fast, 1978). Pliocene: Bowden Member of the Layton Formation, Jamaica (Woodring, 1928). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Genus *NIVERIA* Jousseume, 1884a

Niveria Jousseume, 1884a: p. 100. Type species (by original designation): *Cypraea nivea* Gray, 1824, Recent, Caribbean Sea.

Sulcotrivia F. A. Schilder, 1933b: p. 18. Type species (by original designation): *Cypraea dimidiata* Bronn, 1831, Pliocene, Italy.

Circumscapula Cate, 1979: p. 109. Type species (by original designation): *Trivia myrae* Campbell, 1961, Recent, Golfo de California, México.

Original description.—“Coquille globuleuse cerclée de stries irrégulières, très peu déprimée en dessous; ouverture subcentrale, courbée, étroite; bord columellaire large et déprimé par unsillon longitudinal concave, plissé près du canal, où il forme comme dans la *C. Childreni*, une petite lamelle assez saillante” (Jousseume, 1884a: p. 100).

Revised description.—“Shell solid, globose, ventral area more or less callused; point of spire weakly projecting, spiral ribs extending onto lateral margins; interrupted by deep straight dorsal sulcus, amplifying development of pustules at dorsal extremities of ridges; siphonal canal short and may be truncated in some species; fossula deep, very concave and strongly ridged; columellar area reduced; angulation of inner lip slightly depressed; aperture wide; adapical ridge recurved; exhalant channel deep, not delimited abaxially, outer lip outlines apex in an arc” (Dolin, 1991: p. 56).

Geographic distribution.—Fossil: Italy, France, England, Hungary, Belgium, Canary Islands, North Carolina and Florida. Recent: Mediterranean Sea south to Angola, Caribbean Sea and Florida, and the entire Pacific Panamic Province.

Stratigraphic distribution.—Early Miocene (Aquitanian) to Recent.

Niveria jamaicensis F. A. Schilder, 1932a

Text-figs. 30.1–30.4

Trivia suffusa (Gray). Dall, 1890: p. 168 [not *Niveria suffusa* (J. E. Gray, 1827)].

Trivia (Trivia) pediculus (Linnaeus). Woodring, 1928: pp. 320, 321 [in part], pl. 22, figs. ?6, 7, 8, 9, not 10, 11 = *Pusula* cf. *costipunctata* (G. B. Sowerby II, 1870) [not *Pusula pediculus* (Linnaeus, 1758)].

Pusula (Niveria) suffusa jamaicensis F. A. Schilder, 1932a: p. 95.

Pusula (Niveria) suffusa jamaicensis F. A. Schilder. F. A. Schilder, 1939a: pp. 6, 8.

Niveria (Niveria) suffusa jamaicensis (Schilder). M. Schilder and F. A. Schilder, 1971: pp. 20, 124.

Trivia cf. *suffusa* (Gray). Jung, 1971: p. 180, pl. 7, figs 6, 7.

Niveria jamaicensis (Schilder). Fehse, 2002: p. 25

Niveria jamaicensis (Schilder). Fehse and Grego, 2014: p. 10.

Text-figs. 30.1–30.4. *Niveria jamaicensis* (Schilder, 1932a). NHMW 2017/0124/0212, length 16.7 mm; locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

Type material.—Holotype USNM 369471, length 11.8 mm, width 8.2 mm, height 6.5 mm (specimen figured Woodring, 1928, pl. 22, figs. 8, 9).

Type locality.—Bowden, Jamaica, Bowden Member of the Layton Formation, Pliocene.

Material.—NHMW 2017/0124/0212 (1 specimen; locality NMB 16844); PRI 84867 (2 specimens; locality TU 1210); PRI 84871 (2 specimens; locality TU 1250); PRI 84863 (1 specimen; locality TU 1352); PRI 84857 (1 specimen; locality TU 1422).

Measurements.—Maximum length 16.7 mm, width 12.0 mm, height 9.5 mm.

Original description.—“Shell medium-sized, moderately inflated, dorsal groove long, relatively deep. Aperture narrow, distinctly widened toward base. Threads strongly granular on dorsal surface, varying in number and width.” (Woodring, 1928: p. 320, based on material representing several species). No augmented description was offered by F. A. Schilder (1932a), only a new name for a specimen figured by Woodring (1928: pl. 22, figs. 8, 9).

Remarks.—Woodring (1928: pl. 22, figs. 6–11) illustrated three specimens under the name *Trivia* (*Trivia*) *pediculus* from the Pliocene Bowden Member of the Layton Formation of Jamaica. F. A. Schilder (1932a) noted the group was not conspecific and erected the name *Pusula* (*Niveria*) *suffusa jamaicensis* for one specimen (F. A. Schilder 1932a: pl. 22, figs. 8, 9). This specimen differs from *Pusula pediculus* (Linnaeus, 1758) in having more regular and crowded ribs; its dorsal sulcus is shallower and narrower with some of the ribs distorted but not completely interrupted, as in *P. pediculus*. Two important character traits separate the genera *Niveria* and *Pusula* Jousseaume, 1884a: *Pusula* tends to have fewer, more interrupted or irregular ribs and a wider, smooth dorsal sulcus.

Niveria sanctidominici, which is found at the same locality (NMB 16844) on the Río Cana, Dominican Republic, is immediately separated from *Niveria jamaicensis* by its smaller size and more widely spaced ribs; its shallower dorsal sulcus distorts rather than bisects a greater number of the ribs, and the ribs that are bisected do not form small tubercles at the edge of the sulcus.

Occurrence.—Río Cana (locality NMB 16844); Arroyo Zalaya (locality TU 1227); Río Verde (locality TU 1250); Río Gurabo (locality TU 1352); Arroyo Bellaco (locality TU 1422).

Distribution.—Miocene (indeterminate): ‘Upper Tuff Series,’ Carriacou Island, Grenada (F. A. Schilder, 1939a). Middle Miocene: Grand Bay Formation, Carriacou, Grenada (Jung, 1971). Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper). Pliocene (indeterminate): Bowden Member of the Layton Formation, Jamaica (F. A. Schilder, 1932a, 1939a). Lower Pleistocene: Caloosahatchie [*sic*] Formation [= Caloosahatchee Formation], Florida (F. A. Schilder, 1932a).

Niveria sanctidominici (Maury, 1917a)

Text-figs. 27.3, 27.4; 31.1–31.16

Trivia suffusa variety *sanctidominici* Maury, 1917a: p. 117, pl. 19, fig. 14.

Trivia suffusa variety *sanctidominici* Maury. Maury, 1917b: p. 13.

Trivia suffusa Gray subsp. *sanctidominici* (Maury). Vaughan and Woodring, 1921: pp. 125, 141.

Pusula (*Niveria*) *sanctidominici* (Maury). F. A. Schilder, 1932a: p. 94.

Niveria (*Niveria*) *quadripunctata sanctidominici* (Maury). M. Schilder and F. A. Schilder, 1971: pp. 20, 153.

Trivia suffusa variety *sanctidominici* Maury. Fast, 1978: p. 233.

Text-fig. 31. *Niveria sanctidominici* (Maury, 1917a). 1–4, NHMW 2017/0124/0199, length 9.0 mm. 5–8, NHMW 2017/0124/0200, length 8.0 mm. 9, 10, NHMW 2017/0124/0201, length 9.6 mm. 11, 12, NHMW 2017/0124/0202, length 8.1 mm. 13, 14, NHMW 2017/0124/0203, length 8.3 mm. 15, 16, NHMW 2017/0124/0204, length 9.7 mm. All specimens from locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

Type material.—Holotype PRI 28785, length 7.8 mm, width 5.5 mm.

Type locality.—Bluff 3, Cercado de Mao, Dominican Republic (= locality TU 1294), Cercado Formation, upper Miocene.

Material.—NHMW 2017/0124/0199–0204 (6 specimens; locality NMB 16844); NHMW 2017/0124/0205 (13 specimens; locality NMB 16844); NHMW 2017/0124/0213 (6 specimens; locality TU 1213); NHMW 2017/0124/0222 (1 specimen; locality TU 1354); PRI 84874 (4 specimens; locality TU 1227A).

Measurements.—Maximum length 10.5 mm, width 7.4 mm, height 6.2 mm.

Original description.—“Shell resembling *T. suffusa* but more convex, slightly produced and truncate anteriorly; outer lip somewhat elevated above the last whorl and sub-angulate posteriorly; ribs fine, 35 on the outer margin of the outer lip and 25 on the inner lip; dorsal furrow very straight and sharp on one shell, less sharply defined on the other; aperture narrow widening very slightly anteriorly.” (Maury, 1917a: p. 117).

Remarks.—Maury (1917a: p. 117) noted that “the fossils differ from *T. suffusa*, now living in the Antilles and fossil at Bowden, in their more convex form and narrower and straighter aperture.” *Niveria sanctidominici* differs from *Niveria jamaicensis* (Schilder, 1932a), with which it co-occurs on the Río Cana, in being smaller and less elongated; it also has fewer ribs that are not swollen when interrupted at the dorsal sulcus. *Niveria* sp. from the Gurabo Formation (see below) differs in being more globose with finer ribs and less produced terminals.

Occurrence.—Río Gurabo (locality TU 1213); Río Cana (locality NMB 16844); Río Mao (locality TU 1294); Cañada de Zamba (locality TU 1354); Arroyo Zalaya (locality TU 1227).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; F. A. Schilder, 1932a; Fast, 1978). Lower Pliocene: Gurabo Formation, Dominican Republic (Vaughan and Woodring, 1921; this paper).

***Niveria* sp.**
Text-figs. 32.1–32.8

Material.—NHMW 2017/0124/0224 (1 specimen; locality TU 1215); PRI 84767 (1 specimen; locality TU 1219).

Measurements.—Maximum length 8.2 mm, width 6.3 mm, height 5.5 mm.

Description.—Shell medium sized for genus, strongly globose, oval. Spire covered by callus. Last whorl globose. Terminals weakly produced. Dorsum rounded, completely covered by about 20 narrow, regular ribs that are one-third the width of their interspaces. Dorsal sulcus marked by narrow, shallow, slightly sinuous depression distorting rather than bisecting most ribs, especially mid-dorsum, where ribs are distorted and/or narrowed. Where ribs bisected, they are minimally

thickened adjacent to sulcus. Base convex, with short terminals recurved. Aperture of moderate width, strongly curved adapically, slightly wider anteriorly. Outer lip broadened by labial varix, convex, widest in mid-portion, narrowing towards terminals, bearing 24 sharp denticles. Siphonal and anal canals hardly protruding. Fossula slightly concave, poorly delimited from rest of columella. Columella convex, tapering steeply inwards, bordered internally by a weak carinal ridge. Carinal ridge expanded in fossular region. Columellar edge incomplete, making tooth count impossible.

Remarks.—Unfortunately, this taxon is represented by two specimens: one from the lower Pliocene locality of TU 1215 on Río Gurabo, which has the columella and anterior terminal damaged; and one from locality 1219 on Río Amina, which is complete. There is some difference in shell profile between the two specimens; the one from Río Gurabo (Text-figs. 32.1–32.4) is more inflated than that from Río Amina (Text-figs. 32.5–32.8). However, the sculpture of the specimens is similar in rib thickness and density and the width of the dorsal sulcus.

The specimens differ from *Niveria jamaicensis* in being more globose and in having the terminals less produced; furthermore, the posterior portion of the aperture is far more curved to the left and the dorsal sulcus is shallower and weaker. The same differences separate the specimens from *Niveria sanctidominici*, which also has fewer ribs. Additional material is required to formally describe this species.

Occurrence.—Río Gurabo (locality TU 1215); Río Amina (locality TU 1219).

Distribution.—Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Genus ***PUSULA*** Jousseaume, 1884a

Pusula Jousseaume, 1884a: p. 99. Type species (by original designation): *Cypraea radians* Lamarck, 1810, Recent, Caribbean Sea.

Pustula Roberts in Tryon, 1885: p. 161 [error for *Pusula*].

Vusula Cossmann, 1896: p. 49 [error for *Pusula*].

Original description.—“Coquille semi-ovale, déprimée en dessous, convexe en dessus, arrondie aux extrémités et à bord saillant; face dorsale divisée par un sillon longitudinal profond; côtes circulaires assez fortes, devenant granuleuses ou tuberculeuses près du sillon dorsal; ouverture subcentrale un peu courbe, évasée; bord columellaire à sillon longitudinal à peine marqué” (Jousseaume, 1884a: p. 99).

Revised description.—“Shell size between 4 and almost 25 mm, circular or oval, usually callused. Ribs fully developed,

Text-fig. 32. *Niveria* sp. 1–4, NHMW 2017/0124/0224, length 8.2 mm; locality TU 1215, Río Gurabo. 5–8, PRI 84767, length 12.0 mm; locality TU 1219, Río Amina, Dominican Republic, Gurabo Formation, lower Pliocene.

less numerous, distant and in most species coarse. Dorsal sulcus in most cases wide and smooth, with the ribs sharply bisected and forming nodules or tubercles; spinous in some species. Spire retracted with a variable number of terminal ribs. Ventral and outer labral margin callused and usually edged. Aperture fairly wide. Labrum thickened to a variable degree. Labral teeth coarse and distant. Fossula developed” (Fehse and Grego, 2014, p. 7).

Remarks.—Fehse and Grego (2014) divided the genus into four species complexes based on the arrangement of the dorsal sulcus, condition of the dorsal ribs, and shell coloration. They also introduced two new genera to the *Pusula* complex. The four species complexes and two genera are as follows: The *radians*-species-complex, with a wide, smooth dorsal sulcus; the *pediculus*-species-complex, with a fairly wide, smooth dorsal sulcus; the *californiana*-species-complex of the genus *Pseudopusula*, with a greatly reduced dorsal sulcus; and the *vemacola*-species-complex of the genus *Quasipusula*, with no dorsal sulcus.

Radulae in living species are taenioglossate and have a rectangular rachidian tooth with an elongated, lateral central cusp. The teeth are wing-shaped; the inner marginal teeth are curved with a sharp cusp, and the outer marginal teeth are curved and shorter than the inner marginals.

Geographic range.—Monterey Bay, central California, and the entire Pacific Panamic Province and Islas Galápagos; Bermuda and Florida, circum-Caribbean and Gulf of Mexico to Brazil.

Stratigraphic distribution.—Middle or late Miocene through Recent.

***Pusula pediculus* (Linnaeus, 1758)**

Text-figs. 33.1–33.16

Cypraea pediculus Linnaeus, 1758: p. 724.

Cypraea pediculus var. *indica* Linnaeus 1767: p. 1180 [name not validly established].

Cypraea oniscus Röding, 1798: p. 24.

Cypraea pulex Röding, 1798: p. 24 (*nomen nudum*).

Cypraea pulex Röding. Link, 1807b: p. 92.

Cypraea sulcata Dillwyn, 1817: p. 466.

Not *Cypraea pediculus* Linnaeus. Wood, 1828: p. 84, pl. 17, fig. 60 [= *Trivia monacha* (da Costa, 1778)].

Cypraea pediculus var. *minor* Schlüter, 1838: p. 25.

Cypraea pediculus Linnaeus. Reeve, 1846a: pl. 23, fig. 131.

Cypraea pediculus Linnaeus. Tuomey and Holmes, 1856: p. 127, pl. 27, figs. 3, 4.

Cypraea (Trivia) pediculus Linnaeus. Chenu, 1859: p. 270, fig. 1733.

Trivia pediculus (Linnaeus). Troschel, 1863: p. 214, pl. 18, figs. 2a–c (radula).

Trivia pediculus var. *picturata* Mörch, 1877: p. 49 (*nomen nudum*).

Trivia pediculus (Linnaeus). Gabb, 1881: p. 360.

Cypraea (Trivia) pediculus Linnaeus. Roberts in Tryon, 1885: p. 201, pl. 21, figs. 94, 95.

Trivia pediculus (Linnaeus). Dall, 1889: p. 240.

Trivia pediculus (Linnaeus). Dall, 1890: p. 168.

Trivia pediculus (Linnaeus). Dall, 1903: p. 1584.

Trivia pediculus (Linnaeus). Vaughan, 1919: p. 564.

Trivia pediculus (Linnaeus). Vredenburg, 1920: p. 134.

Trivia pediculus (Linnaeus). Maury, 1922: p. 113.

Cypraea restituta Sullioti, 1922: p. 14.

Text-fig. 33. *Pusula pediculus* (Linnaeus, 1758). 1–4, NHMW 2017/0124/0206, length 12.3 mm. 5–8, NHMW 2017/0124/0207, length 11.8 mm. 9–12, NHMW 2017/0124/0208, length 11.0 mm. 13–16, NHMW 2017/0124/0209, length 10.2 mm. All specimens from locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

Triviella gamma Mestayer, 1927: p. 188, fig. 5.

Not *Trivia* (*Trivia*) *pediculus* (Linnaeus). Woodring, 1928: p. 319, pl. 22, figs. 6, 7 [= *Niveria* cf. *jamaicensis* F. A. Schilder, 1932a], 8, 9 [= *Niveria jamaicensis* F. A. Schilder, 1932a], 10, 11 [= *Pusula* cf. *costipunctata* (G. B. Sowerby II, 1870)].

Triviella gamma Mestayer. Finlay, 1930: p. 250.

Trivia pediculus (Linnaeus). Johnson, 1934: p. 112.

Trivia pediculus (Linnaeus). Perry, 1940: p. 136, pl. 28, fig. 206.

Trivia pediculus (Linnaeus). Jaume, 1946: p. 105.

Trivia pediculus (Linnaeus). Gardner, 1948: pp. 214, 215, pl. 29, figs. 8, 9.

Cypraea pediculus Linnaeus. Dodge, 1953: pp. 111–115.

Not *Trivia* (*Trivia*) *pediculus* (Linnaeus). Olsson and Harbison, 1953: p. 265, pl. 60, figs. 1, 1a [= *Pusula dalli* (Petuch, 1994)].

Trivia pediculus (Linnaeus). Abbott, 1954: p. 177, pl. 21, fig. BB.

Trivia pediculus (Linnaeus). Perry and Schwengel, 1955: p. 148, pl. 28, fig. 206.

Trivia pediculus (Linnaeus). Olsson and McGinty, 1958: p. 15.

Trivia pediculus (Linnaeus). Abbott, 1958: p. 47.

Trivia pediculus (Linnaeus). Nowell-Usticke, 1959: p. 52.

Trivia pediculus (Linnaeus). Warmke and Abbott, 1961: p. 90, pl. 16, fig. f.

Trivia pediculus (Linnaeus). Weisbord, 1962: pp. 16, 22, 28, 226–228, pl. 21, figs. 5–10.

- Cypraea pediculus* Linnaeus F. A. Schilder, 1966a: p. 97.
Trivia pediculus (Linnaeus). Hebard, 1967: p. 41.
Trivia pediculus (Linnaeus). Hoerle, 1970: p. 63.
Trivia pediculus (Linnaeus). Kaufman and Götting, 1970: p. 362, fig. 64.
Trivia pediculus (Linnaeus). Vilas and Vilas, 1970: p. 72, pl. 8, fig. 14.
Niveria (*Niveria*) *pediculus pediculus* (Linnaeus). M. Schilder and F. A. Schilder, 1971: pp. 20, 142.
Trivia pediculus (Linnaeus). Morris, 1973: p. 177, pl. 48, fig. 1.
Trivia (*Pusula*) *pediculus* (Linnaeus). Abbott, 1974: pp. 147, 148, figs. 1623, 1625, pl. 3, fig. 1623.
Trivia (*Pusula*) *suffusa* (Gray, 1827). Abbott, 1974: p. 148, fig. 1625 [not *Trivia suffusa* (Gray, 1827)].
Not *Trivia pediculus* (Linnaeus). Humfrey, 1975: p. 103, pl. 22, fig. 1 [= *Pusula* cf. *costipunctata* (G. B. Sowerby II, 1870)].
Trivia (*Pusula*) *pediculus* (Linnaeus). Rios, 1975: p. 71, pl. 20, fig. 289.
Trivia pediculus (Linnaeus). Lozet and Pétron, 1977: p. 50, fig. 40.
Niveria (*Niveria*) *pediculus pediculus* (Linnaeus). Cate, 1979: p. 49, pl. 14, figs. 55, 55a.
Triviella gamma Mestayer. Cate, 1979: p. 50, pl. 40, fig. 172.
Trivia pediculus (Linnaeus). Manjarres, 1979: p. 36.
Trivia pedicula (Linnaeus). Abbott and Dance, 1982: p. 83, unnumbered fig.
Trivia (*Pusula*) *pediculus* (Linnaeus). H. E. Vokes and E. H. Vokes, 1983: p. 21, pl. 7, fig. 10.
Trivia pediculus (Linnaeus). Bandel, 1984: pp. 78, 79, fig. 120, pl. 7, fig. 2 (radula).
Trivia pedicula (Linnaeus). Bertsch, 1987: p. 25.
Trivia pediculus (Linnaeus). De Jong and Coomans, 1988: p. 64, pl. 35, fig. 331.
Trivia pediculus (Linnaeus). Lipe and Abbott, 1991: p. 50, unnumbered fig.
Trivia pediculus (Linnaeus). Cerridwen and Jones, 1991: p. 101.
Trivia pediculus (Linnaeus). Diaz and Puyana, 1994: p. 165, fig. 610.
Trivia pediculus (Linnaeus). Ramos and Robaina, 1994: p. 101.
Trivia (*Niveria*) *pediculus* (Linnaeus). Rios, 1994: p. 77, pl. 26, fig. 296.
Niveria permagna bermontiana Petuch, 1994: p. 264, pl. 26, fig. E.
Trivia pediculus (Linnaeus). Mikkelsen et al., 1995: p. 111.
Trivia pediculus (Linnaeus). Portell et al., 1995: p. 154.
Pusula (*Pusula*) *pediculus* (Linnaeus). Espinosa et al., 1988: p. 21.
Trivia pediculus (Linnaeus). Carlos and Joaquín, 1998: p. 126.
Trivia pediculus (Linnaeus). Pointier and Lamy, 1998: p. 78, unnumbered fig.
Pusula pediculus (Linnaeus). Fernández Milera, 1998: p. 114, unnumbered fig.
Trivia pediculus (Linnaeus). Macsotay and Campos Villaroel, 2001: p. 56.
Pusula pediculus (Linnaeus). Espinosa and Ortea, 2001: p. 17.
Trivia pediculus (Linnaeus). Redfern (in part), 2001: 53, pl. 27, figs. 226B, D, pl. 108, fig. 226E [not fig. 226A = *Pusula labiosa* (Gaskoin, 1836); not 226C = *Pusula cimex* (G. B. Sowerby II, 1870)].
Pusula pediculus (Linnaeus). Fehse, 2002: p. 28.
Niveria pediculus (Linnaeus). Simone (in part), 2004: p. 113, figs. 34, 54, 59, 60, 98.
Not *Niveria pediculus* (Linnaeus). Simone (in part), 2004: p. 113, figs. 19–21, 97, 390–409 [= *Pusula labiosa* (Gaskoin, 1836)].
Pusula pediculus (Linnaeus). Fehse and Grego, 2005: pl. 7, figs. 2a–f.
Trivia (*Niveria*) *pediculus* (Linnaeus). Rios, 2009: p. 138, fig. 326.
Pusula pediculus (Linnaeus). Jensen and Pearce, 2009: p. 113.
Pusula pediculus (Linnaeus). Lee, 2009: p. 79, fig. 376.
Pusula pediculus (s.l.) (Linnaeus). Landau and Silva, 2010: pp. 41–43, pl. 9, figs. 5a, b.
Trivia pediculus (Linnaeus). Daccarett and Bossio, 2011: pp. 85, 244, fig. 352.
Niveria pediculus (Linnaeus). Simone, 2011: pp. 167, 215.
Pusula pediculus (Linnaeus). Petuch and Sargent, 2011: pp. 81, 132.
Pusula pediculus (Linnaeus). Zhang, 2011: p. 91, fig. 244.
Pusula pediculus (Linnaeus). Redfern, 2013: p. 101, figs. 281A–G.
Pusula pediculus (Linnaeus). Fehse and Grego, 2014: p. 9, pl. 1, figs. 1–8, pl. 2, figs. 9–13, pl. 3, figs. 14–18, pl. 32, fig. 205, pl. 36, figs. 232, 233, pl. 43, figs. 246–249, pl. 45, fig. 253.
Pusula pediculus (Linnaeus). Petuch and Myers, 2014: pp. 141, 255, fig. 7.5A, B.
- Type material*.—*Cypraea pediculus*: neotype (F. A. Schilder, 1966a: p. 97), cabinet of the Linnean Society of London, length 14.6 mm, 10.7 mm width; lectotype (Cate, 1979: p. 50), cabinet of the Linnean Society of London, length 12.1 mm, width 8.7 mm. *Triviella gamma*: holotype NMNZ.M.001747, length 12.0 mm, width 10.0 mm. *Niveria permagna bermontiana*: holotype UF 66218, length 22.0 mm, width 16.2 mm.
- Type locality*.—*Pusula pediculus*, off Pompano Beach, SE Florida, USA (designated by Fehse and Grego, 2014: p. 12); *Triviella gamma*, Bay of Islands, New Zealand (*lapsus*: type locality incorrect, based on Caribbean shell; Fehse and Grego, 2014: p. 14); *Niveria permagna bermontiana*, Capelletti Brothers Pit 11, NW 47th and Florida Turnpike, Miami, Dade County, Florida.
- Previously figured material*.—Hypotype (Gardner, 1948: pp. 214, 215, pl. 29, figs. 8, 9) USNM 325430.
- Material*.—NHMW 2017/0124/0206–0209 (4 specimens; locality NMB 16844); NHMW 2017/0124/0210 (4 specimens; locality NMB 16844); 2017/0124/0211 (1 specimen; locality TU 1215); 2017/0124/0223 (1 specimen; locality TU 1442–1444).
- Measurements*.—Maximum length 11.8 mm, width 8.7 mm, height 7.1 mm.

Original description.—"C. testa transversim sulcata ... Haec media inter Cypraeas and Bullas; Labro exteriori praecedentibus convenit, interiore laevi ad sequentes accedit" (Linnaeus, 1758: p. 724). Added in 1767, "Haec maculas gerit dorsales 3 fuscas. Indica dorso exarato sulco longitudinali; Europaea eo sulco destituta; Angelica tota absque maculis alba." (Linnaeus, 1767: p. 1180).

Revised description.—"Size between 7 and 25 mm, lightweight, solid and ovate. Spire covered by callus. Body whorl ovate, inflated and rounded, about 85% of total height, with both slightly terminals produced [*sic*]. Both terminal tips slightly indented. Dorsum profile evenly rounded, completely covered by ribs — above 18¹⁰ on average — with an incised sulcus mid-dorsally that bisects the ribs. Ribs both sides of the sulcus forming nodules. Ventrums slightly rounded with recurved terminals. Aperture narrow over its entire length widened only barely at the fossular section. Aperture straight but curved posteriorly. Labrum roundly callused, narrow, slightly curved, keeled towards its inner margin. Outer labral margin slightly edged. Labrum bears on its inner margin an average of 15 fine denticles. Siphonal and anal canals follow the shell profile. Columella slightly curved, narrow and tapering steeply inwards. Parietal lip straight, not clearly delimited, crossed by an average of 14 ribs. Fossula concave and not clearly delimited from the rest of the columella. Inner fossular edge protruded" (Fehse and Grego, 2014: p. 10).

Remarks.—The Dominican late Miocene specimens show a neatly incised, narrow dorsal sulcus, with the ribs slightly swollen on either side. The color pattern consisting of three groups of coalescent blotches—one group placed anteriorly, one centrally, and one posteriorly—is clearly preserved. A common shallow water species (Warmke and Abbott, 1961).

Comparisons.—The genus *Pusula*, which includes both fossil and Recent taxa, was recently revised by Fehse and Grego (2014). Several closely similar species occur in the Caribbean. *Pusula labiosa* (Gaskoin, 1836) shares the same present-day distribution as *Pusula pediculus* and is recorded from the Pliocene of Florida as *Pusula dadeensis* Petuch, 1994; it differs from *P. pediculus* in having a more strongly callused periphery (giving the shell a more circular profile), a more elevated dorsum, a more convex venter, and a deeper, wider dorsal sulcus. Another sympatric Caribbean species, *Pusula costispunctata* (G. B. Sowerby II, 1870) differs most notably in having spotted ribs, which are less numerous than in its congeners. *Pusula cimex* (G. B. Sowerby II, 1870) is another Caribbean member of the group which, amongst others, was considered valid by Fehse and Grego (2014). It will be interesting to see if future molecular work supports these distinct species.

Occurrence.—Río Gurabo (locality TU 1215); Río Cana (locality NMB 16844); Río Yaque del Norte (locality TU 1442–1444).

Fossil distribution.—Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Landau and Silva, 2010). Lower Pliocene: Araya Formation, Cubagua Island, Venezuela (Landau and Silva, 2010); Gurabo Formation, Dominican Republic (Landau and Silva, 2010; this paper). Pliocene (indeterminate): Bowden Member of the Layton Formation, Jamaica (Dall, 1903; Woodring, 1928; Gardner, 1948), Costa Rica (Dall, 1889), South Carolina (Tuomey and Holmes, 1856; Du Bar, 1962). Pleistocene (indeterminate): 'Glades' Unit, Florida (Hoerle, 1970; Portell et al., 1995); Barbados (F. A. Schilder, 1932a); Costa Rica (Gardner, 1948). Lower Pleistocene: Waccamaw Formation, North Carolina (Gardner, 1948); Caloosahatchee Formation, Florida (Dall, 1889; Gardner, 1948; Fehse and Grego, 2014). Upper Pleistocene: New Providence Island, Bahamas (Hebard, 1967); Bermont Formation, Florida (Olsson and Harbison, 1953; Petuch, 1994); Fort Thompson Formation, Florida (Olsson and Harbison, 1935; Petuch, 1994; Landau and Silva, 2010); Ironshore Formation, Grand Cayman (Cerridwen and Jones, 1991); La Isabella Formation, Dominican Republic (Landau and Silva, 2010; NHMW coll.); Abisinia Formation, Venezuela (Weisbord, 1962; Fast, 1978).

Recent distribution.—Bermuda (Jensen and Pearce, 2009), Florida, and throughout Caribbean, Bahamas south to Espírito Santo State, Brazil (Fehse and Grego, 2014).

Family ERATOIDAE Gill, 1871

Eratoidae Gill, 1871: p. 9 (as subfamily Eratoinae).

Remarks.—The earliest record of the family Eratoidae is in the early Paleocene (Danian) of Faxø, Denmark, with the appearance of *Johnstrupia faxensis* Ravn, 1933 (M. Schilder and F. A. Schilder, 1971: p. 10; Tracey et al., 1993: p. 148). A possible ancestor may be genus *Zittelia* from the family Colombellinidae, but no Cretaceous species are known (F. A. Schilder, 1933c). By the Eocene the family was widespread in Europe, New Zealand, Australia, and the western United States (M. Schilder and F. A. Schilder, 1971). Numerous Oligocene through Pliocene species are documented from western and southern Europe (Fehse and Landau, 2001a, 2001b, 2003; Fehse and Grego, 2012). M. Schilder and F. A. Schilder (1971) reported Miocene species from New Zealand, Australia, Japan, the Caribbean, Indonesia, and the eastern United States, including Florida. Landau and Fehse (2004) documented Pliocene faunas from southern Spain, and Ladd (1977) described a species from Pliocene of Fiji.

Table 18. Fossil Eratoidae described and/or recorded from the Dominican Republic. Numbers of specimens of four taxa of eratoid gastropods collected in the Cibao Valley for this study.

Taxon	Current Genus	No. of Specimens
<i>Hespererato canae</i> n. sp.		6
<i>Erato chipolana</i> Maury, 1910	<i>Hespererato</i>	12
<i>Erato maugeriae</i> var. <i>domingensis</i> Maury, 1917a	<i>Hespererato</i>	50+
<i>Hespererato praeclusa</i> n. sp.		3

F. A. Schilder (1933c) noted that the Eratoidae differ anatomically and conchologically from all of the other cypraeoideans. However, his generic subdivisions were based solely on shell features. F. A. Schilder (1936) utilized the radula and osphradia in addition to shell morphology to develop his later classifications. This classification (Schilder, 1936) was largely utilized by M. Schilder and F. A. Schilder (1971) as well. Cate (1977) produced the most complete monograph on living eratoids and adopted the classification scheme of M. Schilder and F. A. Schilder (1971). Dolin (1991) included the family in his fossil documentation of the lower Miocene Chipola Formation of Florida. Most recently, Fehse and Landau (2001a, 2001b, 2003) and Landau and Fehse (2004) included eratoids in their publications on western European mollusk species, and Landau et al. (2016) noted the presence of Eratoidae in the Miocene Cantaure Formation of Venezuela. Neogene Eratoidae from the Dominican Republic are listed in Table 18. Higher level systematics above superfamily follow that of Bouchet et al. (2017); lower-level systematics follow M. Schilder and F. A. Schilder (1971). These are the teardrop cowries.

Genus **HESPERERATO** F. A. Schilder, 1932a

Hespererato F. A. Schilder, 1932a: p. 83. Type species (by original designation): *Erato vitellina* Hinds, 1844, Recent, Bodega Bay, Sonoma County, northern California, to Bahía Magdalena, Baja California Sur, México.

Original description.—"Fossula obsolete or nearly so, one or two terminal ridges border the outlet" (F. A. Schilder, 1933c: p. 246).

Revised description.—In most species the fossula is obsolete, slightly concave, or narrow, sloping from the terminal ridge. The number of labial teeth is variable, and teeth may be fine to coarse; columellar teeth obsolete or fine. Apertural lip thickened and callused. Spire projected.

Remarks.—The phylogenetic relationships of the genus are unclear. The earliest species, *Hespererato ampulla* (Deshayes, 1835), appears in the middle Eocene; the next species to appear is *Hespererato rhenana* Schilder, 1933c, from the upper

Oligocene, a notable gap in time. *Hespererato* apparently used this time gap to spread westward into the lower Miocene of eastern North America and the Caribbean (Fehse and Landau, 2001b).

Fehse and Villacampa (2018) incorrectly assigned two fossil Caribbean species, *Erato chipolana* Maury, 1910 (Text-figs. 34.1–34.3), and *Erato domingensis* Maury, 1917a (Text-figs. 34.4–34.6), to the genus *Archierato* Schilder, 1933c. The type species of *Archierato* is *Erato pyrulata* Tate, 1890 (pp. 216, 217, pl. 13, figs. 12, 12a), from the late Eocene of South Australia. *Erato pyrulata* is more globose with a longer and more curved aperture, a shorter and more concealed spire, and coarser teeth than *E. domingensis* and *E. chipolana*. Fehse and Simone (2020) also incorrectly assigned the Caribbean and East Pacific Eratoidea to the genus *Archierato*. None of the species assigned to *Archierato* by Fehse and Villacampa (2018) or Fehse and Simone (2020) compare favorably to the lectotype of *Archierato* (Darragh, 2017: p. 53, fig. 3.3) or to the specimens of *Archierato* figured by Schilder (1933c: fig. 8), Schilder (1935: fig. 1), or Wenz (1941: fig. 2783); hence, the authors have kept the Caribbean species in the genus *Hespererato*.

Geographic distribution.—Italy and the North Sea Basin, North Carolina, Florida, Jamaica, and Martinique to Brazil; northern California to Peru and the Islas Galápagos.

Stratigraphic distribution.—Middle Eocene (Auversian) to Recent (M. Schilder and F. A. Schilder, 1971; Fehse and Landau, 2001b).

***Hespererato canae* n. sp.**
Text-figs. 35.1–35.14

Type material.—Holotype NHMW 2017/0124/0178; paratype 1 NHMW NHMW 2017/0124/0179; paratype 2 NHMW NHMW 2017/0124/0180; paratype 3 NHMW 2017/0124/0190; paratype 4 NHMW 2017/0124/0277; paratype 5 NHMW 2017/0124/0278.

Type locality.—Locality NMB 16844, coquina layer on west bank of Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

Text-fig. 34. *Hespererato* types of Maury. 1–3, *Erato chipolana* Maury, 1910, lectotype, PRI 3464, height 4.1 mm, width 2.9 mm; Bailey's Ferry, Calhoun County, Florida, Chipola Formation, lower Miocene. 4–6, holotype, *Erato maugeriae* variety *domingensis* Maury, 1917a, PRI 28798, length 3.7 mm, width 2.9 mm; Bluff 3 (= locality TU 1294), Cercado de Mao, Dominican Republic, Cercado Formation, upper Miocene.

Text-fig. 35. *Hespererato canae* n. sp. 1–3, holotype, NHMW 2017/0124/0178, length 5.7 mm, width 4.2 mm, height 3.4 mm. 4–6, paratype 1, NHMW 2017/0124/0179, length 5.4 mm, width 4.3 mm, height 3.5 mm. 7–9, paratype 4, NHMW 2017/0124/0277, length 5.5 mm, width 4.3 mm, height 3.2 mm. 10–12, paratype 5, NHMW 2017/0124/0278, length 5.6 mm, width 4.3 mm, height 3.4 mm. Holotype and paratypes 1, 4, and 5 from locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene. 13, 14, paratype 3, NHMW 2017/0124/0190, length 5.5 mm, width 4.3 mm, height 3.4 mm; locality TU 1449, La Barranca, Río Yaque del Norte, Gurabo Formation, lower Pliocene.

Table 19. Measurements of *Hespererato canae* specimens in mm.

Specimen	Length	Width	Height	Locality
Holotype NHMW 2017/0124/0178	5.7	4.2	3.4	NMB 16844
Paratype 1 NHMW 2017/0124/0179	5.4	4.3	3.5	NMB 16844
Paratype 2 NHMW 2017/0124/0180	4.9	3.5	3.0	NMB 16844
Paratype 3 NHMW 2017/0124/0190	5.5	4.3	3.4	TU 1449
Paratype 4 NHMW 2017/0124/0277	5.5	4.3	3.2	NMB 16844
Paratype 5 NHMW 2017/0124/0278	5.6	4.3	3.4	NMB 16844

ZooBank LSID.—urn:lsid:zoobank.org:act:808823A3-D455-4B21-ADF8-68195A048526

Material.—Known only from the type series.

Measurements.—See Table 19.

Diagnosis.—*Hespererato* species with globose last whorl, subobsolete dorsal sulcus, 18–20 coarse labial teeth, subobsolete columellar dentition except in parietal region, and bifid terminal ridge; surface covered in axially elongated pustules.

Description.—Shell small, broadly pyriform, with small, rounded spire enveloped in callus. Last whorl strongly inflated, evenly rounded, with subobsolete dorsal sulcus, constricted at base, venter equally rounded, not depressed. Surface covered in axially elongated pustules. Aperture narrow, curved, not widened anteriorly. Outer lip moderately broad, with 18–20 coarse denticles on inner edge extending outwards to half lip width. Columellar callus absent or reduced to thin wash; fossula area flattened, poorly delimited; row of subobsolete denticles developed at columellar angulation, slightly more strongly developed in parietal portion; terminal ridge bifid.

Remarks.—It is with some surprise that this species was discovered amongst a larger lot of *Hespererato domingensis* from locality NMB 16844 on the Río Cana. To the authors' knowledge, *Hespererato canae* is the only Caribbean species described with strong pustular sculpture. This type of sculpture seems deep-rooted in eratoids, as it crops up in numerous distinct genera, i.e., *Eratoena* Iredale, 1935, *Cypraeerato* F. A. Schilder, 1933c, and *Hespererato* F. A. Schilder, 1933c.

This species is placed in the genus *Hespererato* based on the much reduced fossula. There is little intraspecific variability amongst the specimens at hand.

Comparisons.—The only tropical American eratoid with pustular sculpture is *Hespererato scabriuscula* (Gray in G. B. Sowerby I, 1832) from the tropical American Pacific, but that

species is immediately separated by its more elongated shell, wider aperture, and far more robust apertural dentition.

Etymology.—Named after the type locality of Río Cana. *Hespererato* gender feminine.

Occurrence.—Río Cana (locality NMB 16844); Río Yaque del Norte (locality TU 1449).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (this paper). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper).

Hespererato chipolana (Maury, 1910)

Text-figs. 34.1–34.3; 36.1–36.12

Erato chipolana Maury, 1910: p. 27, pl. 6, fig. 9.

Erato (*Erato*) *domingensis trochala* Woodring, 1928: p. 321, pl. 22, fig. 12.

Erato chipolana Maury. F. A. Schilder, 1929: p. 8.

Erato (*Archierato*) *chipolana* Maury. F. A. Schilder, 1929: p. 8.

Erato (*Archierato*) *chipolana* Maury. F. A. Schilder, 1932a: p. 82.

Hespererato chipolana (Maury). F. A. Schilder, 1933c: pp. 248, 258, 262.

Erato (*Hespererato*) *chipolana* Maury. Gardner, 1947: p. 543.

Hespererato chipolana chipolana (Maury). M. Schilder and F. A. Schilder, 1971: pp. 15, 104.

Hespererato chipolana (Maury). Dolin, 1991: pp. 46–49, fig. 54.

Not *Hespererato chipolana* (Maury). Dolin, 1991: pp. 46–49, figs. 53a–c [= *Archierato antonioi* Fehse and Vallacampa, 2018].

Archierato chipolana (Maury). Fehse and Vallacampa, 2018: p. 26, fig. 2.

Type material.—*Erato chipolana*, lectotype (Brann and Kent, 1960: p. 377) PRI 3464, paralectotype PRI 11006 (ex PRI 3464a) (both ex Cornell University collection); *Erato domingensis trochala*, holotype USNM 135338.

Type locality.—*Erato chipolana*, Bailey's Ferry, Calhoun County, Florida, lower Miocene, Chipola Formation; *Erato domingensis trochala*, Bowden, Jamaica, Pliocene.

Text-fig. 36. *Hespererato chipolana* (Maury, 1910). 1–3, NHMW 2017/0124/0185, length 4.0 mm. 4–6, NHMW 2017/0124/0186, length 3.8 mm. 7–9, NHMW 2017/0124/0187, length 4.4 mm. 10–12, NHMW 2017/0124/0188, length 4.1 mm. All specimens from locality NMB 15907, Río Gurabo, Dominican Republic, Cercado Formation, upper Miocene.

Material.—NHMW 2017/0124/0185–0188 (4 specimens; locality NMB 15907); NHMW 2017/0124/0189 (8 specimens; locality NMB 15907).

Measurements.—Maximum length 4.4 mm, width 3.1 mm, height 2.6 mm.

Original description.—“Shell globose, inflated, rather thin, ribs fine, numerous, about twenty-five on the lip where they form a line of fine but sharply-defined teeth. The ribs extend uninterruptedly over the dorsal area of the shell and occasionally divaricate towards the lateral margins. The shell shows a very faint medial dorsal ridge with barely visible grooves on either side” (Maury, 1910: p. 144).

Revised description.—“Shell small, rather heavy, ovate-conic. Spire short, broad, obtusely tapering. Body obtusely angulated at the periphery, somewhat obliquely constricted in front of the periphery, inclined to flair slightly at the anterior extremity. Conch and protoconch each including $2\frac{1}{2}$ volutions, the suture glazed, however, so that in unmutated specimens it is entirely obscured. Protoconch revealed only by removing the surface enamel; smooth and very highly polished, somewhat naticoid; initial turn minute, inflated, partially immersed; remaining turn and a half increasing more rapidly in altitude than in diameter, flattening towards the close of the nucleus. Opening of conch marked by an abrupt change from the vitreous to the porcellaneous texture. Surface

smooth except for microscopically fine, irregular, blistered lines radiating from the apex to a little in front of the shoulder. Aperture sublinear, oblique. Outer lip sharply angulated at the shoulder, feebly contracted medially, much thickened and serrated along the inner margin by about 15 short, lirate ridges, longest medially and very short and heavy anteriorly, the foremost outlining the entrance to the incipient canal. Inner wall of aperture flattened; a series of irregular denticles developed along the inner margin of the aperture, the three in front produced into oblique and somewhat irregular ridges that simulate collumellar folds. Fossula obsolete. Body constricted anteriorly into an ill-defined canal, squarely truncate or obscurely emarginate at its extremity” (Gardner, 1947: p. 543).

Remarks.—For comparison, see discussion under *Hespererato domingensis* below.

Occurrence.—Río Gurabo (locality NMB 15907).

Distribution.—Lower Miocene: Chipola Formation, USA (Maury, 1910; F. A. Schilder, 1929, 1932a, 1933c; Gardner, 1947; Brann and Kent, 1960; M. Schilder and F. A. Schilder, 1971; Dolin, 1991; Fehse and Vallacampa, 2018). Upper Miocene: Cercado Formation, Dominican Republic (this paper). Pliocene (indeterminate): Bowden Member of the Layton Formation, Jamaica (Woodring, 1928).

Text-fig. 37. *Hespererato domingensis* (Maury, 1917a). 1–3, NHMW 2017/0124/0173, length 4.4 mm. 4–6, NHMW 2017/0124/0174, length 4.5 mm. 7–9, NHMW 2017/0124/0175, length 4.4 mm. 10–12, NHMW 2017/0124/0176, length 5.3 mm. All specimens from locality NMB 16844, Río Cana, Dominican Republic, Cercado Formation, upper Miocene.

***Hespererato domingensis* (Maury, 1917a)**

Text-figs. 34.4–34.6; 37.1–37.12

Erato maugeriae variety *domingensis* Maury, 1917a: p. 118, pl. 21, fig. 8.

Erato maugeriae variety *domingensis* Maury, 1917b: p. 13.

Erato maugeriae subspecies *domingensis* Maury, Vaughan and Woodring, 1921: p. 120.

Erato (*Archierato*) *domingensis* Maury, F. A. Schilder, 1932a: p. 83.

Erato (*Eratopsis*) *domingensis* Maury, F. A. Schilder, 1933c: pp. 249, 258, 263.

Erato (*Eratopsis*) *domingensis* (Maury), M. Schilder and F. A. Schilder, 1971: pp. 13, 111.

Erato maugeriae variety *domingensis* Maury, Fast, 1978: p. 103.

Archierato domingensis (Maury), Fehse and Villacampa, 2018: p. 26, figs. 3a–c.

Type material.—Holotype PRI 28798, length 3.7 mm, width 2.9 mm.

Type locality.—Bluff 3, Cercado de Mao, Dominican Republic (= locality TU 1294), Cercado Formation, upper Miocene.

Material.—NHMW 2017/0124/0173–0176 (4 specimens; locality NMB 16844); NHMW 2017/0124/0177 (50+ specimens; locality NMB 16844); NHMW 2017/0124/0184 (1 specimen; locality NMB 16926); PRI 84776 (7 specimens; locality TU 1294); PRI 84775 (11 specimens; locality TU 1227A).

Measurements.—Maximum length 5.3 mm, width 4.3 mm, height 3.1 mm.

Original description.—“Shell minutely ficiiform, whorls three, suture indistinct, spire very short, obtuse, last whorl very globose posteriorly, contracted and slightly produced anteriorly; aperture linear, nearly as long as the shell, margin of outer lip much thickened, minutely crenulated within; inner lip perfectly smooth except for a longitudinal ridge” (Maury, 1917a: p. 118).

Revised description.—Shell small, pyriform, strongly inflated at high-placed shoulder, spire moderately low, smooth surface. Teleoconch of three whorls; spire whorls moderately low, convex, separated by superficial linear suture; last whorl strongly globose above mid-whorl, constricted at base. Aperture moderately narrow, almost straight, not widened anteriorly. Outer lip moderately narrow, bearing broad labial varix, somewhat alate adapically; labial varix fused to penultimate whorl, 16–19 fine denticles restricted to inner edge. Anterior terminal relatively long, margined exteriorly by callus. Columellar callus thickened and expanded over entire venter, fossula hardly developed, poorly delimited; columellar angulation forming narrow ridge, with a few subobsolete denticles in parietal portion; terminal ridge simple.

Remarks.—As can be seen in the series illustrated (Text-fig. 37.1–37.12), there is little intraspecific variation. Although always inflated at the shoulder, some shells are more inflated

than others, and the thickness of the labial varix is slightly variable, probably increasing with ontogeny.

Comparisons.—*Hespererato chipolana*, originally described from the lower Miocene Chipola Formation of Florida, differs from *Hespererato maugeriae* (Gray in G. B. Sowerby I, 1832) from the present-day Caribbean in having a more elevated spire and longer anterior terminal, giving it a less squat appearance. The outer lip is less alate adapically and the columellar teeth are less strongly developed than in *H. maugeriae*; *H. maugeriae* usually has relatively well-developed denticles on the columella in the parietal area and abapically, separated by a smooth mid-columellar area. The size of the two species is comparable.

Hespererato domingensis differs from both of the above-mentioned species in having a squatter shell—which is more globose just above mid-whorl and more constricted at the anterior terminal—and a relatively strongly alate adapical portion to the outer lip. *Hespererato domingensis* is found together with *Hespererato canae* at Río Cana (locality NMB 16844), but *H. canae* is immediately separated by its larger size, more evenly globose and less pyriform shell shape, and the presence of surface pustules.

Occurrence.—Río Mao (localities NMB 16926; TU 1294); Río Cana (locality NMB 16844); Arroyo Zalaya (locality TU 1227A).

Distribution.—Upper Miocene: Cercado Formation, Dominican Republic (Maury, 1917a, 1917b; Vaughan and Woodring, 1921; F. A. Schilder, 1932a; Fast, 1978). Lower Pliocene: Gurabo Formation, Dominican Republic (this paper)

***Hespererato praeclusa* n. sp.**

Text-figs. 38.1–38.9

Type material.—Holotype NHMW 2017/0124/0178; paratype 1 NHMW 2017/0124/0179; paratype 2 NHMW NHMW 2017/0124/0180.

Type locality.—Locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Dominican Republic, Baitoa Formation, lower–middle Miocene.

ZooBank LSID.—urn:lsid:zoobank.org:act:FF3E3290-30BC-4C0A-9FF7-BB48929069F4.

Material.—Known only from the type series.

Measurements.—See Table 20.

Diagnosis.—*Hespererato* species with last whorl inflated in adapical portion, low spire, 15–18 coarse labial teeth, alate outer lip, subobsolete columellar dentition that is slightly stronger in parietal region, simple terminal ridge, strongly produced anterior terminal, smooth surface.

Description.—Shell small, pyriform, strongly inflated at high-placed shoulder, spire low, smooth surface. Teleoconch of two whorls; spire whorl low, flat, separated by superficial linear suture; last whorl strongly globose above mid-whorl, constricted at base. Aperture moderately narrow, almost straight, not widened anteriorly. Outer lip moderately narrow, bearing broad labial varix, alate adapically; labial varix fused to penultimate whorl, 15–21 coarse denticles extending outwards over inner half of outer lip. Anterior terminal long, margined exteriorly by callus. Columellar callus thin, expanded over entire venter, fossula hardly developed, poorly delimited; columellar angulation forming narrow ridge, with a few subobsolete denticles in anterior and parietal portions; terminal ridge simple.

Remarks.—Cate (1977: p. 362) commented on the difficulties in separating species within the *Hespererato columbella* (Menke, 1847) species group, which included *Hespererato maugeriae*, *Hespererato panamensis* (Carpenter, 1856) and *Hespererato marginata* (Mörch, 1860). Cate suggested there were good reasons for lumping all the species together, but concluded that they could be separated into a Panamic Pacific species group based on shell morphology and color; this group of extant species includes *H. columbella* (= *H. panamensis*; = *H. marginata*) and *H. maugeriae* in the Caribbean.

If species boundaries are unclear in the extant faunas, these problems are compounded when dealing with species over time. Not only is the color—so often used as a distinguishing feature in cypraeids, ovulids, and their kind—lacking, soft parts are also obviously lacking, and preservation is often imperfect.

Closely related species groups with representatives found today on either side of the Isthmus of Panama must have had a common ancestor prior to the closure of the Central American Seaway. It is herein suggested that *Hespererato praeclusa* may be just such a species. It seems closer to the Panamic Pacific *Hespererato columbella* than *Hespererato maugeriae*.

Comparisons.—*Hespererato praeclusa* and the Panamic Pacific *Hespererato columbella* share an elongated pyriform shell shape with a relatively long anterior terminal. *Hespererato praeclusa* differs in having a narrower aperture with labial dentition extending outwards onto the outer lip, whereas in *H. columbella* it is restricted to the inner lip edge. The fossil species also has a more alate adapical portion to the outer lip

Text-fig. 38. *Hespererato praeclusa* n. sp. 1–3, holotype, NHMW 2017/0124/0181, length 5.3 mm. 4–6, paratype 1, NHMW 2017/0124/0182, length 6.2 mm. 7–9, paratype 2, NHMW 2017/0124/0183, length 5.2 mm. All specimens from locality TU 1363/1364, Arroyo Hondo, Río Yaque del Norte, Baitoa Formation, lower–middle Miocene.

Table 20. Measurements of *Hespererato praeclusa* specimens in mm.

Specimen	Length	Width	Height	Locality
Holotype NHMW 2017/0124/0181	5.3	3.6	3.0	TU 1363/1364
Paratype 1 NHMW 2017/0124/0182	6.2	3.8	3.2	TU 1363/1364
Paratype 2 NHMW 2017/0124/0183	5.2	3.3	3.0	TU 1363/1364

and weaker columellar dentition than most specimens of *H. columbella*, but, as can be seen in the series illustrated by Cate (1977: figs. 44, 44a–g), these features are highly variable.

The lectotype of *Hespererato panamensis* illustrated by Cate (1977: fig. 45), who considered it to be a synonym of *Hespererato columbella*, is very similar to *Hespererato praeclusa*.

The Caribbean *Hespererato maugeriae* differs from *Hespererato praeclusa* in having a squatter shell with a lower spire and shorter anterior terminal, finer teeth on the inner lip that are restricted to the inner edge, and usually stronger columellar dentition. *Hespererato domingensis*, from the younger upper Miocene Cercado Formation of the Dominican Republic, is intermediate in form between *H. praeclusa* and *H. maugeriae*; the height of the spire and length of the anterior terminal are greater than in *H. maugeriae*, but less than *H. praeclusa*. It has a narrow aperture similar to that of *H. maugeriae* and *H. praeclusa* and shares a weak columellar dentition with *H. praeclusa*.

Etymology.—Latin “*prae-*,” prefix meaning before, and “*clusus*, -a, -um,” adjective meaning closed or shut in; this species lived before the closure of the CAS. *Hespererato* gender feminine.

Occurrence.—Río Yaque del Norte (locality TU 1363/1364).

Distribution.—Lower–middle Miocene: Baitoa Formation, Dominican Republic (Maury, 1917a).

ACKNOWLEDGMENTS

The authors extend their heartfelt thanks to the following researchers, curators, collection managers, and colleagues for numerous loans, collections access, specimen information, and images, literature, and personal insights and encouragement. By institution we thank Elana Benamy, Paul Callomon, Katy Estes-Smargiassi, and Gary Rosenberg (ANSP); Bushra Hussaini (AMNH); Reggie Kawamoto (BPBM); the late Jean DeMouthe, Christine (Chrissy) Garcia, Lou Marincovich Jr., Peter U. Rodda, and Peter Roopnarine (CASG); Terry Gosliner and Elizabeth Kools (CASIZ); Richard L. Squires (CSUN, Geological Sciences, retired); Harry F. Filkorn, Austin J.W. Hendy, George L. Kennedy, the late Phillip G. Owen, the late LouElla R. Saul, Mary Stecheson, and Lindsay Walker (LACMIP); the late James H. McLean and Jann E. Vendetti (LACM, Malacology Department); John Taylor

(NHMUK); the late Peter Jung, René Panchaud, and Olivier Schmidt (NMB); Warren Allmon, Jonathan R. Hendricks, the late Peter Hoover, Leslie Skibinski, Wendy Taylor, and Vicky Wang (PRI); Daniel L. Geiger (SBMNH); Mark Goodwin, David Haasl, Carole S. Hickman, Pat Holroyd, David R. Lindberg, and Karen Wetmore-Grycewicz (UCMP); the late E. Alison Kay (UHI); the late Warren C. Blow, Jann Thompson, and Thomas R. Waller (USNM). Geerat Vermiej (UCD, Earth and Planetary Sciences), Felix Lorenz (cowries.info, Buseck-Beuern, Germany) and Dirk Fehse (ZSM) are thanked for information and supplying reprints and pdfs. Librarians Mali Griffin, Mark Herbert, Richard Hulser, and the late Don McNamee (LACM research library) and Jean Crampon, Melinda Hayes, and Suzanne Henderson (USC research libraries) all aided in acquisition of rare and obscure references. Ángel Valdés (CPP) kindly translated an early version of the abstract from English to Spanish. LG sincerely thanks his wonderful wife Cathy L. Groves (LACM Echinoderms Department, retired) for her support, patience, and insights over the years and for all of the “working vacations” while visiting numerous museum collections. An enormous thanks to Emily Vokes (TU, emeritus, retired) for her help, advice, and support during this project and to Leslie L. Skibinski and Vicky Wang (PRI), who provided excellent photographs and collection numbers for all the cypraeids in the PRI collection. Thanks also to Carlos Marques da Silva (University of Lisbon, Portugal), who not only helped with fieldwork in the Dominican Republic during several expeditions, but also helped with artwork in the paper. Finally, Felix Lorenz (cowries.info, Buseck-Beuern, Germany) and Judith T. Smith (USNM) reviewed the manuscript and offered helpful suggestions and caught many of our errors; to both of them we are sincerely grateful.

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Note: **Bold-faced name** indicates the valid species or higher taxon name. **Bold-faced number** indicates the primary page(s) on which that species or higher taxon is treated.

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Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York 14850 U. S. A.

ISSN 0007-5779

ISBN 978-0-87710-533-6 \$40.00
5 4 0 0 0 >
9 780877 105336
US \$40.00