THE NAUTILUS

Volume 132, Numbers 3–4
December 21, 2018
ISSN 0028-1344

A quarterly devoted
to malacology.

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The subscription rate for volume 133 (2019) is US $65.00 for individuals, US $102.00 for institutions. Postage outside the United States is an additional US $10.00 for regular mail and US $28.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

Change of address: Please inform the publisher of your new address at least 6 weeks in advance. All communications should include both old and new addresses (with zip codes) and state the effective date.

THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews National Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

THE NAUTILUS

Volume 132, Numbers 3–4
December 21, 2018
ISSN 0028-1344

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STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

1. Publication Title, THE NAUTILUS.
2. Publication No. 0028-1344.
3. Filing Date, December 3, 2018.
4. Issue Frequency, Quarterly.
5. No. of Issues Published Annually, Four.
6. Annual Subscription Price, US $102.00.
7. Complete Mailing Address of Known Office of Publication, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA
8. Complete Mailing Address of Headquarters, same as 7.
9. Full Names and Complete Mailing Addresses of Publisher, The Bailey-Matthews Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957 USA
   Editor, Dr. José H. Leal, address as above.
10. Owner, Shell Museum and Educational Foundation, Inc., address as above.
11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities, None.
12. The purpose, function, and nonprofit status of this organization and the tax exempt status for federal income tax purposes has not changed during the preceding 12 months.
13. Publication Name, THE NAUTILUS.
14. Issue Date for Circulation Data Below, July 29, 2018

15. Extent and Nature of Circulation	Average 12 months	Single Issue
a. Total Number of Copies	260	260
b. Paid Circulation		
1. Paid/Requested Outside-County Mail Subscriptions	216	228
2. Paid In-County Subscriptions	0	0
3. Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution	0	0
4. Other Classes Mailed Through the USPS	13	16
c. Total Paid and/or Requested Circulation	229	244
d. Free Distribution by Mail		
1. Outside-County	11	11
2. In-County	0	0
3. Other Classes Mailed Through the USPS	0	0
4. Free distribution outside the Mail	0	0
e. Total Free or Nominal Rate Distribution	11	11
f. Total Distribution	240	255
g. Copies not Distributed	20	05
h. Total	260	260
i. Percent Paid Total	95%	96%

16. Electronic Copy Circulation		
a. Paid Electronic Copies	0	0
b. Total Paid Print Copies + Paid Electronic Copies	229	244
c. Total Print Distribution + Paid Electronic Copies	240	255
d. Percent Paid (Both Print & Electronic Copies)	95%	96%

The genus *Cerion* (Gastropoda: Pulmonata: Cerionidae) on San Salvador [Watling Island], Bahamas: A geometric morphometric analysis of shell morphology

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ABSTRACT

Morphometric analyses of shell shape of living specimens of *Cerion* inhabiting San Salvador Island segregate samples into two primary phenotypes, one inhabiting the western and southern coasts of the island, the other the eastern and much of the northern coast. These are concordant with phenotypes identified in prior morphometric studies. **Lectotypes are designated for *Cerion watlingense* Dall, 1905; *C. inconspicuum* Dall, 1905; *C. inconspicuum lacunorum* Dall, 1905; and *C. coloni* Bartsch, 1924.** The lectotype of *Cerion watlingense* Dall, 1905 falls within the western and southern phenotype, and is the oldest name available for this taxon. The lectotype of *Cerion coloni* Bartsch, 1924, a validly introduced, but previously unrecognized taxon, and the holotype of *Cerion rodrigoi* Gould, 1997 both fall within the group containing the east coast populations, with *Cerion coloni* Bartsch, 1924 being the oldest available name for this phenotype. A third, previously unrecognized phenotype, represented by a single inland population, is morphologically similar to the lectotype of *Cerion inconspicuum* Dall, 1905, which is the oldest available name for this phenotype. The geographical distribution and chronological succession of these phenotypes since the late Pleistocene is reviewed in the context of both the single and multiple colonization models for the arrival of *Cerion* on San Salvador, and the evolutionary and taxonomic corollaries of each model are discussed.

INTRODUCTION

Nearly all modern papers dealing with land snails of the genus *Cerion* are prefaced by an acknowledgment of the extreme morphological diversity among the many, small populations of these snails. This is usually followed by a lamentation (e.g., Woodruff, 1978) about the profusion of names [ca. 600] that have been applied to the various phenotypes, mostly in the late 19th and early 20th centuries. Nearly all of these named taxa are allopatric, but many interbreed freely when brought into contact (see e.g., Bartsch, 1920; Woodruff and Gould, 1987). Throughout the range of *Cerion* (from the Keys and barrier islands of tropical Florida, throughout the Bahamas, Greater Antilles, Cayman Islands, western Virgin Islands, and the Dutch Antilles, but absent from Jamaica, the Lesser Antilles, and coastal Central and South America), there are but three reported cases in which two different phenotypes co-occur sympatrically, one in Cuba (Mayr, 1963), and two on Great Inagua (Gould and Woodruff, 1990; Goodfriend and Gould, 1996).

Earliest records of Cerionidae date from the Cretaceous of Montana (Roth and Hartman, 1998), yet the overwhelming majority of taxa (>98%) are from late Pleistocene, Holocene, and especially Recent faunas, particularly those of Cuba (29%) and the Great Bahama Bank (51%) (Harasewych, 2012: Table 1). Changes in sea levels brought about by Pleistocene glaciations would have joined populations of the numerous adjacent islands on shallow banks such as the Great Bahama Bank during glacial periods and isolated them during interglacial sea level rises, facilitating hybridization and amplifying morphological diversity over multiple eustatic cycles (Harasewych, 2012).

Although the distribution of cerionids throughout most of the islands of the tropical western Atlantic was the result of overland dispersal followed by the break-up of GAARlandia (Greater Antilles + Aves Ridge Land Bridge) and the displacement of Antillean blocks to the northeast by the advancing Caribbean Tectonic Plate (Itturalde-Vinent, 2006: fig. 13), the lack of a land connection between the islands of the Bahamas and the Greater Antilles precluded overland colonization. Rather, the Bahamian Islands must have been populated by propagules dispersed from the Greater Antilles either by rafting or by hurricanes (Harasewych, 2012: 124). Clench (1938: 495) reported that the fauna of the Bahamas archipelago likely dates only from the Pleistocene and has reached the Bahamas by fortuitous means, noting (Clench, 1938: 484–485) that the species of the Great

Table 1. Populations of Recent of *Cerion* from San Salvador (Watlings Island) included in this study.

Population	STATION	LOCATION	LATITUDE	LONGITUDE	CATALOG NUMBER	N	GROUP
1	BP	Barker's Point	24°06.61' N	74°30.87' W	USNM 1110076	10	1
2	VH	Victoria Hill	24°05.83' N	74°31.27' W	USNM 1110077	10	1
3	EA	E of airport	24°03.85' N	74°30.90' W	MCZ IP 190243-190252	10	3
4	CT	N of Cockburn Town	24°03.24' N	74°32.16' W	USNM 590160	10	1
5	SU	Sugarloaf	24°00.43' N	74°31.89' W	USNM 1110078	8	1
6	G1234	Sugarloaf	24°00.15' N	74°32.17' W	MCZ IP-190212-190221	10	1
7	GB	Grotto Bay	23°57.26' N	74°33.63' W	USNM 1110079	10	1
8	WQ	Watling's Quarry	23°57.23' N	74°32.87' W	USNM 1110080	10	1
9	SH1	W of Sandy Hook	23°56.85' N	74°29.91' W	USNM 1110081	10	1
10	SH2	E of Sandy Hook	23°57.17' N	74°29.32' W	USNM 1110082	10	1
11	TT	The Thumb	24°00.80' N	74°27.35' W	USNM 1110088	10	2
12	G193b	W of Storr's Lake	24°02.72' N	74°27.17' W	MCZ IP 190195-190204	10	2
13	G194	W of Storr's Lake	24°03.52' N	74°27.19' W	MCZ IP 190205-190211	7	2
14	G1225	Columbus Monument	24°04.06' N	74°25.80' W	MCZ IP 190264-190273	9	2
15	G1240	NE of Granny Lake	24°02.89' N	74°27.19' W	MCZ IP-190222-190231	10	2
16	CC	Crab Cay	24°03.93' N	74°25.80' W	USNM 1110087	9	2
17	HB	Hanna Bay	24°07.14' N	74°27.03' W	USNM 1110085	4	2
18	MH	Man Head Cay	24°07.54' N	74°26.97' W	USNM 1110086	8	2
19	NP1	North Point	24°07.65' N	74°27.44' W	USNM 1110083	8	2
20	NP2	North Point	24°07.22' N	74°27.37' W	USNM 1110084	10	2
21	GC	Green Island (Cay)	24°08.33' N	74°30.51' W	USNM 359519	10	2

Bahama Bank were closely allied to those of Cuba, while the species of the easterly islands (Crooked Island Group to Caicos Island) were affiliated with species from Haiti. He hypothesized that relationships among the terrestrial molluscan faunas of this region are due to island proximity and the paths of hurricanes.

San Salvador is a small island on the eastern margin of the Bahamas platform that has remained isolated by deep water, with little change in island area during the eustatic sea level fluctuations since at least the Pliocene. Its living and fossil *Cerion* fauna had been spared some of the excesses of early taxonomists, yet has been well studied by modern researchers, particularly in the areas of ecology and chronostratigraphy, due largely to the presence of the Gerace Research Centre (formerly Bahamian Field Station) on the island. The genus *Cerion* is well represented in the fossil record of San Salvador, with a documented dated presence spanning the past 140,000 years (Hearty and Schellenberg, 2008).

In the present study, we analyze the morphology of *Cerion* shells from representative populations spanning the island of San Salvador in order to determine the number of phenotypes and their distribution, and to reconcile these with the type specimens of all taxa described from San Salvador or Watling Island. A second series of analyses incorporates measurements from a small subset of well-preserved, adult fossil specimens for which ages have been determined (Hearty and Schellenberg, 2008). These analyses follow the chronology of patterns of phenotype distribution from the Pleistocene to the Recent to the extent possible given the sampling.

Conclusions of earlier works on the *Cerion* of San Salvador are reviewed in the context of our findings.

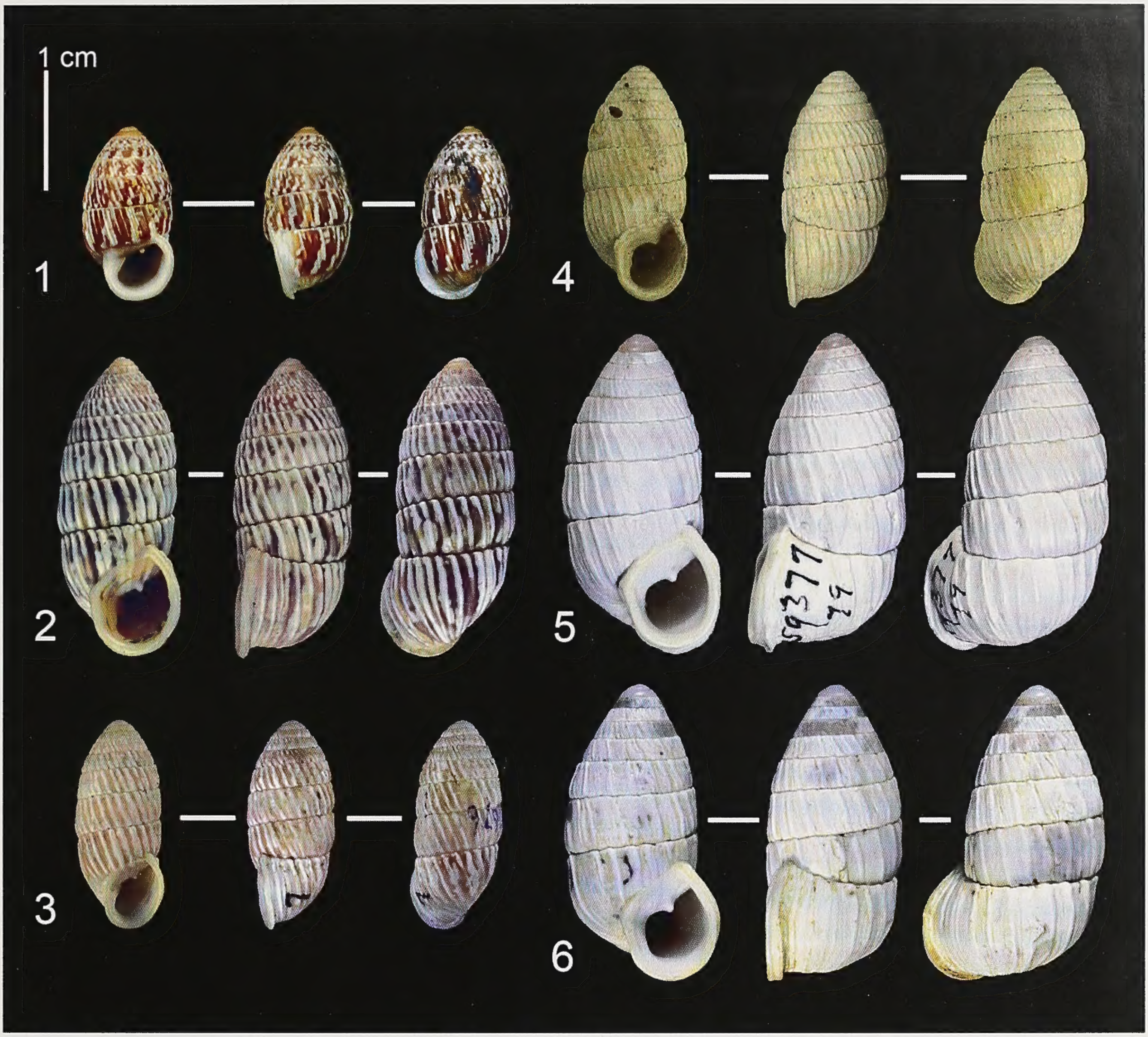
TAXONOMIC HISTORY

Known as Guanahani to the native Lucayan inhabitants, the island was named San Salvador by Christopher Columbus when he first sighted land in 1492. It was settled by John Watling in the 17th century and became known as Watlings Island. The name San Salvador was officially transferred from what is now Cat Island to Watlings Island in 1925 as historians concluded that this was the island where Columbus first landed in the New World.

Dall (1894: 117) reported on the molluscan fauna of Watling Island based on material sent to him. He identified as *Cerion (Strophiops) glans* (Küster, 1844) a single, rather small specimen taken from about a pint [0.473 L] of beach drift from Watling Island lagoon during a U. S. Fish Commission sampling. Dall (1905: 438) later wrote that no *Cerion* had previously been noted from Watling Island, and that his earlier report of *C. glans* from this island was due to an error.

Pilsbry (1902: 265) described the subspecies *Cerion eximium fraternum* (Figure 1) as being from San Salvador, based on material attributed to Bland. Clench (1938: 531) reported this taxon from Little San Salvador (now also known as Half Moon Cay), an island between Eleuthera and Cat Cay. He noted that the exact type locality for this taxon is unknown, but "as Bland had received other species of Cat Island material from near the center of the island, it is quite probable that his *fraternum* material came from the same area." As Pilsbry's publication predated the renaming of Watlings Island, it seems clear that *Cerion eximium fraternum* was described from Cat Island (called San Salvador at the time) and does not occur on the island that is known as San Salvador today.

In his report on land snails collected in the Bahamas, Dall (1905: 438–439) proposed two new species, *Cerion*



Figures 1–6. Apertural, lateral, and dorsal views of primary type specimens of *Cerion* described as from San Salvador. **1.** *Cerion eximium fraternum* Pilsbry, 1902. Lectotype (designated by Baker, 1963: 206). ANSP 7418. San Salvador (Bland). **2.** ***Cerion (Strophiops) watlingense* Dall, 1905.** The specimen illustrated by Dall (1905: pl. 58, fig. 7) **is here designated as the lectotype for this taxon. USNM 132970.** Watling Island [San Salvador]. **3.** ***Cerion (Strophiops) inconspicuum* Dall, 1905.** The specimen illustrated by Dall (1905: pl. 58, fig. 2) **is here designated as the lectotype for this taxon. USNM 37676.** Watling Island. **4.** ***Cerion (Strophiops) inconspicuum lacunorum* Dall, 1905.** The specimen illustrated by Dall (1905: pl. 58, fig. 4) **is here designated as the lectotype for this taxon. USNM 127494,** Watling Island, on the shores of the lagoon. **5.** ***Cerion coloni* Bartsch, 1924. Lectotype (designated herein), USNM 359377**, Columbus Point (Crab Cay), San Salvador, Bahamas. **6.** *Cerion rodrigoi* Gould, 1997. Holotype, MCZ IP 190264. Windswept terrace of Crab Cay adjacent to the Columbus Monument, San Salvador, Bahamas. Scale bar = 1 cm for all images.

watlingense (Figure 2) and *Cerion inconspicuum* (Figure 3), both from Watling Island. He also described the variety *Cerion inconspicuum lacunorum* (Figure 4) from the shores of the lagoon on Watling Island.

Paul Bartsch conducted fieldwork on San Salvador in August of 1923, noting in a report of his visit (Bartsch, 1924) that he had gathered approximately 25,000 specimens during his two weeks on the island. This published report included a photograph (Bartsch, 1924: fig. 41) of seven specimens of *Cerion* on a leaf and was captioned "*Cerion coloni*, new species, ... taken at the base of the Columbus Monument, San Salvador." As this associates a name with an illustration prior to 1931, it is an available name (ICZN 2012, Article 12.2.7). The taxon

Cerion coloni Bartsch, 1924, (Figure 5) was not recorded in Clench's (1957) catalog of the Cerionidae, nor in Ruhoff 's (1973) listing of Bartsch's zoological taxa. Unaware of Bartsch's publication, Gould (1997) described *Cerion rodrigoi* (Figure 6) from the same locality.

Many subsequent researchers (e.g., Woodruff, 1978; Poth et al. 2010; Rose, 1990) have regarded the *Cerion* fauna of San Salvador to consist of a single variable species, while others (e.g., Baldini et al., 2007:174; Hearty and Schellenberg, 2008) have elected to avoid species nomenclature, "as neither proof nor consensus exists with regard to species level taxonomy".

MATERIALS AND METHODS

A geometric morphometric analysis of shell shape was performed on 193 specimens of *Cerion* snails from 21 populations spanning San Salvador Island (Table 1). Figure 7 illustrates the location and a representative specimen from each population.

Specimens were individually photographed in an apertural orientation using a digital camera (Nikon D300) with the lens axis oriented perpendicular to the coiling axis of the shell. Images were taken at a distance of 35–40 cm in order to minimize image distortion and parallax error. To avoid the effects of allometry, only adult specimens, free of repaired breaks and with a well-preserved embryonic shell and a fully formed terminal adult aperture having an expanded and reflected lip indicative of terminal growth (Gould and Woodruff, 1978: 381), were selected for analysis.

Shells were digitized using TPSDIG2 (Rohlf, 2005). A total of 24 points were selected to capture shell shape (Figures 8–9). All points were treated as landmarks. These points cover most of the ratios used for classical characterization of *Cerion* shell morphometry (Gould et al., 1974). Taking several photographs of the same specimen ensured the reproducibility of the measurements by checking that the deviation in landmark positioning was minimal. Thus, the same *Cerion* shell (maximum length 25.56 mm) was photographed 10 times, even with different optics in the camera. The maximum error in landmark positioning was 0.13 mm (0.51 % referenced to the size of the shell). The mean error was 0.06 mm (0.23 % relative to the size of the shell). Landmarks were aligned by a standard generalized least squares (GLS) procedure. Procrustes coordinates and centroid sizes (CS) were generated by COORDGEN6h (Sheets, 2003–2005). CS provides a measure of the geometric size of each specimen, and is computed as the square root of the sum of squared distances from each landmark to the centroid of each specimen's configuration of landmarks (Zelditch et al., 2004). Partial warp scores (PWS) were derived from the 24 landmarks used for capturing the shape of the shells upon Procrustes alignment and calculation of the consensus reference form. PWS were used as shape variables in our analyses. PWS and their principal components (PC, also known as relative warps) were computed using PCAGEN8, which is included in the Integrated Morphometrics Package software suite (IMP 8, Sheets, 2003–2014). CS and the first principal component (PC1) of the partial warps accounted for 92.2% variance in the dataset. Gaussian clustering of these variables (CS and shape PC1 scores) was used to detect population clusters, with the number of clusters determined using the Bayesian Information Criterion (BIC) as implemented in MCLUST Version 5 software package for R (Scrucca et al., 2016). This program tests different models of clustering, and the fit of each model to the dataset is assessed by means of the Bayesian information criterion.

In our system the best-fit model (BIC –332.56, log L = –132.0738, df = 13, for n = 193) indicated 3 components or clusters of variable volume and equal shape and orientation (VEE model). The pairwise Procrustes distances between groups of populations based upon shell morphometry were obtained with TWOGROUP8 (Sheets, 2003–2014) using resampling methods (400 bootstraps). The significance of the Goodall's F-test was assessed by a bootstrapped F-test. Discriminant Function Analysis (DFA) using PWS+CS as variables, and morphometric grouping as factor was performed with the programs STATGRAPHICS CENTURION XVII and CVAGEN8 (Sheets, 2003–2014). The latter program was also used for generating the two-dimension (2D) scatter plots and the corresponding deformation grids and vectors. Discrimination was statistically significant along both DF1 and DF2 axes (DF 1: Wilk's $\Lambda = 0.0852$, $\chi^2 = 413.8103$. df=90, $p < 2.22045 \times 10^{-16}$; DF 2: Wilk's $\Lambda = 0.4458$ $\chi^2 = 135.7141$, df = 44, $p = 2.7677 \times 10^{-11}$).

RESULTS

A geometric morphometric analysis of the shells of 193 specimens from 21 living populations of *Cerion* from San Salvador Island was conducted. A Principal Component Analysis of the PWS yielded two statistically significant components that represent 62.4 % of the overall variation in shape in our sample. Shell height of *Cerion* from San Salvador is known to exhibit a strongly bimodal distribution (Fronabarger et al., 1997). Gaussian clustering of CS and shape PC1 data was used to determine the different morphometric groups in our sample according to size and shape by the program MCLUST in R. The best-fit model indicated three components or clusters of variable volume and equal shape and orientation (Figure 10).

This analysis indicates that the pattern of distribution of size and shape in our sample of *Cerion* shells is best represented by three separate groups, partitioned among three different phenotypes. We obtained the initial composition of each of the groups directly from MCLUST, taking into consideration that the group assignment for specimens falling in the overlap region among clusters may be subjected to increased uncertainty (Figure 11). Final assignment of individuals to each of the three groups was determined by checking the composition of each of the populations against the suggested grouping resulting

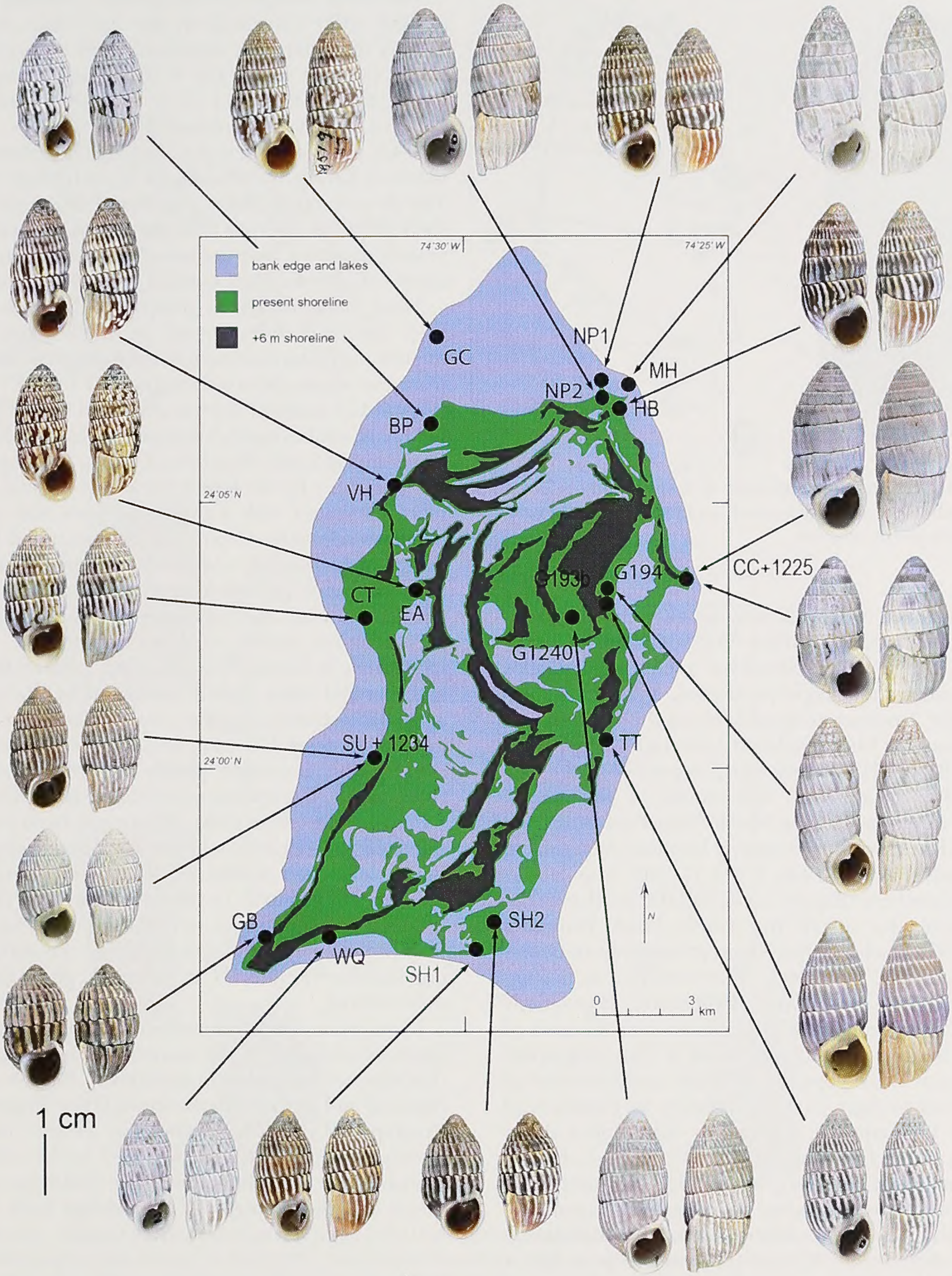
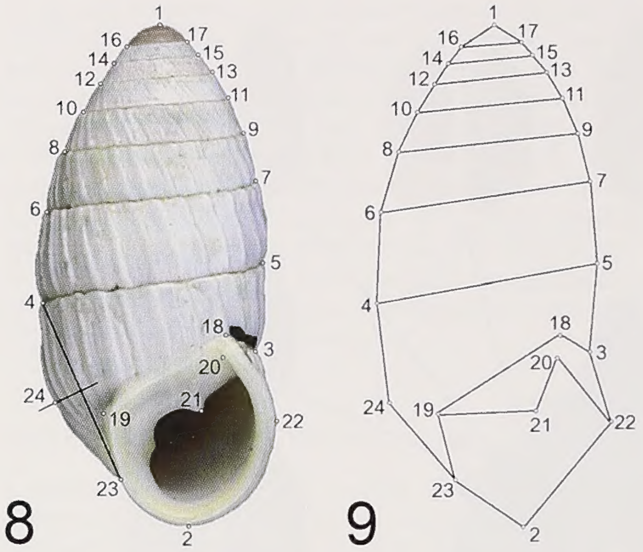


Figure 7. Map of San Salvador, Bahamas. Locations of sampled populations (solid circles) are identified by alphanumeric station designations (see Table 1). A representative specimen from each station is shown.

from MCLUST Gaussian clustering. Individuals from each of the populations studied were all members of the same group with the exception of populations VH and CT, which fell into the region of overlap between Group 1 and Group 2, and thus had a higher uncertainty in group classification.

Phenotype 1 (Group 1) includes all individuals from populations: BP, VH, CT, SU, G1234, GB, WQ, SH1, and



Figures 8–9. Position of landmarks. **8.** A specimen of *Cerion coloni* Bartsch, 1924, showing **9.** positions of the landmarks used in the morphometric analyses.

SH2. Phenotype 2 (Group 2) includes all individuals from populations: TT, G193b, G194, G1225, G1240, CC, HB, MH, NP1, NP2, and GC. Phenotype 3 (Group 3) includes all individuals from a single population, EA.

Phenotype 1 occurs exclusively along the western and southern coasts of San Salvador to the mouth of the lagoon (Figure 7, BP to SH2). Phenotype 2 occurs along the east coast of the island, from the mouth of the lagoon northward to the base of the North Point Peninsula (Fig. 7, TT to NP2), as well as at several locations inland from the east coast (Fig. 7, G193b, G194, G1240). Populations from an isolated cay (Figure 7, GC) off the north coast as well as from the tip of the North Point Peninsula (Figure 7, NP1) include phenotypes primarily from Group 2 but with several individuals from Group 1, indicating areas of potential overlap or hybridization. Populations VH and CT appear on the plot clustered in the area of overlap of between Phenotypes 1 and 2. The geographic distribution of these populations in the western coast of the island led to their final classification as members of Phenotype 1. Phenotype 3 is known only from a single population inland from the west coast (Figure 7, EA).

Confirmation of the composition of these morphometric groups was accomplished by means of Discriminant Function Analysis (DFA). Discrimination was statistically significant along both DF1 and DF2 axes (Figure 12). A DFA using the above group composition as a factor and PWS+CS as variables classified correctly 190 out of 193 specimens (98.4 %). In the jack-knifed assignment test, the rate was 90.7 % (175 correct out of 193). Using shape-only variables (i.e. leaving CS out of the analysis) the correct classification rate was 97.4 % (89.1 % in the jack-knifed test). Figures 13 to 24 represent the relative position of the specimens from each of the populations in discriminant space.

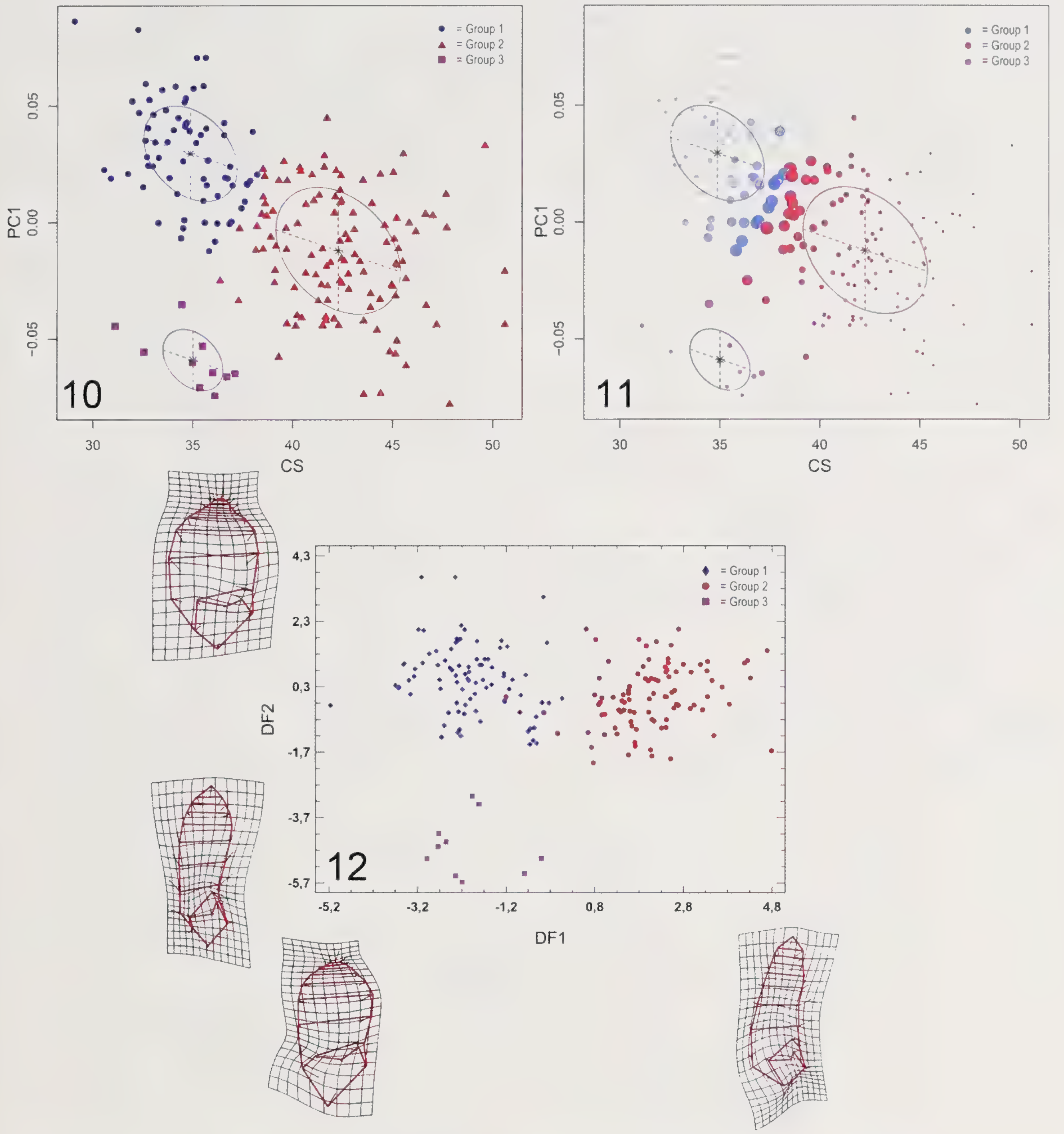
The three morphometric groups resulting from this analysis differ statistically in size and shape. ANOVA indicates that there are significant differences in CS between Group 1 (mean CS = 35.79) and Group 2 (mean CS = 43.05) (F = 311.37, p = 0.0000), and between Group 2 and Group 3 (mean CS = 34.98) (F = 79.85, p = 0.0000). However, there is no significant difference in size between Group 1 and Group 3 (F = 0.80, p = 0.3735). The three groups exhibit significant differences in mean shell shape, as inferred from the calculated pairwise Procrustes distances between means and the corresponding results of bootstrapped Goodall's F-tests (Table 2).

Thus, individuals from groups 1 and 3 do not differ in shell size, but differ greatly in shell shape. The distinguishing features of each of the groups can be extracted from the shape deformation implied by DF1 and DF2 (Figure 12). Group 1 is separated from Group 2 along the DF1 axis, while Group 3 is separated from group 1 and 2 along the DF2 axis. Members of Group 2 can be separated from Group 1 by the larger size of their shells, which are more elongated with a projecting apex and a relatively narrower aperture. Group 1 is characterized by smaller shells, with broadest whorls at mid-length, and a more depressed apex, giving a general oval appearance and with a relatively wider aperture. Members of Group 3 exhibit shell features similar to those of Group 1. However, individuals in Group 3 display a less inflated shell shape, with parallel sides slightly narrowing at the mid-length and with a convex profile towards the apex. Shells of individuals from Group 1 are relatively broader at the center, with a straight profile towards the more protruded apex. The aperture in Group 3 is narrower than in Group 1. Apart from these differences in size and shape, the shells of individuals in groups 1 and 3 also exhibit a more developed sculpture of axial ribs compared to members of group 2. In the latter, the axial ribs may be reduced or even absent in certain specimens. This feature provides additional support for the assignment of populations VH and CT to Group 1, given their strong axial ribbing.

Using this morphometric framework, primary type specimens of each of the named taxa from San Salvador (Lectotypes designated in captions to Figures 2–5) were digitized and analyzed by means of DFA (Figure 25). The lectotype of *Cerion watlingense* clearly falls within Group 1 (probability 98.8%), and is the oldest name available for this phenotype. The lectotype of *Cerion coloni* and the holotype of *C. rodrigoi* both fall within

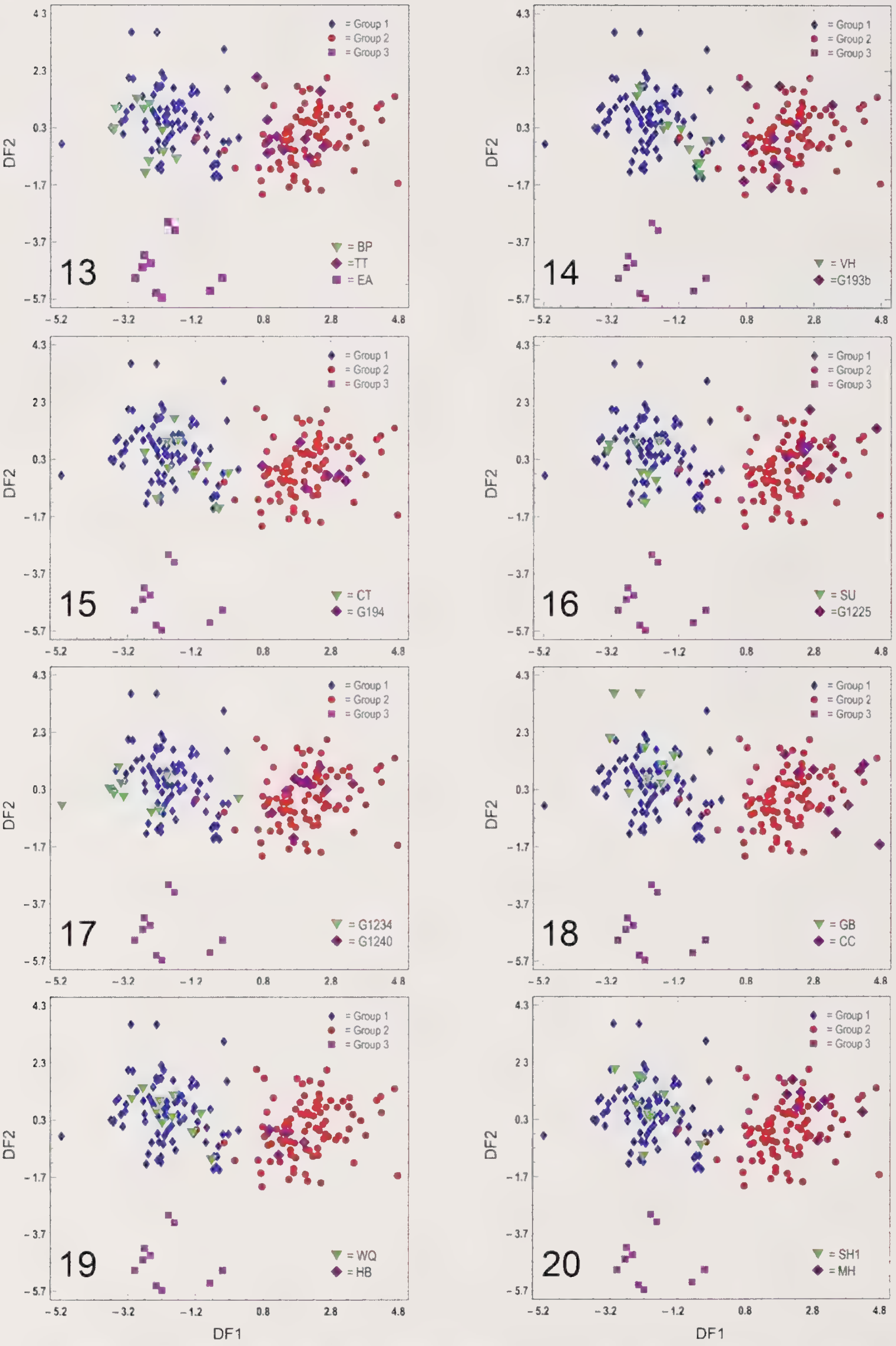
Table 2. Comparison of pairwise Procrustes distances between groups of specimens as defined by shell phenotype, based upon shell morphometry. The significance of the Goodall's F-test was assessed by a bootstrapped F-test (400 replications).

Group	Group	Procrustes distance	Goodall's-F	p
1	2	0.0361	30.03	0.0025
1	3	0.0823	31.25	0.0025
2	3	0.0577	16.26	0.0025



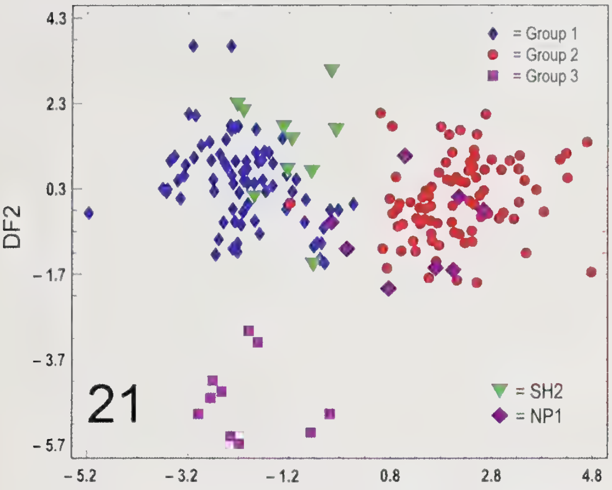
Figures 10–12. Plots of the first principal component (PC1) versus Centroid size (CS). **10.** Symbols indicate classification corresponding to the best-fit model as determined by MCLUST. Component means are marked, and ellipses with axes are drawn corresponding to their covariances. **11.** Classification uncertainty as determined by MCLUST. Symbol size proportional to degree of uncertainty. **12.** Discriminant Function Analysis (DFA) of the shapes and sizes of the shells of 193 specimens corresponding to 21 populations of *Cerion* snails from San Salvador Island, using Partial warp scores (PWS) + Centroid size (CS) as variables and considering morphometric group as classification factor. The 2D scatter plot of the DF1 and DF2, and the corresponding deformation grids and vectors are shown.

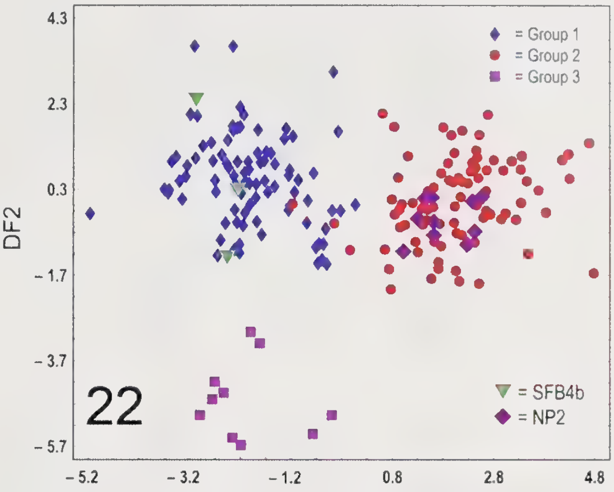
Group 2 (probabilities > 99.9%), with *C. coloni* being the oldest available name for this phenotype. The lectotypes of *Cerion inconspicuum* and *Cerion inconspicuum lacunorum* have morphologies that are intermediate between Group 1 and Group 3 with the algorithm assigning them to Group 3 at 95 % probability for *C. inconspicuum*, and 51.4 % for *C. inconspicuum lacunorum*. *Cerion inconspicuum* is the oldest available name for this phenotype.

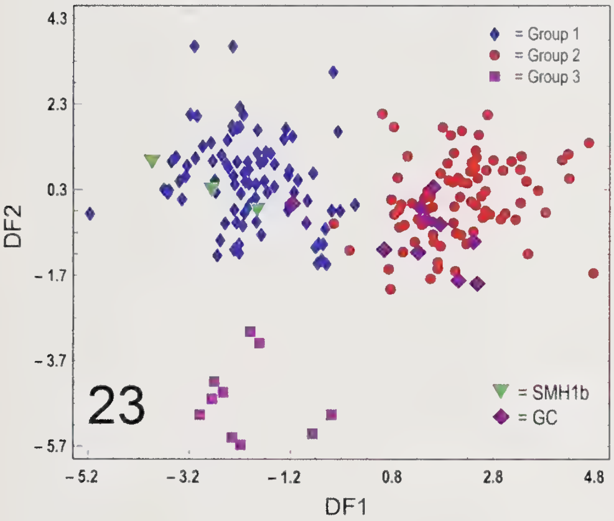


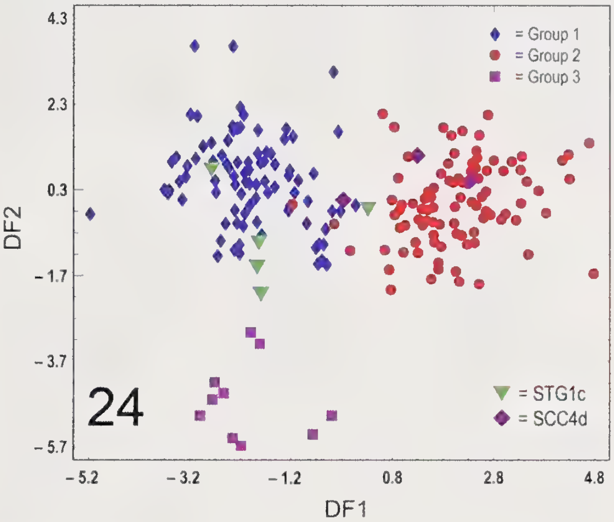
Figures 13–24. Positions of specimens from individual living (Figures 13–23) and fossil (Figures 22–24) populations in the discriminant space.

A number of well-preserved fossil specimens that had been dated by amino acid racemization in a previous study (Hearty and Schellenberg, 2008) were digitized, scored, and classified by DFA as had been done with the type material. The oldest well-preserved specimens suitable for morphometric analyses were from French Bay (between WQ and SH1 on Fig. 7). All three specimens from SFB4b(1) (Figure 26) (Hearty and Schellenberg, 2008:









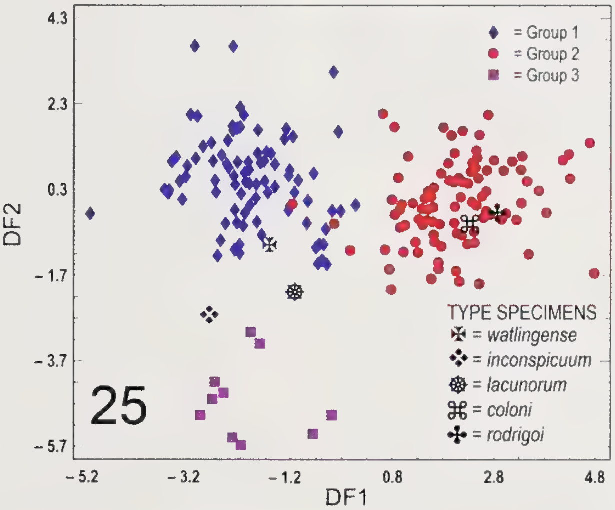
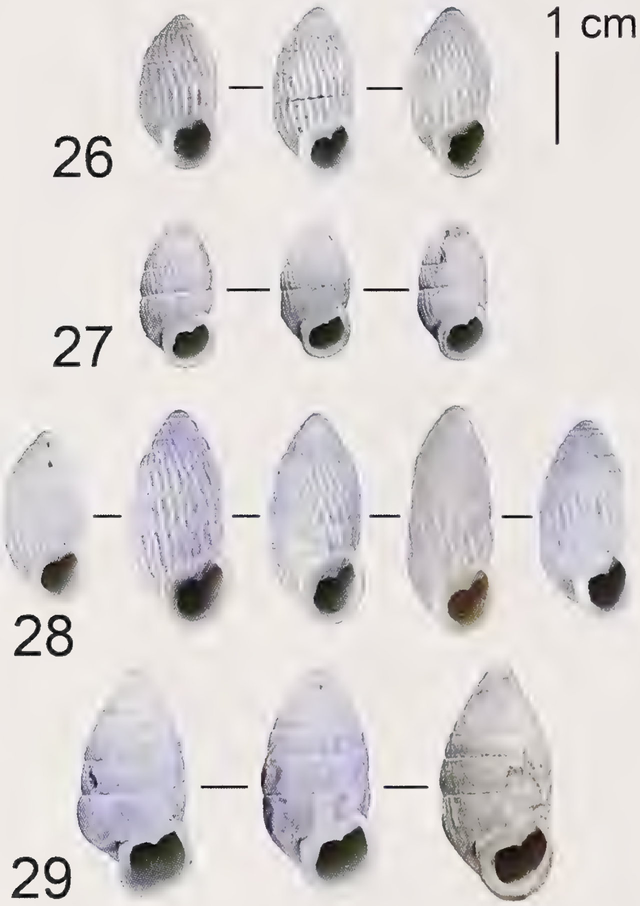


Figure 25. Positions of primary type specimens in the discriminant space.

Fig. 2, Table 2) fell well within Group 1 (Figure 22) (probabilities > 99 %), indicating that this phenotype has been represented on the southern coast of San Salvador between 125,000 and 140,000 years before present. Three fossil specimens from Man Head Cay SMH1b (Figure 27) (Hearty and Schellenberg, 2008: Fig. 2, Table 2) also fell well within Group 1 (Figure 23) (probabilities > 99.8 %), indicating that this was the only phenotype occurring on



Figures 26–29. Fossil specimens of San Salvador Cerion used in morphometric analyses. **26.** Three specimens from the French Bay Member of the Grotto Beach Formation [station SFB4b(1), Hearty and Schellenberg, 2008: Fig. 2, Table 2], (125,000–140,000 years before present). **27.** Three specimens from Man Head Cay [station SMH1b, Hearty and Schellenberg, 2008: Fig. 2, Table 2], (90,000–110,000 years before present). **28.** Five specimens from The Gulf [Station STG1c1, Hearty and Schellenberg, 2008: Fig. 2, Table 2], (80,000–90,000 years before present). **29.** Three specimens from Crab Cay [SCC4d (1–2), Hearty and Schellenberg, 2008: Fig. 2, Table 2], (70,000–80,000 years before present).

Man Head Cay between 90,000 and 110,000 years before present. Modern *Cerion* on Man Head Cay are all of Group 2 (Figure 20). Fossil samples STG1c1 (Figure 28) (Hearty and Schellenberg, 2008: Fig. 2, Table 2) from The Gulf (very near SH1 on Figure 7) were morphologically diverse (Figure 24), with three falling within Group 1 (probabilities > 99 %), 1 within Group 2 (probability 93 %) and one questionably within Group 3 (probability of only 61.9 %), indicating that in addition to phenotype 1, phenotypes 2 and possibly 3 were present on San Salvador between 80,000 and 90,000 years before present, although in a region of the island where phenotypes 2 and 3 do not occur today. Three fossil samples from Crab Cay (Figure 29) [SCC4d(1–2), Hearty and Schellenberg, 2008:Fig. 2, Table 2] near the geographic center for Group 2 in the modern fauna, reveal that both Group 1 (probability > 95 %) and Group 2 (probabilities > 99 %) (Figure 24) were present at this location between 70,000 and 80,000 years before present.

DISCUSSION

Despite minor differences in the number and types of measurements and analytical algorithms, our results concur with prior morphometric analyses (e.g. Hearty et al., 1993; Fronabarger et al., 1997; Hearty and Schellenberger, 2008) in identifying two primary shell phenotypes of *Cerion* living on the island of San Salvador, one centered along the western coast (Group 1), the other along the eastern coast (Group 2) of the island. The presence of a third phenotype (Group 3) with a very restricted inland distribution has not been previously reported, since prior studies had not sampled in the area in which it occurs.

A number of these studies had dealt with morphological changes in *Cerion* shells throughout the continuous fossil record that spans 140,000 years. Hearty et al. (1993: Fig. 6) had reported that a single phenotype was present on San Salvador in the Grotto Beach Formation (MIS 5e), the Gulf Unit (MIS 5a), and the Man Head Unit (MIS5a), but that a different phenotype was present in the later Almgreen Cay Formation (MIS5a). They noted that the more recent Holocene Rice Bay Formation contained shells with both phenotypes. They had also documented (Hearty et al., 1993: Fig. 7) a significant increase in shell length and especially in shell width within the Almgreen Cay Formation (70,000–90,000 years before present). Hearty and Schellenberg (2008) subsequently reported that changes in the morphology of *Cerion* shells on San Salvador over the past 140,000 years appear to be continuous and generally directional, and that a trend of increasing gross shell size characterizes each of the interglacial phases (MIS 5e, MIS 5a and MIS 1). They also commented that live-collected *Cerion* have a range in gross morphology that nearly encompasses that of the entire fossil sequence.

In morphometric analyses of living and fossil *Cerion* shell morphology, Fronabarger et al. (1997) concluded that variation is dependent on geography, and suggested that environment affects shell shape. They also noted that variation seen between living and fossil populations is the same as the variation seen in the geographic distribution of living samples.

These studies interpret the considerable variation in shell morphology, both geographic and chronostratigraphic, based on the premise that there was but a single colonization of San Salvador by *Cerion*, and that all variation resulted from subsequent differentiation within a single lineage. Rose (1990) attributed the different morphologies to intraspecific variation, with the larger, thicker ribs found on shells that inhabited the eastern coast being a response to predation by crabs and rodents. Hearty and Schellenberg (2008) attributed rapid changes in shell size during MIS 5a as responses to environmental factors due to climate change during this interglacial period with its warmer and wetter climate. They concluded that multiple *Cerion* extinctions and recolonizations during the past 140,000 years are improbable due to the continuous fossil record, and that multiple species are unlikely to occur on San Salvador.

Gould (1997) noted the intermediate position of San Salvador between the "two major geographic domains of Bahamian *Cerion*" and concluded that the *Cerion* fauna of the island is descended from propagules from both geographic regions. He considered *Cerion watlingense* (Group 1) to be derived from the "ribby" bank-edge phenotype (see Gould and Woodruff, 1986) of the Great Bahama Bank, while the "triangular" phenotype, which he named *Cerion rodrigoi* (a junior synonym of *C. coloni* Bartsch, 1924) (Group 2) to have originated in the southeastern Bahamian islands. He speculated that a third phenotype, corresponding to the "mottled", bank interior phenotype of the northern Bahamas, would either be absent or restricted to the interior of San Salvador because the island has no bank-interior coast (a coast that was inland when eustatic sea level fell, exposing larger banks during glacial periods). He commented that it was not known whether the "ribby" and "mottled" phenotypes represent distinct, monophyletic lineages throughout the northern Bahamas, or whether the phenotypes arise independently and convergently as adaptations to common environments.

Our findings of three distinct *Cerion* phenotypes on San Salvador are congruent with Gould's hypotheses. Phenotype 1 corresponds to *Cerion watlingense*, derived from a propagule originating on the Great Bahama Bank, has been present on San Salvador since at least 125,000 to 140,000 years before present, and was widespread throughout the island, occurring at Man Head Cay by 90,000 to 110,000 years before present. Phenotype 2 corresponds to *Cerion coloni*, and is believed to be derived from a propagule originating in the southern Bahamas. Based on our limited sampling of fossil specimens, earliest records are known from the southeastern corner of San Salvador between 80,000 and 90,000 years before present, although in a region of the island where this phenotype does not occur today. This phenotype appears to have expanded its range northward along the eastern coastline of San Salvador, where it likely replaced or hybridized with Phenotype 1. It co-occurred with phenotype 1 at Crab Cay between 70,000 and 80,000 years before present, but is the only phenotype present along the east coast in the modern fauna, including at Man Head Cay, which was inhabited exclusively by phenotype 1 between 90,000 to 110,000 years before present. Phenotype 2 continued to expand westward along the northern coast of the island, including to several of the offshore cays. Populations at the northern tip of North Point Peninsula and Green Cay are dominated by Phenotype 2, although vestiges of Phenotype 1 still remain at these localities. The presence of a third, morphologically distinct phenotype (Group 3) on San Salvador, corresponding to the "mottled" phenotype of the northern Bahamas, is presently known from a single population in the interior of the island, in agreement with Gould's prediction.

Analyses of shell morphology of living and fossil *Cerion* occurring on San Salvador may be interpreted in the context of several biogeographic scenarios, each with different evolutionary and systematic consequences. The single introduction hypothesis predicts that all *Cerion* living on San Salvador are part of a monophyletic clade, and all have a most recent common ancestor not shared with *Cerion* from other islands. As such, they may all be members of a single species, *Cerion watlingense*, or the phenotypes may have differentiated sufficiently to comprise either separate species or subspecies of *C. watlingense*. If the multiple introduction hypothesis is correct, *Cerion watlingense* as well as *Cerion inconspicuum* would be more closely related to species from the Great Bahama Bank, while *Cerion coloni* would be closer to species from the southern Bahamas. A molecular phylogeny with appropriate sampling should resolve between these two hypotheses and provide insights into the processes by which *Cerion* achieve and modify their patterns of extreme morphological diversity.

ACKNOWLEDGMENTS

We are grateful to Dr. Paul Hearty for his extensive fieldwork on San Salvador [supported by NSF award EAR 0106936 (Goodfriend, Gould, and Harasewych PI's) through a subcontract to Dr. Hearty], and for depositing the voucher material for his published study, including dated fossil specimens, in the collections of the National Museum of Natural History, Smithsonian Institution. We also thank Jessica Cundiff and Adam Baldinger of the Museum of Comparative Zoology for making available specimens in their care. We thank the reviewers, Dr. James Carew and Dr. Timothy Pearce, for their helpful comments and suggestions.

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How many micromollusks are there? A case study on species richness in Hawai‘i, with the description of a new species of *Murdochella* (Gastropoda: Epitoniidae)

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ABSTRACT

Four statistical metrics (Chao1, Chao2, ACE, and rarefaction) were used to estimate the total number of species of shelled micromollusks based on composition of nine benthic samples collected from the sublittoral zone off Wailea, Maui, Hawai‘i. There was a total of 250 species in the nine samples analyzed, and the estimated total number of species of shelled micromollusks in this area, based on the statistical metrics, was 317–375 species. *Murdochella tricingulata* new species is described and *Pelycidion habei* (Kay, 1979) is discussed.

Additional Keywords: Biodiversity, endemism, oceanic island, Indo-West Pacific

INTRODUCTION

This study estimates the species richness of shelled marine micromollusks off of Wailea, Hawai‘i. Micromollusks are defined as having shells smaller than 5 mm as adults (Geiger et al., 2007). There are only 1,300 named species of shelled marine mollusks in Hawai‘i (Severns, 2011), out of an estimated 37,000 species in the entire Indo-West Pacific (Contrafatto and Minelli, 2011). This difference is likely because of Hawaii‘s geographic isolation. Biodiversity in the Indo-West Pacific peaks around the islands of Southeast Asia, and decreases outward from there (Severns, 2011). Endemism of Hawaii‘s malacofauna is 21%, which is the world's highest. Severns has recorded 394 micromollusk species (Severns, 2011). Estimates for the total number of named mollusk species in the world reach 70,000–76,000, while estimates including undescribed species go as high as 200,000 (Rosenberg, 2014).

The shells in this study were part of a thanatocoenosis, or death assemblage; the composition of the samples is assumed to represent the composition of the surrounding areas. We used non-parametric calculations of species richness, which estimated the total number of species based on the relative abundance of rare and common species in the sample. An area from which a sample with a relatively high number of rare species was taken is estimated to have a high number of unfound species, because a high number of rare species indicates high species heterogeneity and low sampling intensity (Gotelli et al., 2007).

MATERIALS AND METHODS

Nine dredged samples from six locations off Wailea, Maui, Hawai‘i, at depths of 85–140 meters were collected and kindly made available by M. Severns (Figure 1, Table 1). The bulk sediment samples were sorted, and all specimens were deposited at the Santa Barbara Museum of Natural History (SBMNH: Table 1); some paratypes were also deposited in the Bernice P. Bishop Museum, Honolulu, Hawai‘i, USA (BPBM). Identifications were based primarily on Kay (1979), Okutani (2000), Severns (2011), and Okutani (2017).

A rarefaction curve was generated to display the average species accumulation of each sample and was extrapolated to an estimate for the species richness of the entire area using the iNEXT function from the R package (Chao et al., 2016; Hsieh et al., 2016). Species richness estimators used in this study were ACE (abundance-based coverage estimate) (Chazdon, 1998), as well as Chao1 and Chao2 (Chao, 1984). ACE and Chao1 combine all the samples, while Chao2 considers each sample in the study separately and constructs an estimate by comparing the samples. In the R package Vegan (Oksanen et al., 2017) the estimateR and specpool functions estimated Chao1, ACE, Chao2 and their standard errors, respectively.

Images of select shells were taken by scanning electron microscopy (SEM). Standard methods were applied for uncoated specimens (Geiger et al., 2007). Light microscope z-stack images were taken using a Zeiss Axioskop 2plus compound microscope (Zeiss, Oberkochern, Germany). A Cognisys (Traverse City, Michigan, USA)

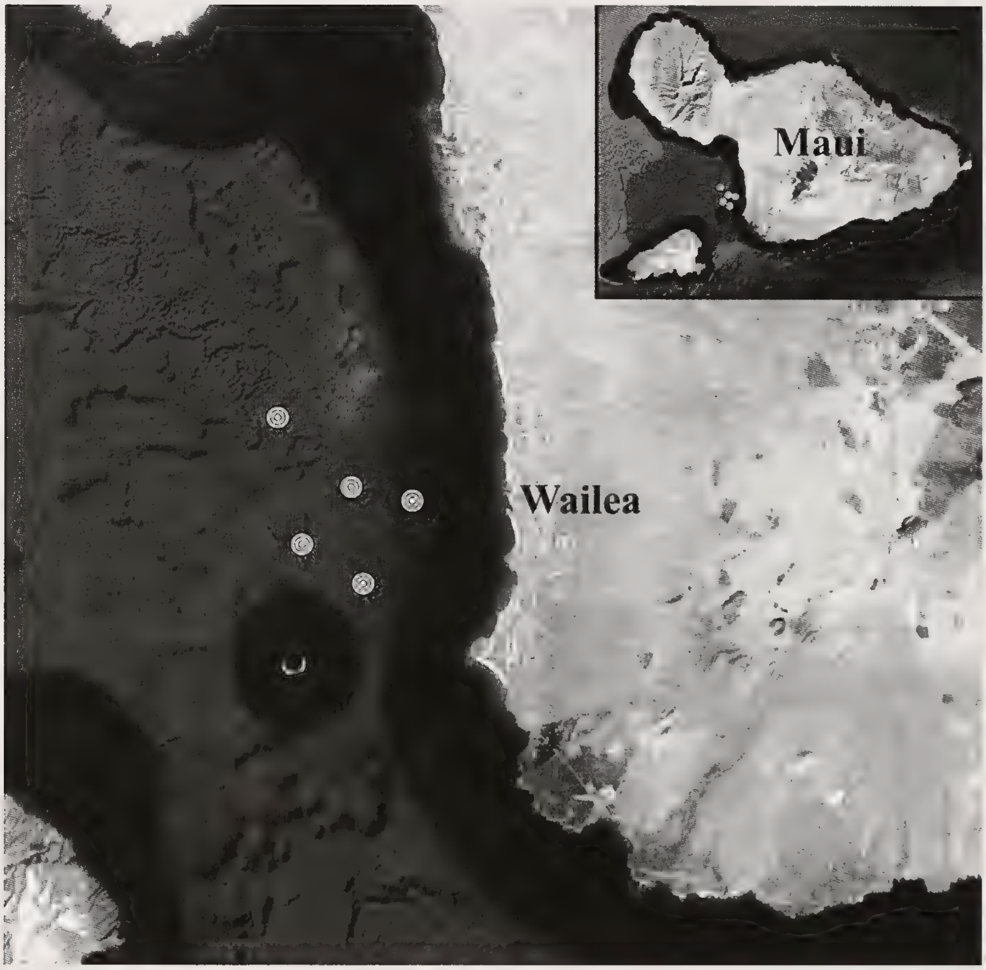


Figure 1. Map of Maui. Markers indicate locations of samples.

stepping motor connected to a Cognisys StackShot controller and programmed through ZereneStacker (Richland, Washington, USA) was coupled to the fine focus of the microscope with a custom adapter (Aben Machine Products, Canoga Park, California, USA). Step size was calculated based on depth of field of numerical aperture (2.4–152 μm). Images were acquired with a Canon 5DsR digital SLR camera; RAW files were processed with DxO Optics Pro (DxO Labs, Paris, France), and stacked with ZereneStacker using the Pmax algorithm. Further digital imaging was carried out in AffinityPhoto (Serif Ltd., Nottingham, UK).

RESULTS

Diversity Estimates: A total of 4,233 shells belonging to 250 discrete morphospecies were recovered from the samples. The estimates that used abundance data for the total number of species in the area encompassed a 95% confidence interval of 288–404 species (rarefaction, ACE, Chao1: Figure 2, Table 2). All three abundance estimates had overlapping 95% confidence intervals, which suggests that the different methods of estimating species richness were consistent, and thus more likely to be accurate. On the order of three-quarters of species of micromollusks in the overall sampled area were represented in the individual samples.

To explore the possible correlation between number of specimens and species in the sample and diversity estimates, ACE and Chao1 were applied to each of the nine samples (Table 3). Estimated species richness correlated positively with sample size, but that correlation was insignificant ($r^2 < 0.38$, $p >> 0.1$: Figure 3). Similarly, depth was found to have no effect on number of specimens found ($r^2 = 0.06$, $p >> 0.1$: Figure 4).

New Records: The Hawaiian malacofauna has recently been treated by Severns (2011), including 394 micromollusks. Although Hawai'i is among the best studied tropical areas and despite it being a rather low diversity region relative to its tropical latitude, the faunal inventory is far from complete. Exciting finds such as the highly distinctive *Severnsia strombeulima* Geiger, 2016 highlight the potential for new species discoveries, particularly in micromollusks (Geiger, 2016). Some additions to the Hawaiian malacofauna stemming from the present study are detailed below.

Table 1. Sample sites of this study. SBMNH: range of SBMNH registration numbers for the particular site. WP: Severns GPS waypoints.

Sample site	Location	Coordinates	Depth	SBMNH
WP267-424	2.5 mi W off Wailea	20.673° N, 156.482° W	101 m	424489–424607, 424609, 453258
WP502-506	3.6 mi W off Wailea	20.689° N, 156.500° W	85–88 m	265846–265857, 265859–265934
WP714-716	1.5 mi NE of Molokini	20.651° N 156.479° W	120–125 m	266363–266380, 452777–452856
WP384-394	1.5 mi W of Wailea	20.670° N 156.467° W	92 m	266251–266296
WP267-468	2.3 mi W of Wailea	20.673° N 156.482° W	88 m	266081–266181
WP267-496	2.3 mi W of Wailea	20.673° N 156.482° W	88–92 m	266008, 265984–266007, 266009–266046, 266048–266054
WP404-640	3.5 mi W of Wailea	20.660° N 156.494° W	139–141 m	266297–266333
WP404-713	3.5 mi W of Wailea	20.660° N 156.494° W	139–140 m	266334–266362, 424916, 424917, 453262
WP641-642	3.5 mi W of Wailea	20.673° N 156.482° W	124–132 m	454728–454731, 454733–454738, 454740–454750, 454752–454762, 454764, 454765, 454767–454815, 454817–454819, 454859–454915, 457572

SYSTEMATICS

Epitoniidae Berry, 1910 (1812)

Murdochella Finlay, 1926

Diagnosis: Shell high-spired, many fine, low, axial lamellae, crossed by few spiral cords. Base flattened. Protoconch bulbous, smooth.

Type Species: *Scala levifoliata* Murdoch and Suter, 1906, by original designation.

Remarks: The genus is currently known from New Zealand (*M. alacer* Finlay, 1926, *M. levifoliata*) Australia (*M. macrina* Iredale, 1936), Antarctica (*M. antarctica* Dell, 1990), South Africa (*M. crispata* Kilburn, 1985, *M. lobata* Kilburn, 1985), and Alaska (*M. turritelliformis* Brown, 2018).

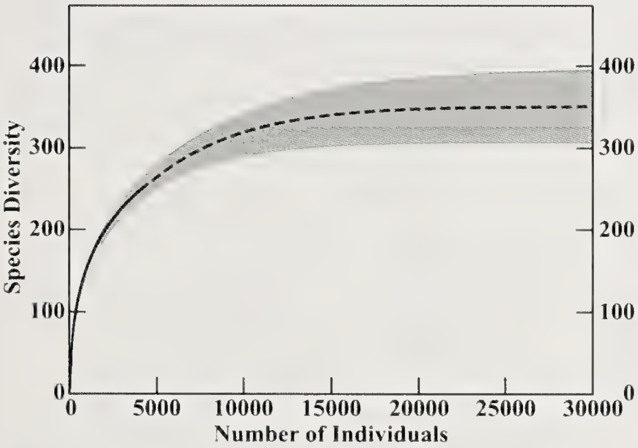


Figure 2. Interpolated (solid line) and extrapolated (dashed line) rarefaction curve of all samples. The shaded region is 95% confidence interval. The asymptote is at 350 species, 95% confidence interval covers 305–394 species.

Murdochella tricingulata new species
(Figures 5–14)

Description: Shell high-spired, holotype 2.7 mm (Figures 5–6), to 4.5 mm (Figure 9). Shell off-white to dark-tan. Protoconch bulbous, smooth. Up to ten teleoconch whorls. First whorl with more widely spaced, stronger axial cords, no spiral sculpture (Figures 6, 8). Second whorl with spacing and strength of axial lamellae as on remainder or teloconch, peripheral spiral cord distinct, adsutural spiral cord indistinct (Figures 5, 7, 9–11, 13, 14). Subsequent whorls with three spiral cords: strongest to just below periphery, second at two-thirds towards suture, last just above suture. Height of lamellae variable, some specimens with irregular distal horizontal extensions towards anterior (Figure 12). Base concave with pericolumellar cord. Aperture subquadratic.

Type Material: Holotype SBMNH 266361; Paratypes: SBMNH 266300 (two); Severns WP 404-640 (one) (all from type locality); SBMNH 452826 (nine); BPBM 284613 (two); Severns WP 714–716 (three), all from 2.78 km NE Molokini, Maui, Hawai'i, USA, 20°39.047′ N, 156°28.759′ W, 131–136 m; SBMNH 454728 (five); Severns WP 641–642 (two), all from off Wailea, Maui, Hawai'i, USA, 20°39.29′ N, 156°29.56′ W, 136–144 m.

Type Locality: Off Wailea, Maui, Hawai'i, USA, 20°29′38″ N, 156°29′38″ W, 152–154 m.

Etymology: Latin *tri-* = three, *-cingulata* referring to the spiral cords; noting the three spiral cords.

Remarks: *Murdochella tricingulata* is most similar to *M. levifoliata* with the very tight axial lamellae and strong, stepped spiral cords in the lower half of the whorl. The Hawaiian species is overall more slender, and has three distinct spiral cords, as compared to two in *M. levifoliata*. Both *M. antarctica* and *M. macrina* have more rounded whorls with less prominent spiral cords (Dell, 1990;

Table 2. Species richness estimates (95% confidence intervals) based on rarefaction curve, ACE, Chao1, and Chao2.

	All specimens combined			Separate samples
Species in samples	Rarefaction curve	ACE	Chao1	Chao2
250	350 (305–394)	343 (323–363)	346 (288–404)	425 (341–509)

Beechey, 2008; Engl, 2012). The South African (Transkei) *M. crispata* has clathrate sculpture with spiral cords well above the periphery of the whorls, while *M. lobata* has fewer but strong axial lamellae but no spiral cords (Kilburn, 1985). *Murchochella turritelliformis* Brown, 2018 from the Aleutian Islands, Alaska (Brown, 2018), has a proportionally wider shell and more numerous spiral cords.

The new species exhibits a moderate degree of variability in the sculpture, which appears gradual/clinal among the 19 specimens available. Accordingly, no further taxonomic separation is justified. The lamellae can be rather low (height less than half distance between lamellae) to rather high (height greater than distance between lamellae). The specimens with higher lamellae have trapped debris between the lamellae, which cannot be removed by sonication. The specimens with high lamellae tend to develop extremely fine and irregular distal horizontal extensions towards the anterior part of the shell. Those extensions are always pure white in color, contrasting with the off-white to dark-tan background color. The specimens with higher lamellae also appear slightly broader. As this difference in shape can be accounted for by the projecting sculpture, the shape of the main body of the shell is very similar in all specimens.

***Pelycidion habei* (Kay, 1979)**

(Figures 15–19)

Remarks: Severns (2011: pl. 36, figs 8–9) showed two putative species of *Pelycidion* from Hawai'i, the holotype of *P. habei* and *Pelycidion* sp. They differ nominally in the glassy (*P. habei*) vs. opaque white (*P.* sp.) shell color, the degree the whorls are inflated or incised at suture, respectively, and the apparent smooth (*P. habei*) vs. finely clathrate (*P.* sp.) shell sculpture. The illustrations in Kay (1979: 27, i–j) reveal fine clathrate sculpture, which suggests that the apparent differences in the images in Severns (2011) are either due to specimen condition or photographic technique, but that they are not systematically relevant. The three specimens illustrated by SEM here (Figures 15–17) show quite a bit of variability with respect to degree of incision of the whorls are intermediate between the specimens figured by Severns (2011). It suggests that there is only a single species of *Pelycidion* in Hawai'i.

DISCUSSION OF DIVERSITY

All diversity measures are estimates, and one needs to be aware of their inherent limitations. While an estimator based on incidence data such as Chao2 can be useful because it takes distribution heterogeneity into account, in this study estimators using abundance data such as ACE and Chao1 were more useful because of the small number of samples analyzed and the fact that the samples in this study were of different sizes. The Chao2 estimate is known to stabilize above 30 samples (Gotelli, 2011), while this study was based on only nine samples. Regardless, even though the Chao2 estimate is much larger than the others, the Chao2 confidence interval includes the other estimates.

All models used in this study are minimum richness estimators (O'Hara, 2005). Richness estimates of a particular area have been found to be correlated with sample size, suggesting underestimation due to low sample size (Żmihorski et al., 2013). Here, this correlation was positive but insignificant ($r^2 < 0.38$, $p >> 0.1$, Figure 3). Because of the correlation between richness estimate and sample size, estimates are ideally compared between samples of equal numbers of individuals from different locations to compare species richness (Chao, 2016). The samples in this study had unequal numbers of specimens (66–650), though the raw sediment samples had approximately the

Table 3. ACE and Chao1 species richness estimates and standard error for each sample. WP: Severns GPS waypoints.

Sample Site	Number of specimens in sample	Number of species in sample	ACE estimate	ACE 95% confidence interval	Chao1 estimate	Chao1 95% confidence interval
WP267-624	196	77	85	75–95	81	73–89
WP502-506	102	56	123	109–137	110	54–166
WP714-716	432	64	87	77–97	90	60–120
WP384-394	195	37	72	62–82	61	33–89
WP267-468	617	84	129	117–141	131	87–175
WP404-640	66	28	40	36–46	39	23–55
WP404-713	73	30	51	47–55	43	25–61
WP641-642	650	96	115	105–125	121	95–47
WP267-496	294	57	126	112–140	163	49–277

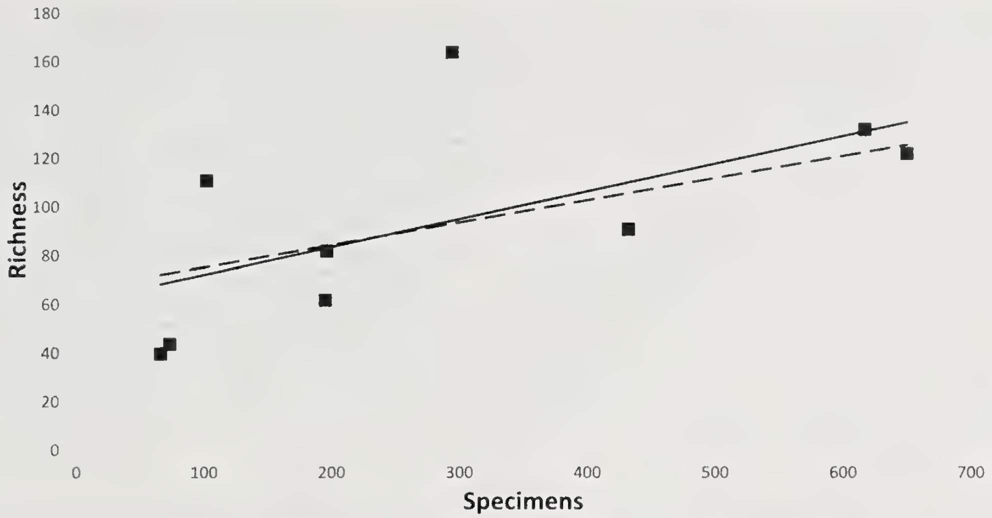


Figure 3. Species richness estimates of samples over number of specimens in sample. Statistically insignificant positive correlation ($r^2 < 0.38$, $p >> 0.1$). Diamonds: ACE estimate. Squares: Chao1 estimate. Solid line: Chao1 regression. Dashed line: ACE regression.

same volume and were collected within kilometers of each other. Depth (88–141 m) as a factor explaining those differences could be ruled out ($r^2 = 0.06$, $p >> 0.1$, Figure 4). The observed differences appear to reflect true environmental heterogeneity.

The estimated number of species for each sampling site was 62–88% lower than that for the whole area, which shows high distribution heterogeneity. The sum of sample species richness is much greater than the total species richness due to many common species among samples. Estimating species richness is known to be more difficult for highly diverse locations (Chao, 2016), such as Maui. Comparison of the data presented here is challenging, because of the absence of comparable studies at other localities. An environmental impact report (Russo et al., 2018) from a waste water treatment outfall site at 33 m off Oahu listed 165 species of mollusks of all sizes from approximately 4,500 individuals. Samples were collected by SCUBA diver and small cores, hence, included the full size-range of organisms. Diversity estimators calculated from the raw data were highly consistent (this study). Chao1 estimates a species richness of 193±12SE, 95% confidence interval 169–217, and ACE estimated 197± 7SE, 95% confidence interval 183–211 (this study). The different size compositions of the two studies make direct comparison difficult. Based on the species list, we estimate that less than half the species in Russo et al. (2018) are of comparable small size as in our samples from Maui; that proportion is conservative and in rough agreement with other studies (Aravind et al., 2008; Middlefart et al., 2016: see also below). Accordingly, the contrast of of species richness of micromollusks alone is even more remarkable: Oahu ~80 found, ~100 estimated; Maui 250 found, ~350 estimated. These differences suggest

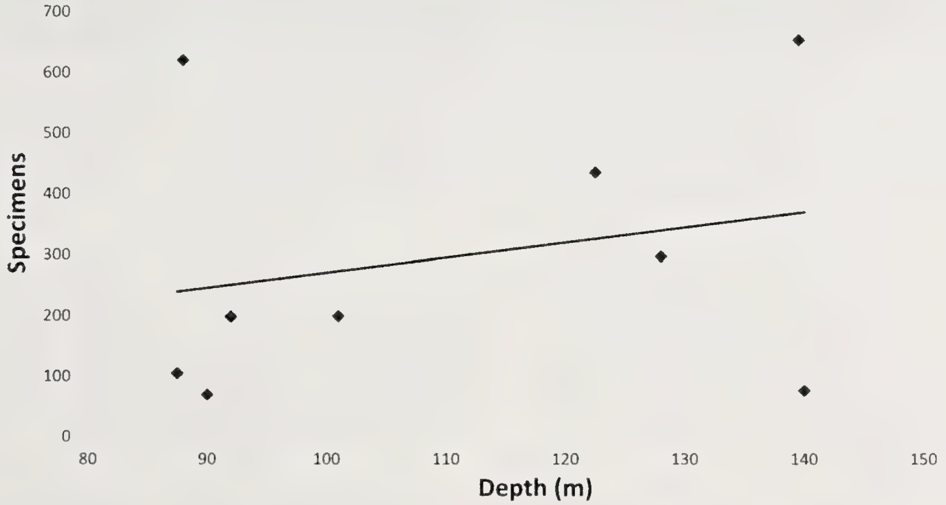
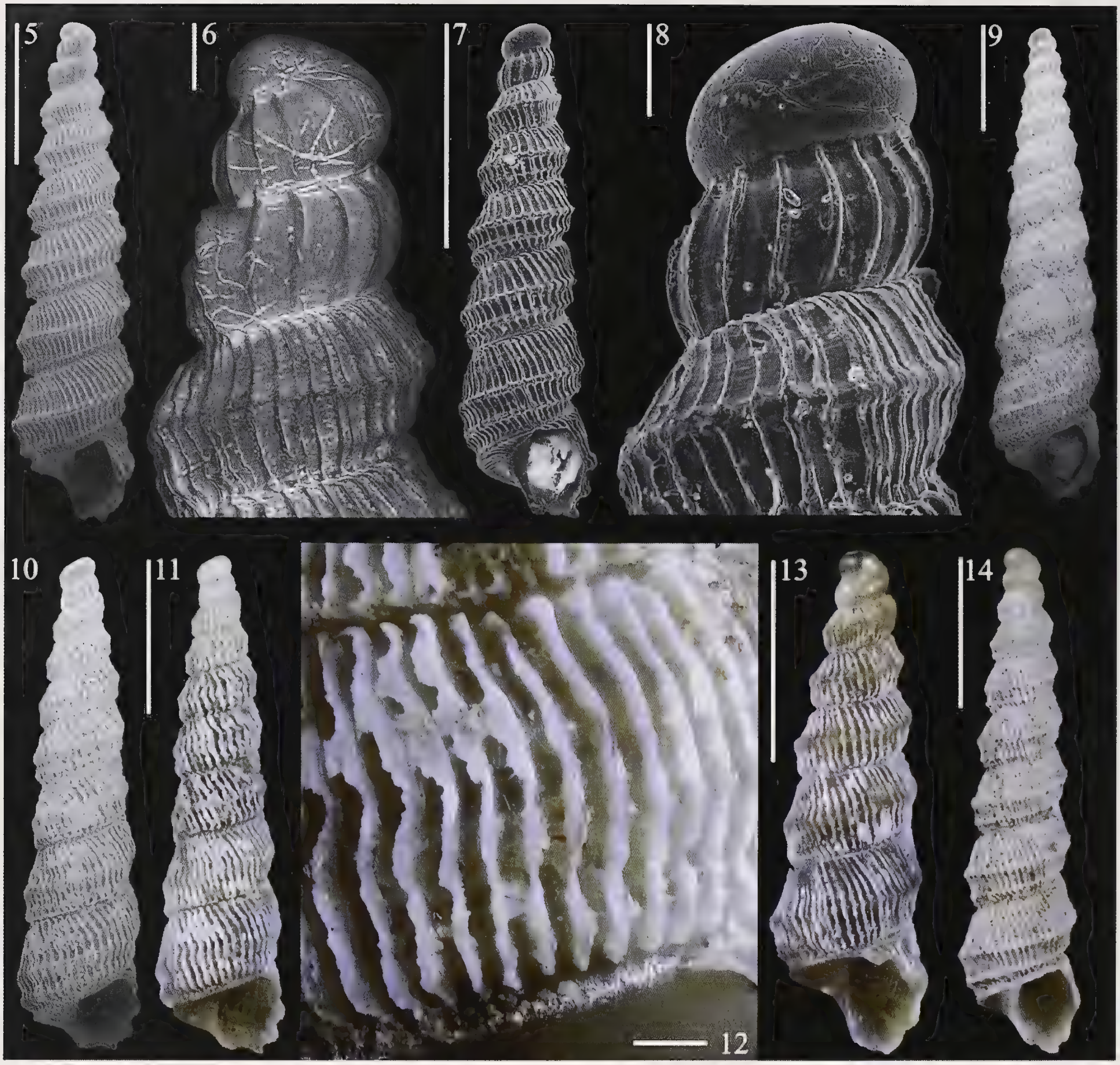


Figure 4. Linear regression of mean depth vs number of specimens found ($r^2 = 0.06$, $p >> 0.1$).

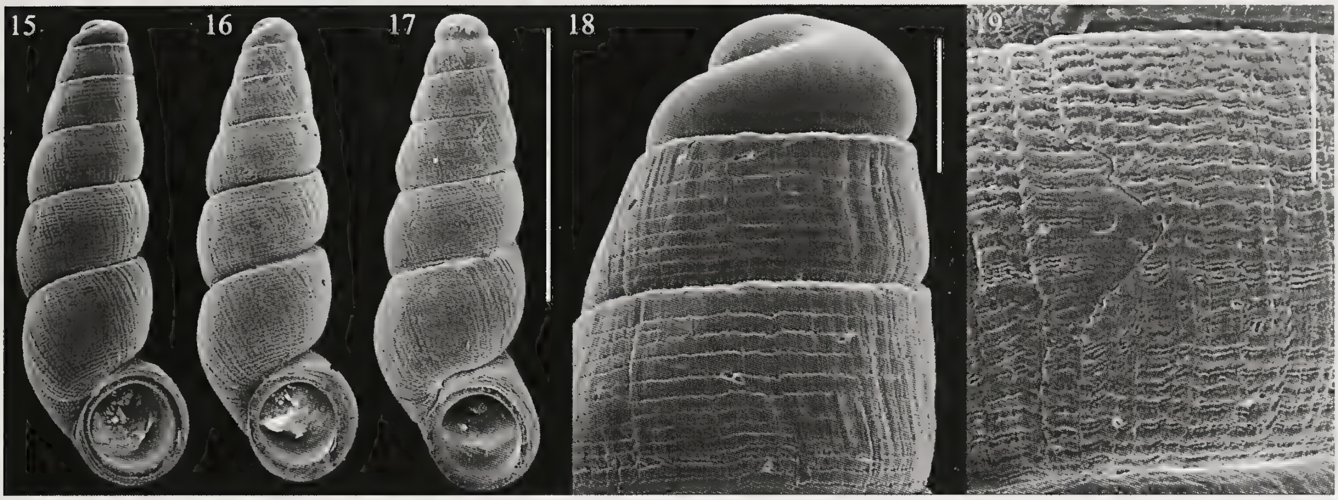


Figures 5–14. *Murdochella tricingulata* new species. **5–6.** Holotype SBMNH 266361. **5.** Shell. **6.** Detail of protoconch and early teloconch. **7–12.** Paratypes SBMNH 454728. **7.** Shell of small specimen with low sculpture. **8.** Protoconch of 7. **9.** Largest specimen known (4.2 mm). **10.** SEM image. **11.** Photograph of 10. **12.** Enlargement of lamellae with irregular distal horizontal extensions towards anterior. **13–14.** Paratype SBMNH 452826. **13.** Dark-colored specimen with strong axial lamellae. **14.** Lighter colored specimen with lower axial lamellae. Scale bars shells = 1 mm. Scale bars details = 100 μm.

environmental heterogeneity and that the sites sampled in this study are more biodiverse than the site sampled in Oahu. Differences in depth may account for the difference in diversity, as the Oahu samples were taken at 33 m and the Maui samples were taken from 85–141 m. Anthropogenic effects were discounted by Russo et al. (2018) as similar species composition and numbers of species were found in control sites.

Bouchet (2002) recorded 864 species smaller than 4.1 mm off Koumac, New Caledonia. The higher number of species found in New Caledonia is probably due to the fact that the sampling area was larger (295 km^2 vs 18 km^2) with greater habitat diversity, and the fact that New Caledonia is less isolated than Maui. The absolute latitudes of both areas are similar (Koumac 20.5°S, Maui: 20.7°N).

Many micromollusks are missed in habitat assessments because they are smaller than the holes in the mesh used to sort shells out of a sand sample. Additionally, some micromollusks require the use of a scanning electron



Figures 15–19. *Pelycidion habei* (Kay, 1979). SBMNH 454742. **15–17.** Shells. **18.** Protoconch of 15. **19.** Enlargement of body sculpture from 15. Scale bar shells = 1 mm. Scale bars details = 100 μm.

microscope to observe distinguishing characteristics (Middlefart et al., 2016). Despite relatively few studies on micromollusks, they appear to be very common. Of the 269 recorded gastropod species of the Western Ghats, 40% were micromollusks (Aravind et al. 2008), and 33% of recovered species of mollusks from a study in New Caledonia were micromollusks (Middlefart et al., 2016).

The present study shows that even a rather well-studied area such as Hawai'i still harbors a significant percentage of undescribed species. Given Hawaii's high rate of marine endemism, it highlights the need for strong conservation measures to protect the yet to be recognized biodiversity.

ACKNOWLEDGMENTS

BC was supported in part by a generous donation from Laura Francis, Education and Outreach coordinator at NOAA Channel Islands National Marine Sanctuary, and the Sea Forward Fund. Jenna Rolle (SBMNH) kindly provided insights into diversity estimates. Marta deMaintenon and Cynthia Hunter helped with constructive comments to improve the manuscript and provided reports on samples from Oahu. José H. Leal provided editorial guidance. Regina Kawamoto (BPBM) provided the registration number for one paratype lot.

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Catalog of the taxonomic updates of northeastern Pacific Late Cretaceous shallow-marine bivalves and gastropods named from 1874 to 1966

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ABSTRACT

Published taxonomic updates of northeastern Pacific (southern Alaska to Baja California, Mexico) shallow-marine Late Cretaceous bivalves and gastropods named between 1874 and 1960, are catalogued for the first time. Of the 143 species (including "varieties,") 68 are bivalves and 75 are gastropods. These species were named prior to the usage of more effective paleontologic procedures initiated by Willis P. Popenoe in 1957. The junior homonym *Inoceramus pacificus* Anderson and Hanna, 1935 is renamed as ***Inoceramus georgeedavisi* new name Squires**.

Additional Keywords: Vancouver Island, California, *Inoceramus*

INTRODUCTION

The purpose of this paper is to catalog, for the first time, the taxonomic name changes of shallow-marine species of Late Cretaceous bivalves and gastropods, which were named by early molluscan paleontologists (between 1874 and 1966) in the region extending from southern Alaska to northern Baja California, Mexico. This region corresponds to the "Northeast Pacific Subprovince (NEP)" of Kauffman (1973: fig. 1). Squires (2018) provided a discussion of the geologic setting and paleoclimate conditions of this paleo-biotic subprovince.

Stemming from his field work in California in the 1860s, William M. Gabb was the first paleontologist to collect and name Cretaceous shallow-marine mollusks from the NEP region. His monumental contributions were catalogued by Groves and Squires (2018). Subsequent NEP paleontologists during the late 1880s to the late 1950s were, in alphabetical order, Frank M. Anderson, Ralph Arnold, James G. Cooper, Donald H. Dailey, E. B. Hall and Arthur W. Ambrose, Roy D. McLellan, Charles W. Merriam, Michael A. Murphy, Earl L. Packard, Willis P. Popenoe, Peter U. Rodda, Clarence A. Waring, Charles A. White, and Joseph F. Whiteaves. Although Anderson's Late Cretaceous monograph was published in 1958, his research was actually done in the 1940s. He died in 1945, and the volume was published posthumously 13 years after his death.

Starting in the late 1950s, there was a fundamental transformation in how NEP Late Cretaceous bivalves and gastropods were studied. Popenoe (1957: 430) implemented a method that relied mainly on his own large and well-curated collection of fossils; a collection now residing at the Natural History Museum of Los Angeles County Museum of Natural History. "His method of careful collecting, the recording of precise geographic locality and stratigraphic position, and accurate identifications has resulted in so much more orderly knowledge of the Late Cretaceous molluscan faunas that it now seems impossible that these faunas could have been in such confusing disarray as when he began his studies" (Saul et al., 1989: 117). Popenoe selected a representative number of specimens from each major formation in which they occur and then carefully cleaned the hinges of bivalves and the apertures of gastropods. Careful cleaning of these critically important morphologic areas allowed for a much better basis for the systematic placement of taxa. He used detailed biostratigraphy to more accurately show lineages of species and their evolutionary trends. Initially, he relied only on ammonite data for biostratigraphic control but later (Popenoe et al., 1960) added inoceramid-bivalve zones. Saul, who was mentored by Popenoe, perfected the method begun by him and greatly helped to introduce it to current NEP molluscan paleontologists. The method relies on new biologic and stratigraphic data in order to keep everything updated. In the last 20 years or so, there have been many updated systematic and biostratigraphic studies of NEP

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bivalves and gastropods, and these studies are the basis of this present paper. It is relevant to mention that species named after the onset of Popenoe's transformation are much less prone to being changed, than those named prior to it. There are, nevertheless, many other bivalves and gastropods, named prior to 1960, which are in need re-investigation. More name updates will be made in the future.

MATERIALS AND METHODS

The information was largely extracted from the literature. Study area papers concerning Late Cretaceous bivalves and gastropods but without any taxonomic updates were not included. Cold-seep taxa are not included. The authors are listed in alphabetical order. Bivalves are listed before gastropods, but a few of the listed species concern only gastropods. The species names, which are also in alphabetical order, include the parenthesized genus name in which the author originally placed the species, along with its date, page, figure number(s), and holotype number, unless otherwise noted. The museum type-specimens numbers were mostly gleaned from the cited literature. The CASG numbers were derived from its in-house records. The USNM numbers were derived from the USNM online database [natural history.si.edu/rc]. All of the "original" information is followed by the updated name (in bold) and the currently known geologic age, geographic range (listed from north to south), and reference(s) concerning the updates of the species. For the geologic age, standard (European) geologic stages of the Late Cretaceous are used, with the sequence from older to younger being Cenomanian, Turonian, Coniacian, Santonian, Campanian, and Maastrichtian.

Abbreviations used in conjunction with type-specimen numbers are: CASG: California Academy of Sciences, San Francisco; GSC: Geological Survey of Canada, Ottawa, Ontario; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Department, Los Angeles; LSJU, Leland Stanford Junior University, Stanford, California [collection now at CASG]; UCMP: University of California, Berkeley, Museum of Paleontology,; UO, University of Oregon, Eugene, Oregon; USNM, National Museum of Natural History, Smithsonian Institution. Abbreviations used for geographic areas are: BX (Baja California, Mexico), CA (California), QC (Queen Charlotte Islands, British Columbia, VI (Vancouver Island area, British Columbia; including adjacent islands along eastern coast), WA (Sucia Island, Washington).

ANDERSON

Bivalves

anaana (*Pholadomya*) Anderson, 1902: 73, pl. 7, fig. 151; plastohypotypes UCMP 30251, 30252. ***Liopistha anaana*** **(Anderson, 1902)**, Turonian, CA. Popenoe (1937: 384), Anderson (1958: 119).

banosensis (*Glycymeris*) Anderson, 1958: 98–99, pl. 73, figs. 1–3; CASG 28310.01. ***Glycymerita banosensis*** **(Anderson, 1958)**, late Campanian to latest Maastrichtian, CA, BX. Squires (2010: 908).

bowersiana (*Trigonia*) Anderson, 1958: 116, pl. 26, fig. 8; CASG 252.01. ***Musagonia bowersiana*** **(Anderson, 1958)**, Turonian, CA. Cooper (2015: 27); no age update found.

branneri (*Trigonia*) Anderson, 1958: 112, pl. 17, fig. 5; UO 26859. ***Louella fitchi*** **(Packard, 1921)**. Cenomanian/Turonian boundary, OR, CA. Saul (1978: 53), Cooper and Leanza (2017: 330).

buttensis ("*Trigonocallista*") Anderson, 1958: 140, pl. 59, figs. 1, 1a; CASG 27838.15. ***Calva (Egelicalva) buttensis*** **(Anderson, 1958)**, early Campanian, AK, VI, CA. Saul and Popenoe (1992: 36).

churchi (*Trigonia*) Anderson, 1958: 115, pl. 17, figs. 6, 7; CASG 1788.01. ***Notoscabrotrigona evansana*** **(Meek, 1858)**, early to late Campanian, VI, CA. Jones (1960: 436), Cooper (2015: 25).

colusaensis (*Trigonia*) Anderson, 1958: 110, pl. 1, fig. 6; lectotype UCMP 12171. ***Yaadia leana*** **Gabb, 1876**, early Turonian to Coniacian, OR, CA. Saul (1978: 33).

contracostae (*Inoceramus*) Anderson (1958: 103, pl. 18, figs. 3, 4), CASG 29084.01, two forms: a a Coniacian species of ***Sphenoceramus?*** and a Coniacian? to Santonian species of ***Mytiloides?***, CA. Kauffman (1977: 189).

duplicostatus (*Inoceramus*) Anderson, 1958: 100, pl. 17, figs. 3, 4; CASG 61724.02. ***Mytiloides duplicostatus*** **(Anderson, 1958)**, Turonian, CA. Kauffman (1977: 189).

eolobatus (*Inoceramus*) Anderson, 1958: 99, pl. 18, fig. 13; CASG 1291.01. ***Inoceramus crippsi?*** **Mantell, 1822**, early to mid Cenomanian, CA. Kauffman (1977: 188).

gabbiana (*Mactra*) Anderson, 1902: 74, pl. 7, fig. 156; CASG 1. ***Cymbophora gabbiana*** **(Anderson, 1902)**, Turonian, CA. Saul (1974: 1084).

glennensis (*Inoceramus*) Anderson, 1958: 99, pl. 17, figs. 1, 2; CASG 61629.01 ***Mytiloides*** sp., most likely *M. opalensis elongata* (Seitz, 1934), early Turonian, CA. (Kauffman, 1977: 188).

hemphilli (*Trigonia*) Anderson, 1958: 115, pl. 52, figs. 9, 9a, 9b. CASG 994. ***Popenoella hemphilli*** (Anderson, 1958), early Maastrichtian, CA. Saul (1978: 50), Cooper and Leanza (2017: 329).

jacksonensis (*Inoceramus*) Anderson, 1958: 100, pl. 43, figs. 1, 2; not in CASG database. ***Inoceramus crippsi?*** **Mantell, 1822**, early to mid Cenomanian, OR. Kauffman (1977: 188).

klamathensis (*Inoceramus*) Anderson, 1958: 104, pl. 18, figs. 1, 2; syntypes CASG 61914.01, 61914.02. ***Sphenoceramus lingua?*** **(Goldfuss, 1836)**, Coniacian? to Campanian, CA. Kauffman (1977: 186).

klamathonia (*Trigonia*) Anderson, 1958: 112, pl. 30, fig. 4., CASG 61873. ***Notoscabrotrigona klamathonia*** **(Anderson, 1958)**, Turonian. Cooper (2015: 25), CA.

meekianus (*Inoceramus*) Anderson, 1958: 101, pl. 22, figs. 5, 6; CASG 228.01. ***Mytiloides meekianus*** **(Anderson, 1958)**, Coniacian?, WA. Kauffman (1977: 180).

pentzana (*Glycymeris*) Anderson, 1958: 98, pl. 74, figs. 2, 2a; CASG 61874.01. ***Glycymeris veatchii*** **(Gabb,**

1864), Turonian to late Campanian; VI, CA, BX. Squires (2010: 902).

pacifica (*Opisoma*) Anderson, 1958: 122, pl. 26, figs. 5–6; CASG 29118.03. ***Opis* (*Hesperopis*) *triangulata* (Cooper, 1894)**, late Campanian through early late Maastrichtian, CA, BX. Squires and Saul (2009: 1329).

pacificus (*Inoceramus*) Anderson and Hanna (1935: 29, pl. 10, fig. 4); CASG 1430.01, early Maastrichtian, BX (Miller and Abbott, 1989: 63, fig. 1). Anderson and Hanna's name is a junior homonym of *Inoceramus pacificus* Woods (1917: 28, pl. 14, figs. 1, 2) from Upper Cretaceous (lower Santonian) strata on South Island of New Zealand (Crampton et. al, 2000: 322, fig. 12). Anderson and Hanna's junior homonym is renamed herein as ***Inoceramus georgeedavisi* new species Squires**, in honor of the late George Edward Davis, geologist and molluscan paleontologist.

pacificus (*Pectunculus*) Anderson, 1902: 74, pl. 7, fig. 159; voucher GASG 70504. ***Glycymeris pacifica* (Anderson, 1902)**, late Cenomanian to Turonian, OR, CA, BX. Squires (2010: 898).

peninsularis (*Corbis*) Anderson and Hanna, 1935: 31, pl. 10, fig. 1; UCMP 36119. ***Calva* (*Calva*) *peninsularis* (Anderson and Hanna, 1935)**, latest Campanian and early Maastrichtian, CA, BX. Saul and Popenoe (1992: 17).

roguensis (*Avicula*) Anderson, 1958: 106, pl. 38, fig. 7; CASG 445.17. ***Pteria pellucida* (Gabb, 1864)**, Turonian to Santonian, OR, CA. Squires (2014: 221).

rosarioensis (*Opis*) Anderson and Hanna, 1935: 31, pl. 10, figs. 2, 3; UCMP 36120. ***Opis* (*Hesperopis*) *rosarioensis* (Anderson and Hanna, 1935)**, early middle to middle late Campanian, CA, BX. Squires and Saul (2009: 1322).

shastaensis (*Glycymeris*) Anderson, 1958: 97, pl. 19, figs. 8–10; CASG 27830.01. ***Glycymeris veatchii* (Gabb, 1864)**, Turonian to late Campanian, VI, CA, BX. Squires (2010: 902).

taffi, ("*Trigonocallista*") Anderson, 1958: 139; CASG 27836.01. ***Calva* (*Egelicalva*) *taffi* (Anderson, 1958)**, Coniacian to Santonian, CA. Saul and Popenoe (1992: 34).

wheelerensis (*Trigonia*) Anderson, 1958: 116, (unfig.); CASG 10632. ***Yaadia leana* (Gabb, 1877)**, Coniacian to early Turonian, OR, CA. Saul (1978: 33).

Gastropods

argonautica (*Cypraea*) Anderson, 1958:177, pl. 21, figs. 4, 4a; CASG 61856.05. ***Protocypraea argonautica* (Anderson, 1958)**, Turonian, OR, CA. Lorenz (2017: 205).

bellavistana (*Acteonina*) Anderson, 1958: 157, pl. 29, fig. 2; CASG 1293.01. ***Paosia californica* (Gabb, 1864)**, late Cenomanian to Turonian, VI, OR, CA, BX. Squires and Saul (2004a: 492).

berryessensis (*Acteonina*) Anderson, 1958: 157, pl. 29, fig. 3; CASG 3192.01. ***Paosia californica* (Gabb, 1864)**, late Cenomanian to Turonian, VI, OR, CA, BX. Squires and Saul (2004a: 492).

berryessae (*Cypraea*) Anderson, 1958: 176, pl. 63, figs. 2, 2a, 2b; CASG 31918.02. ***Protocypraea berryesae* (Anderson, 1958)**, Turonian, CA. Lorenz (2017: 205).

biconica (*Gosavia*) Anderson, 1958: 175, pl. 75, figs. 3, 3a; CASG 61935.01. ***Konistra biconica* (Anderson, 1958)**, Turonian, CA. Saul and Popenoe (1993: 381).

colusaensis (*Acteonina*) Anderson, 1958: 158, pl. 21, fig. 14; CASG 1291.05. ***Paosia colusaensis* (Anderson, 1958)**, late Albian to early Cenomanian, CA. Squires and Saul (2004a: 491).

condoniana (*Anchura*) Anderson, 1902: 76, pl. 8, fig. 179; CASG 445.30. ***Anchura* (*Helicaulax*) *condoniana* Anderson, 1902**, Turonian, OR, CA. Saul and Popenoe (1993: 354).

crossi (*Volutoderma*) Anderson, 1958: 174, pl. 16, figs. 3, 3a; CASG 61934.02. ***Cydas crossi* (Anderson, 1958)**, Turonian, CA. Saul and Popenoe (1993: 362).

frazierensis Acteonella Anderson, 1958: 161, pl. 29, figs. 7, 7a; CASG 28103. ***Trochactaeon* (*Trochactaeon*) *frazierensis* (Anderson, 1958)**, Turonian, CA. Sohl and Kollmann (1985: 79).

garzana (*Phasianella*) Anderson, 1958: 162, pl. 73, fig. 5; CASG 28311.02. ***Tylostoma? garzana* (Anderson, 1958)**, late early to early late Maastrichtian, CA. Squires and Saul (2004b: 27).

gualalaensis (*Cypraea*) Anderson, 1958: 176, pl. 62, figs. 8, 8a; CASG 61918.01. ***Protocypraea gualalaensis* (Anderson, 1958)**, early Maastrichtian, CA. Lorenz (2017: 205).

jacksonensis Volutoderma Anderson, 1958: 174, pl. 21, fig. 1; CASG 445.16. ***Drilluta jacksonensis* (Anderson, 1958)**, Turonian, OR, CA. Saul and Popenoe (1993: 368).

nortonensis Bullina Anderson, 1958: 178, pl. 21, figs. 13, 13a; CASG 61850.03. ***Ellipsoscapha nortonensis* (Anderson, 1958)**, Campanian, CA. Stecheson (2004: 102).

packardi Acteonella Anderson, 1958: 160, pl. 29, figs. 4, 4a, 4b; not in CASG database. ***Trochactaeon* (*Trochactaeon*) *packardi* (Anderson, 1958)**, Turonian. Sohl and Kollmann (1985: 83).

robertiana (*Nerinea*) Anderson, 1958: 155, pl. 66, fig. 3; UCMP 33954. ***Turritella chaneyi* Merriam, 1941**, early Maastrichtian, CA. Saul (1983: 81), Saul and Squires (1998: 465).

roguensis (*Acteonina*) Anderson, 1958: 158, pl. 30, figs. 5, 5a; CAS 61906.01. ***Paosia californica* (Gabb, 1864)**, late Cenomanian to Turonian, VI, OR, CA, BX. Squires and Saul (2004a: 492).

rustica (*Acteonella*) Anderson, 1958: 161, pl. 29, fig 5; CASG 33721.01. ***Trochactaeon* (*Trochactaeon*) *frazierensis* (Anderson, 1958)**, Turonian, CA. (Sohl and Kollmann, 1985: 79, 85).

stewarti (*Nerinea*) Anderson, 1958: 155, pl. 30, figs. 2, 3; CASG 61842.02. A cold-seep epitoniid, ?middle Turonian, CA. Saul and Squires (1998: 465).

ursula (*Acteonina*) Anderson, 1958: 158, pl. 63, fig. 4; CASG 31210.01. ***Paosia ursula* (Anderson, 1958)**, Coniacian, CA. Squires and Saul (2004a: 494).

ursulagorda (*Acteonina*) Anderson, 1958: 159, pl. 63, fig. 5; CASG 31210.02. ***Paosia ursula* (Anderson, 1958)**, Coniacian, CA. Squires and Saul (2004a: 494).

siskiyouensis (*Gyrodes*) Anderson, 1902: 76, pl. 8, figs. 167, 168; CASG 41. ***Natica conradiana* (Gabb, 1864)**, Turonian, OR, CA. Popenoe et al. (1987: 92).

yrekensis (*Acteonina*) Anderson, 1958: 157, pl. 29, fig. 2; CASG 61847.01. ***Paosia californica* (Gabb, 1864)**, late Cenomanian to Turonian, VI, OR, CA, BX. Squires and Saul (2004a: 492).

ARNOLD

Bivalve

stantoni (*Mactra*) Arnold, 1908: 357, pl. 31, fig. 3; USNM 31001. ***Cymbophora stantoni* (Arnold, 1908)**, Campanian, CA. Saul (1974: 1076).

Gastropod

pescaderoensis (*Turritella*) Arnold, 1908: 358, pl. 31, fig. 7; CASG 69777. ***Turritella chicoensis pescaderoensis* Arnold,** 1908, late Campanian, CA. Saul (1983: 64).

COOPER

Bivalves

triangulata (*Corbula*) Cooper, 1894: 49, pl. 2 [not 4], fig. 42; lectotype CASG 624. ***Opis* (*Hesperopis*) *triangulata* (Cooper, 1894),** late Campanian to early Maastrichtian, CA, BX. Squires and Saul (2009: 1329).

bowersiana (*Cucullaea*) Cooper, 1894:48, pl. 5, figs. 61, 62; CASG 66028.0. ***Calva* (*Egelicalva*) *bowersiana* (Cooper, 1894)**, late early through late Campanian, VI, CA. Saul and Popenoe (1992: 39).

Gastropods

capuloides (*Siphonaria*) Cooper, 1894: 47, pl. 2, figs. 38, 39; CASG 612. ***Vasculum? capuloides* (Cooper, 1894)**, late Campanian to possibly early Maastrichtian, CA. Coan (1981: 160).

cretaceum (*Sistrum* (*Ricinula*?)) Cooper, 1896: 330, pl. 47, figs. 1, 2; neotype LACMIP 9997. ***Perissitys cretacea* (Cooper, 1896)**, Coniacian, CA. Popenoe and Saul (1987: 12).

fairbanksi (*Cerithium*) Cooper, 1894: 44, pl. 1, fig. 12; not in GASG database. Possibly ***Anchura***, late Campanian to possibly early Maastrichtian, CA. Coan (1981: 163).

kempiana (*Calliostoma*) Cooper, 1894: 46 [pl. 2 [not 3], figs. 33, 34; CASG 610. ***Calliostoma kempianum* Cooper, 1894**, late Campanian to possibly early Maastrichtian, CA. Coan (1981: 165).

normalis (*Tornatella*) Cooper, 1894: 46, pl. 2 [not 3], figs. 36, 37; CASG 625. ***Eoacteon normalis* (Cooper, 1894)**, late Campanian to possibly early Maastrichtian, CA. Coan (1981: 168).

DAILEY and POPENOE

Bivalves

apletos (*Glycymeris*) Daily and Popenoe, 1966: 8, pl. 1, figs. 1, 5, 6; LACMIP 8891. ***Glycymerita veatchii* (Gabb, 1864)**, middle Turonian to late Campanian, VI, CA. Squires (2010: 902).

pozo (*Corbula*) Daily and Popenoe, 1966:19, pl. 5, figs. 6–10; LACMIP 8916. ***Panzacorbula pozo* (Daily and Popenoe, 1966)**, early Campanian to early late Maastrichtian, CA. Squires and Saul (2004c: 117).

Gastropod

ainiktos (*Pseudoglauconia*?) Daily and Popenoe, 1966: 21, pl. 6, figs. 3, 5, 6; LACMIP 8291. ***Bullamirifica ainiktos* (Dailey and Popenoe, 1966)**, middle through late Campanian, CA, BX. Squires and Saul (2005: 141).

HALL and AMBROSE

Gastropod

branneri (*Cerithium*) Hall and Ambrose, 1916: 70, unfigured; CASG 69804. **Cerithium? teslaensis** Hanna, 1924:162, Late Cretaceous, CA. See Wiedey (1929: 25, pl. 1, fig. 6).

McLELLAN

Bivalves

suciensis (*Cucullaea*) McLellan, 1927: 132, pl. 17, figs. 4–6; UWBM 15010, ***Glycymerita veatchii* (Gabb, 1984)**, middle Turonian to late Campanian, VI, WA, CA, BX. Squires (2010: 902).

suciensis (*Glycymeris*) McLellan, 1927: 131, pl. 17, figs. 7, 8; UWBM 15008, ***Glycymerita veatchii* (Gabb, 1864)**, middle Turonian to late Campanian, VI, WA, CA, BX. Squires (2010: 902).

MERRIAM

Gastropod

tolenasensis (*Turritella*) Merriam, 1941: 62, pl. 1, figs. 14, 15; UCMP 15328. ***Turritella hearni* Merriam, 1941**, Turonian and probably early Coniacian, CA. Squires and Saul (2006a: 54).

MURPHY AND RODDA

Gastropods

allisoni (*Gyrodes*) Murphy and Rodda, 1960:842, pl. 101, figs. 18–20; LACMIP 9828. ***Natica? allisoni* (Murphy and Rodda, 1960)**, Cenomanian, OR, CA. Popenoe et al. (1987: 92).

greeni (*Gyrodes*) Murphy and Rodda, 1960:843, pl. 101, figs. 27–29; LACMIP 9830. ***Gyrodes* (*Sohlella*?) *greeni* Murphy and Rodda, 1960**, Cenomanian, CA. Popenoe et al. (1987: 79).

stewarti (*Sollariella*) [sic] Murphy and Rodda, 1960:839, pl. 103, figs. 4, 5; LACMIP 9821. ***Igonoia stewarti* (Murphy and Rodda, 1960)**, late Cenomanian, CA. Squires (2011a: 142).

PACKARD

Bivalves

alisoensis (*Tellina*) Packard (1922: 426, pl. 33, fig. 3); UCMP 12309. ***Laternula? alisoensis* (Packard,**

1922), middle Campanian, CA. Elder and Saul (1993: pl. 2, figs. 1, 2).

angulata (*Meretrix*) Packard (1922: 425, pl. 33, fig. 5); UCMP 12307. ***Etea angulata* (Packard, 1922)**, Campanian, CA. Saul (1982: 73).

californica (*Exogyra*) Packard, 1922: 421, pl. 27, fig. 5; UCMP 12320. ***Costagyra californica* (Packard, 1922)**, Turonian, CA. Squires (2017: 39).

californiana (*Trigonia*) Packard, 1921: 17, pl. 2, fig. 2; UO 6 (lost, but CASG 568 is a plaster cast of it). ***Popenoella californiana* (Packard, 1921)**, Turonian, CA. Saul (1978: 39), Cooper and Leanza (2017: 329).

chicoensis (*Spisula*) Packard, 1916: 300, pl. 27, figs. 6, 7; UCMP 12205. ***Willimactra* (*Petromactra*) *truncata* (Gabb, 1864)**, early to late Campanian, VI, CA. Saul (1973: 23).

cordiformis (*Cucullaea*?) Packard, 1922: 417, pl. 24, fig. 1; UCMP 12311. ***Cucullaea* (*Idonearca*) *cordiformis* Packard, 1922**, late Campanian, CA. Saul (1982: 68).

coronaensis (*Cardium*) Packard, 1922: 424, pl. 30, fig. 2; UCMP 12281. ***Pachycardium coronaense* (Packard, 1922)**, Turonian, CA. Popenoe (1937: 388).

crescentica (*Ostrea*) Packard, 1922: 420, pl. 26, fig. 3 [not fig. 4]; UCMP 12318. ***Curvostrea crescentica* (Packard, 1922)**, Turonian, CA. Squires (2017: 29).

demessa haidana var. (*Acila* (*Truncacila*)) Packard in Schenck, 1936: 50, pl. 2, figs. 3, 4, 6, 10; CASG 69081. ***Acila* (*Truncacila*) *haidana* Packard in Schenck**, latest Albian (probably) to early Turonian, QC, CA. (Squires and Saul, 2006b: 92).

deschutesensis (*Trigonia*) Packard, 1921: 24, pl. 10, fig. 3; UO 9. ***Notoscabrotrigonia oregana* (Packard)**. middle Albian?, perhaps middle or late Cenomanian, OR. Jones (1960: 437), Cooper (2015: 25).

evansana var. *oregona* (*Trigonia*) Packard, 1921: 26, pl. 9, fig. 7; UO 4. ***Notoscarbrotrigona oregano* (Packard)**, middle Albian to perhaps middle or late Cenomanian, OR. Jones (1960: 437), Cooper (2015: 25).

fitchi (*Trigonia*) Packard, 1921: 20, pl. 6, fig. 3; pl. 7, fig. 2; UO 26859. ***Louella fitchi* (Packard, 1921)**, early to middle Turonian, OR, CA. Saul (1978: 53), Cooper and Leanza (2017: 330).

hardingensis (*Homomya*) Packard, 1922: 423, pl. 32, figs. 1a, 1b; UCMP 12291. ***Liopistha* (*Psilomya*) *hardingensis* (Packard, 1922)**, Turonian, CA. Popenoe (1937: 383).

inezana (*Trigonia*) Packard, 1921: 27, pl. 8, figs. 1a, b; pl. 9, fig. 1, pl. 10, fig. 1; UCMP 31464. ***Notoscabrotrigona evansana* (Meek, 1858)**, Coniacian through Campanian, VI, OR, CA. Jones (1960: 436), Cooper (2015: 25).

inornata (*Exogyra*) Packard, 1922: 420, pl. 27, fig. 1; UCMP 12284. ***Phygraea inornata* (Packard, 1922),** Turonian, CA. Squires (2017: 46).

lapidis (*Astarte*) Packard, 1922: 423, pl. 30, figs. 4a, 4b; UCMP 12285. ***Eriphyla lapidis* (Packard, 1922)**, Campanian?, CA. Popenoe (1937: 387).

nitida (*Meretrix*) var. *major* Packard, 1922: 425, pl. 33, fig. 2; UCMP 12279. ***Calva* (*Egelicalva*) *bowersiana* (Cooper, 1894)**, late early through late Campanian, WA, CA. Saul and Popenoe (1992: 39).

ovoides (*Astarte*) Packard, 1922, 424: pl. 30, fig. 1; UCMP 12280. ***Eriphyla ovoides* (Packard, 1922)**, late Turonian to Coniacian?, CA. Popenoe (1937: 386), Saul (1982: 72).

striatus (*Spondylus*) Packard, 1922: 422, pl. 29; UCMP 12276, [a junior homonym renamed as ***Spondylus fucatus* Hanna, 1924**: 181], late Campanian to early Maastrichtian, CA. Elder (1991: E10).

subnodosa (*Lima*) Packard, 1922:421, pl. 28; UCMP 12275. ***Spondylus subnodosus* (Packard, 1922)**, late Campanian to early Maastrichtian, CA, BX? Elder (1991: E10).

sulcata (*Astarte*?) Packard, 1922: 424, pl. 33, fig. 6; UCMP 12305, [a junior homonym renamed as *Astarte*? *acerba* Hanna, 1924: 157 and as *Astarte*? *earllergyi* Anderson, 1958: 121; now ***Alleinacin acerba* (Hanna, 1924)**]. Turonian, CA. Squires and Ritterbush (1981: 896).

taxidonta (*Ostrea*) Packard, 1922: 420, pl. 26, fig. 2; UCMP 12317. ***Acutostrea taxidonta* (Packard, 1922**), Turonian, CA. Squires (2017: 32).

Gastropods

californica (*Gyrodes*) Packard, 1922: 429, pl. 35, figs. 2a, 2b; UCMP 12300. ***Euspira shumardiana* (Gabb, 1864)**, late Campanian, CA. Popenoe (1937: 398).

californiensis (*Lysis*) Packard, 1922: 431, pl. 37, figs. 2, 3; UCMP 12287. ***Lysis suciensis* (Whiteaves, 1879)**, late early Campanian to early Maastrichtian, VI, WA, CA, BX. Saul and Squires (2008b: 128).

dubius (*Siphonalia*) Packard, 1922: 431, pl. 35, fig. 5; UCMP 12304. ***Saturnus dubius* (Packard, 1922)**, Turonian, CA. Saul and Popenoe (1993: 367).

nodosa (*Alaria*) Packard, 1922: 430, pl. 26, figs. 5a, 5b; UCMP 12297. ***Latiala nodosa* (Packard, 1922)**, Turonian, CA. Saul (1998: 132).

pseudoalveata (*Amauropsis*) Packard, 1922: 429, not pl. 35, figs. 1a, 1b, 3; UCMP 12301. ***Ampullina packardi* Popenoe, 1937**, early to middle Campanian, CA. Popenoe (1937: 399), Stecheson (2004).

suciaensis (*Cerithium*?) Packard, 1922: 430, pl. 35, fig. 4; UCMP 12303. ***Zebalia suciaensis* (Packard, 1922)**, middle Campanian, WA, CA. Squires and Saul (2003a: 43).

vetus (*Aporrhais*) Packard, 1922: 431, pl. 36, fig. 1; UCMP 12298. ***Alarimella veta* (Packard, 1922)**, Turonian, CA. Saul (1998: 134).

tumida (*Bullaria*) Packard, 1922: 433, pl. 37, fig. 4; UCMP 12289, [a junior homonym renamed as ***Bullaria obtenta* Hanna, 1924**: 159], Turonian, CA. Saul (1982: 72).

WARING

Bivalves

chicoensis (*Isocardia*) Waring, 1917: 62, pl. 8, fig. 3; LSJU 399. Probably *Clisocolus cordatus* Whiteaves, 1879: 157, middle Campanian, CA. Popenoe (1937: 390); Smith, 1978: 332).

cordata (*Macrocallista*) Waring, 1917: 62, pl. 8, fig. 1; not in CASG database. ***Paraesa? lens* (Gabb, 1864)**, Campanian, VI, WA, CA. Saul (1993: 976).

cowperi (*Pecten* (*Propeamusium*)) [sic] Waring, 1917: 63, pl. 7, figs. 1, 2; syntypes CASG 61644. ***Propeamussium* (*Parvamussium*) *cowperi* (Waring, 1917)**, late middle Campanian, CA. Sundberg (1989: 61–62). A "variety" of *cowperi* occurs in a Paleocene wood-fall (chemosynthetic) deposit in northern Japan (Amano et al., 2018: 636).

triangulatus (*Crassatellites*) Waring, 1917: 59, pl. 9, fig. 1; syntype CASG 397. ***Cymbophora triangulata* (Waring, 1917)**, late Campanian, CA. Saul (1974: 1083).

Gastropods

compressus (*Gyrodes*) Waring, 1917: 67, pl. 9, fig. 6; CASG 61958.01. ***Euspira compressa* (Waring, 1917)**, middle Campanian, CA. Stecheson (2004: 64).

crassa (*Cancellaria*) Waring, 1917: 66, pl. 9, fig. 5; CASG 61644.06. [a junior homonym renamed as ***Cancellaria simiana* Hanna, 1924**: 160], probably middle Campanian, CA. No age update found.

plicata (*Turris*) Waring, 1917: 68, pl. 9, fig. 3; not in CASG database, [a junior homonym renamed as ***Surcula binotata* Hanna, 1924**: 181], Late Cretaceous undifferentiated, CA. No age update found.

rotundus (*Pugnellus*) Waring, 1917: 67, pl. 9, fig. 10; LSJU 402. ***Lispodesthes rotundus* (Waring, 1917)**, middle Campanian to early Maastrichtian, CA. Dailey and Popenoe (1966: 22), Stecheson (2004: 43).

templetoni (*Solariaxis*) Waring, 1917: 68, pl. 9, fig. 22; not in CASG database. ***Atira ornatissima* (Gabb, 1864)**, latest Santonian to late Campanian, VI, CA, BX. Squires (2010: 1025).

WHITE

Gastropods

californiensis (*Nerita*) Orcutt, 1887 (based on White's, 1885: 12, pl. 5, figs. 7, 8 of *Nerita* sp.); lectotype USNM 13411a. ***Nerita* (*Bajanerita*) *californiensis* (Orcutt, 1887)**, late Campanian to early Maastrichtian, BX. Squires (1993: 1085).

condoni (*Trophon*) White, 1889: 21, pl. 3, figs. 4, 5; syntypes USNM 20122. ***Praesargana condoni* (White, 1889)**, Turonian, CA. Saul and Popenoe (1993: 360).

dilleri (*Scobinella*) White, 1889: 25, pl. 4, figs. 1–3; syntypes USNM 20123. ***Carota dilleri* (White, 1889)**, Turonian, VI, OR, CA, BX. Saul and Popenoe (1993: 374).

dowelli (*Gyrodes*) White, 1889: 19, pl. 3, figs. 8, 9; USNM 20126. ***Gyrodes* (*Gyrodes*) *dowelli* White, 1889**, Turonian, VI, OR, CA. Popenoe et al. (1987: 75).

euryostomous (*Trochus* (*Oxystele*)) White, 1885: 12, pl. 5, figs. 9–11; not in USNM online database. ***Homalopoma euryostoma* (White, 1885)**, early Campanian to early Maastrichtian, BX. Kiel and Aranda-Manteca (2002: 29).

gabbi (*Fulguraria*) White, 1889: 23, pl. 3, fig. 1; lectotype USNM 20112. ***Volutoderma averillii* (Gabb, 1864)**, early Campanian, VI, CA. Saul and Squires (2008a: 226).

hilgardi (*Fulgur*) White, 1889: 22, pl. 3, figs. 2, 3; USNM 20117. ***Pentzia hilgardi* (White, 1899)**, early Campanian to early Maastrichtian, WA, CA, BX. Squires and Saul (2003b: 57); Stecheson (2004: 83).

marcidulus (*Faunus*) White, 1889: 20, pl. 4, figs. 12, 13; USNM 20127. ***Liocium marcidulum* (White, 1889)**, early Campanian, CA. Squires and Saul (2003c: 149).

nexilia (*Ceratia*) White, 1889: 21, pl. 3, figs. 13, 14; lectotype USNM 20119a. ***Acirsa nexilia* (White, 1889)**, early to late middle Campanian, WA, CA. Squires and Saul (2003a: 39).

obstricta (*Stomatia*) White, 1889: 18, pl. 4, figs. 10, 11; USNM 20124. ***Ariadnaria obstricta* (White, 1889)**, late Coniacian? to Santonian, CA. Saul and Squires (2008b: 122).

obtusa (*Mesalia*) White, 1889: 20, pl. 4, figs. 6, 7]; lectotype USNM 20116a. ***Acirsa obtusa* (White, 1889)**, late Santonian to early late Campanian, CA. Squires and Saul (2003a: 36).

oppansus (*Lysis*) White, 1889: 17, pl. 4, figs. 14, 15; USNM 20115. ***Lysis duplicosta* Gabb, 1864**, Campanian, WA, CA. Saul and Squires (2008b: 125).

pillingi (*Cerithium*) White, 1885: 13, pl. 5, figs. 3–6; USNM 13408. ***Echinoaxis pillingi* (White, 1885)**, early Campanian to early Maastrichtian, BX. Kiel and Aranda-Manteca (2002: 33).

totium-sanctorum (*Cerithium*) White, 1885: 13, pl. 5, figs. 12, 13; USNM 13409. ***Tympanotonos* (*Exechocirsus*) *totiumsanctorus* (White, 1885)**, early Campanian to early Maastrichtian, BX. Kiel and Aranda-Manteca (2002: 34).

wallaense (*Solarium*) White, 1885: 14, pl. 5, figs. 1, 2; USNM 13412 ***Trochacanthus wallalense* (White, 1885)**, early Campanian to early Maastrichtian, CA, BX. Squires (2011b: 3).

WHITEAVES

Bivalves

cretacea (*Conchocele*) Whiteaves, 1874: 266, plate of fossils (figs. 2, 2a); vouchers CASG 61850.04, 61850.5. ***Thyasira cretacea* (Whiteaves, 1874)**, exact age unknown, VI. Whiteaves (1903: 383).

cumshewaensis (*Arca* (*Nemodon*)), Whiteaves (1900: 294; illustrated by Whiteaves 1884: 235, pl. 31, figs. 8, 8a, 8b); lectotype GSC 4915 (see Smith, 1978: 335). **Navonavis cusmshewaensis (Whiteaves, 1900)**, late Santonian, QC. Haggart and Higgs (1989: 61).

meekana (*Tellina*) Whiteaves, 1874: 268, plate of fossils (fig. 6); GSC 5730. ***Paraesa? lens* (Gabb, 1864)**, Campanian, VI, WA, CA. Saul (1993: 976).

nanaimoensis (*Tellina*) Whiteaves, 1903: 376, pl. 46, fig. 3; GSC 5729. ***Willimactra* (*Petromactra*) *truncata* (Gabb, 1864)**, early to late Campanian, VI, CA. Saul (1973: 23).

suciense (*Laevicardium*) Whiteaves, 1879: 154, pl. 18, fig. 2; GSC 5713. ***Cymbophora suciensis* (Whiteaves, 1879)**, Campanian, WA, CA. Saul (1974: 1079) used an unnecessary emendation of Whiteaves' name "*suciense*," instead of using the name "*suciensis*."

suciensis (*Linearia*) Whiteaves, 1879: 146, pl. 17, fig. 12; GSC 5824 (Bolten, 1992: 235). No new name found, hinge characters are unknown, and the only known specimen has been lost (Squires and Goedert, 1994: 262); thus, this bivalve is a *nomen dubium*, early middle Campanian, WA. Squires and Graham (2014: fig. 2).

suciensis (*Teredo*) Whiteaves, 1879: 135, pl. 17, figs. 1, 1a; syntypes GSC 5752, 5752 a–d (Bolton, 1992: 239). No new name found, but this fossil cannot be assigned to "*Teredo*," whose certain identification requires soft-part morphology, early late Campanian, VI. Squires and Graham (2014: fig. 2).

vancouverensis (*Opis*) Whiteaves, 1879: 158, pl. 18, figs. 4, 4a; GSC 5691. ***Opis* (*Hesperopis*) *vancouverensis* Whiteaves, 1879**, middle to late Campanian, VI. Squires and Saul (2009: 1328).

Gastropods

canadensis (*Gyrodes*) *conradiana*? var. Whiteaves, 1903: 365, unfigured; GSC 5777. ***Gyrodes* (*Sohlella*) *canadensis* Whiteaves, 1903**, Santonian to earliest Campanian, VI. Popenoe et al. (1987: 85).

dakotensis vancouverensis var. (*Serrifusus*) Whiteaves, 1879: 119, pl. 15, fig. 6. GSC 5794 (Bolton: 1965: 74). ***Serrifusus vancouverensis* Whiteaves, 1879**, possibly early Maastrichtian, VI. Anderson (1958: 171).

harveyi (*Cerithium*) Whiteaves, 1903: 362, pl. 43, fig. 7; syntypes 5933, 5933a (Bolton, 1965: 11). ***Alamirifica? harveyi* (Whiteaves, 1903)**, Coniacian to early Campanian, VI. Saul and Squires (2003: 448).

intermedium (*Mesotoma*?) Whiteaves, 1903:360, pl. 43, fig. 4; syntypes 5956, 5956 a–d (Bolton, 1965: 44). ***Acirsa nexilia* (White, 1889)**, early Campanian to late middle Campanian, WA. Squires and Saul (2003a: 39).

lallierianum suciense var. (*Cerithium*) Whiteaves, 1879: 122, pl. 15, figs. 10, 10a; lectotype GSC 5764b. ***Belliscala suciense* (Whiteaves, 1903)**, middle to early late Campanian, WA. Squires and Saul (2003a: 33).

newcombii (*Mesostoma*?) Whiteaves, 1903: 361, pl. 43, fig. 5; GSC 5298 (Bolton, 1965: 45). ***Confusiscala newcombii* (Whiteaves, 1903)**, latest Santonian to middle Campanian, WA. Squires and Saul (2003a: 40).

nodulosa (*Fasciolaria*) Whiteaves, 1874: 268, figs. 7, 7a (not 7b); lectotype GSC 5766. ***Forsia popenoei* Saul, 1988**. Late early to middle Campanian, VI, CA. Saul (1988: 10), Squires and Graham (2014: fig. 2).

occidentalis radiatula? var. (*Solariella*) Whiteaves, 1903: 368, pl. 45, figs. 5, 5a; GSC 5918. ***Igonoia occidentalis* (Whiteaves, 1903)**, Santonian. Squires (2011a: 144).

suciense (*Mesostoma*) Whiteaves, 1903: 359, pl. 44, fig. 7; lectotype GS 5764b. ***Belliscala suciense* (Whiteaves, 1879)**, middle Campanian to early late Campanian, WA. Squires and Saul (2003a: 33).

suciensis (*Cypraea*) Whiteaves, 1895: 127, pl. 3, fig. 5; GSC 5937. ***Palaeocypraea suciensis* (Whiteaves, 1895)**, early middle Campanian, WA. Groves (1990: 275); Squires and Graham (2014: fig. 2); Lorenz, 2017: 210).

suciensis (*Surcula*) Whiteaves, 1879: 115, pl. 15, figs. 1, 1a; syntypes GSC 5784, 5784 a–b (Bolton, 1965: 79). ***Amuletum?* (*Lutema*)? *suciensis* (Whiteaves, 1879)**, early middle Campanian, WA. Erickson (1974: 223), Squires and Graham (2014: fig. 2).

suciensis carinifera var. (*Stomatia*) Whiteaves, 1879: 128, pl. 16, fig. 4; lectotype GSC 5771. ***Lysis suciensis* (Whiteaves, 1879)**, late early Campanian to early Maastrichtian, VI, WA, CA, BX (including Baja Sur). Saul and Squires (2008b: 128).

suciensis carinifera var. (*Stomatia*) Whiteaves, 1879: 128, pl. 16, fig. 5; lectotype UCMP 11975. ***Lysis duplicosta* Gabb, 1864**, early to late Campanian, WA, no. CA. Saul and Squires (2008b: 125).

tenuis nanaimoensis var. (*Potamides*) Whiteaves, 1879: 121, pl. 15, figs. 9, 9a; lectotype GSC 5763a. ***Anchura nanaimoensis* (Whiteaves, 1879)**, middle to late Campanian, VI. Elder and Saul (1996: 390).

ACKNOWLEDGMENTS

Peter Roopnarine and Christine Garcia provided CASG type-specimen numbers. Lindsey T. Groves (LACM, Malacology Department) provided detailed information. Lorenz (2017), provided some type-specimen numbers, critically reviewed the manuscript, and gave valuable comments about it.

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Anatomy of *Engoniophos unicinctus* from Isla Margarita, Venezuela (Gastropoda: Caenogastropoda: Nassariidae), with a discussion on the buccinid-nassariid relationship

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ABSTRACT

The taxonomic position of *Engoniophos unicinctus* (Say, 1826) in the family Nassariidae is comfirmed based on morphological results. Our detailed anatomical analysis reveals some disparities with typical nassariids, e.g., having a non-serrated operculum, a simpler and proportionally smaller head, and the absence of epipodial tentacles. However, the similarities in shell and radula are present and are easily noticeable, which corroborates the taxonomic data and the positioning of *E. unicinctus* within the Nassariidae.

Additional Keywords: Anatomy, Buccinidae, Neogastropoda, Taxonomy

INTRODUCTION

The families Nassariidae and Buccinidae are among the most diverse within the Caenogastropoda. They occur from the poles to the equator, inhabiting a wide variety of environments, from shallow water to abyssal ocean depths (Harasewych, 1998; Hayashi, 2004). Members of the families are small- to medium-sized (20–250 mm), with ovate to fusiform, weakly shouldered shells, an open siphonal canal, columella lacking plicae, and axial sculpture usually consisting of broad ribs limited to early whorls. These families have a rich fossil record dating from the lower Cretaceous (Taylor and Morris, 1980), together with Fasciolariidae, Melongenidae, and Cancellariidae, while other neogastropod families appeared between the late Cretaceous and early Paleocene (Tracey et al., 1993).

The systematics of both families are poorly understood, and there is no consensus as to their limits and their relationships (Simone, 2011). Ponder (1974) considered the Buccinidae closely related to the Nassariidae, Fasciolariidae, and Melongenidae, based on the absence of accessory salivary glands and an anal gland. This close affinity was emphasized by Kantor (1996), based on shared characteristics such as a long or very long proboscis, the loss of glandular dorsal folds, and a tendency toward the reduction of the gland of Leiblein. The molecular systematics work by Galindo et al. (2016) provided a hypothesis for the systematic relationships within the Nassariidae.

Buccinids are usually distinguished from the nassariids by having a radula with three or more cusps on the central teeth, lateral teeth with two large flanking cusps (Golikov, 1980; Kantor, 1990a), and zero to five intermediate cusps (Harasewych, 1998). These radular distinctions, however, have not been observed in *Engoniophos unicinctus* (Say, 1825), which shows shell and radula greatly similar to those of the Nassariidae (Bandel, 1984). This led some authors to suggest its relocation to Nassariidae, and not in Buccinidae as it is traditionally allocated (Bandel, 1984; Faber, 2004).

The present paper is part of a larger project aiming at an improvement of the taxonomic knowledge on the Buccinoidea. Focusing in a problematic species with a clear duality of familiar attribution, we intend to discuss its morpho-anatomical attributes which has been published on nassariids and buccinids, and provide new data on the species.

MATERIALS AND METHODS

Specimens examined in this study are deposited in the collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). A list of examined specimens is given after the species description. Shells were broken prior to soft-tissue extraction. Specimens were immersed in 70% ethanol and dissected by standard techniques under a stereomicroscope. The terminologies of Arnold (1965) and Simone (2011) were employed for shell characters, and Diver's (1931) whorl-counting method was applied. Details of the radula were examined under the scanning electron microscope (SEM) at the MZSP. The synonymic list presented herein is restricted to taxonomic and occurrence papers.

Abbreviations used in anatomical drawings: **aa**, anterior aorta; **ab**, albumen gland; **ae**, anterior oesophagus; **ag**, albumen gland; **an**, anus; **au**, auricle; **bg**, buccal ganglia; **br**, subradular membrane; **ce**, cerebral ganglion; **cg**, cement gland; **cm**, columellar muscle; **co**, cement gland orifice; **cv**, ctenidial vein; **df**, dorsal fold of buccal mass; **dg**, digestive gland; **dl**, gland of Leiblein duct; **ep**, posterior oesophagus; **es**, oesophagus; **fp**, female pore; **fs**, stomach folds; **ft**, foot; **ge**, suboesophageal ganglion; **gi**, gill; **hg**, hypobranchial gland; **kd**, kidney; **m1–m11**, odontophore muscles; **mb**, mantle border; **me**, medium oesophagus; **mj**, julgal muscle; **mo**, mouth; **mt**, mantle; **ne**, nephrostome; **ng**, nephridial gland; **nr**, nerve ring; **oc**, odontophoral cartilage; **od**, odontophore; **og**, osphradium ganglion; **os**, osphradium; **ot**, oral tube; **ov**, pallial oviduct; **oy**, ovary; **pa**, posterior aorta; **pb**, proboscis; **pd**, penial duct; **pe**, penis; **pf**, propodial expansion; **pg**, pedal gland; **po**, palial oviduct; **pp**, penial papilla; **pr**, propodium; **pu**, pleural ganglia; **ra**, radula; **rm**, retractor muscle of proboscis; **rn**, radular nucleus; **rs**, radular sac; **rt**, rectum; **sd**, salivary duct; **sf**, siphon; **sg**, salivary gland; **so**, salivary duct orifice; **su**, suboesophageal ganglia; **te**, tentacle; **va**, vaginal atrium; **vd**, vas deferens; **ve**, ventricle; **vo**, visceral oviduct; **ye**, eye.

RESULTS

Family Nassariidae Iredale, 1916
Subfamily Photinae Gray, 1857

Genus *Engoniophos* Woodring, 1928

Type Species: *Phos erectus* Guppy, 1873 by original designation. Miocene, Jamaica.

Engoniophos unicinctus (Say, 1826)

(Figures 1–25)

Nassa unicincta Say, 1826: 211–212 (pl. 57, figs 1, 1a); Tryon, 1873: 35 (fig. 55), 1882: 245.
Nassa pallida Powys, 1835: 96.
Nassa guadelupensis Petit de la Saussaye, 1852: 171 (pl. 2, figs 3–4).
Strongylocera textilina Mörch, 1852: 80 (Lister, pl. 965, fig. 20).
Phos guadalupensis [sic]: Arango, 1880: 201.
Phos guadeloupensis [sic]: Tryon, 1881: 219 (pl. 83, figs 512, 520).
Nassa textilina: Tryon, 1882: 243.
Phos unicinctus: Dall, 1889: 178; Gardner, 1926: 460.
Strongylocera unicincta: Dall and Simpson, 1901: 402.
Engoniophos guadelupensis: Warmke and Abbott, 1962: 115 (pl. 21, fig. F); Humfrey, 1975: 150; Bandel, 1976: 99 (fig. 3a–b).
Engoniophos unicinctus: Rehder, 1962: 131; Warmke and Abbott, 1962: 116 (pl. 21, fig. J); Work, 1969: 672; Abbott, 1974: 220 (fig. 2428); Vokes and Vokes, 1983: 26 (pl. 14, fig. 21); Bandel, 1984: 142 (fig. 235; pl. 16, fig. 6); Jong and Coomans, 1988: 83 (pl. 38, fig. 455); Díaz and Puyana, 1994: 187; Ramos and Robaina, 1994: 102; Faber, 2004: 8; Buitrago et al., 2006: 639; Cruz and Gándara, 2006: 132; Fernández and Jiménez, 2007: 5; Reyes et al., 2007: 384; Rosenberg et al., 2009: 650.
Pallacera unicincta: Macsotay and Campos, 2001: 88.

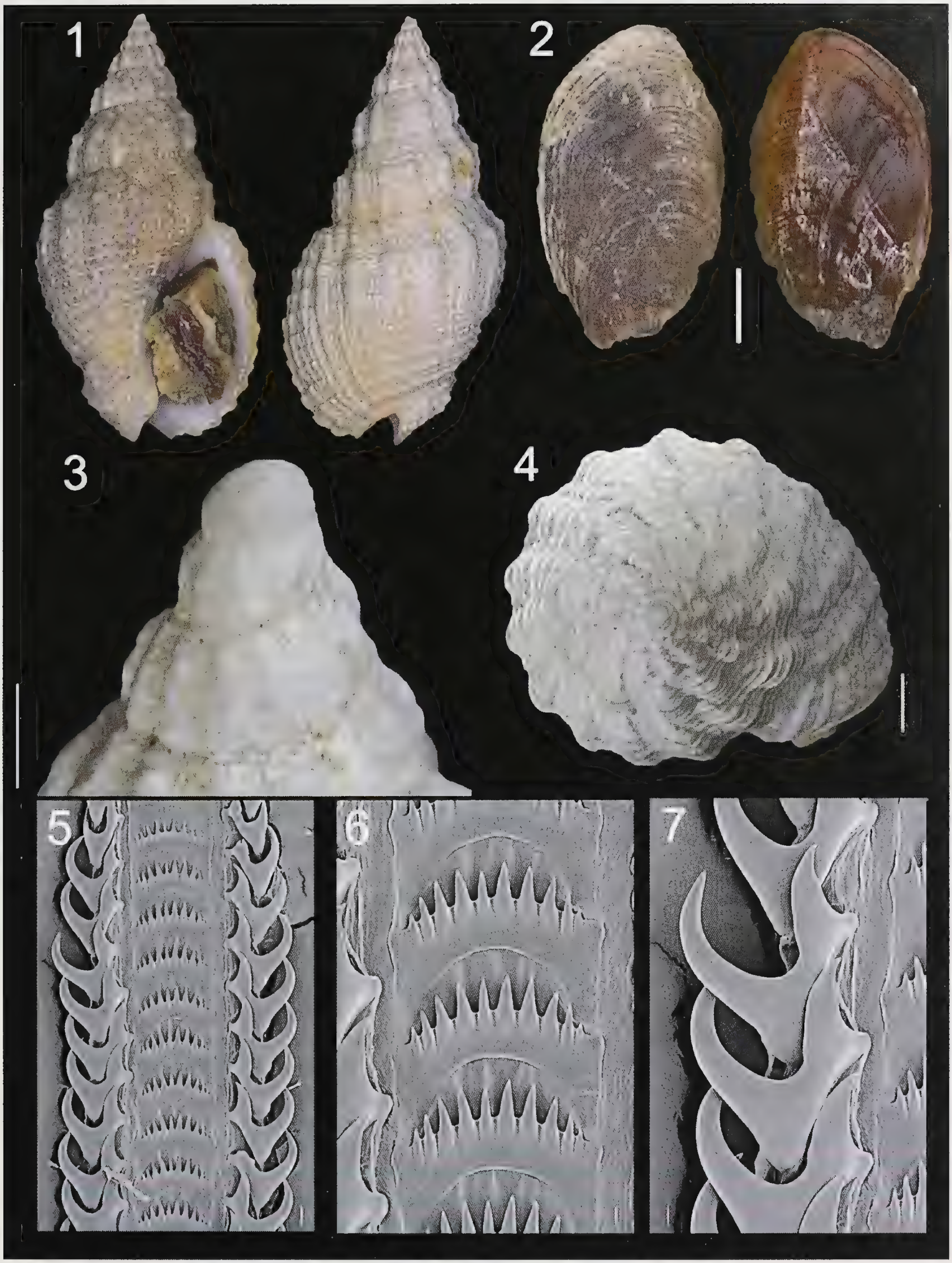
Type Locality: Coast of South Carolina (Say, 1826 in error; see Woodring, 1964: 269).

Distribution: Lower Caribbean to Venezuela (Macsotay and Campos, 2001).

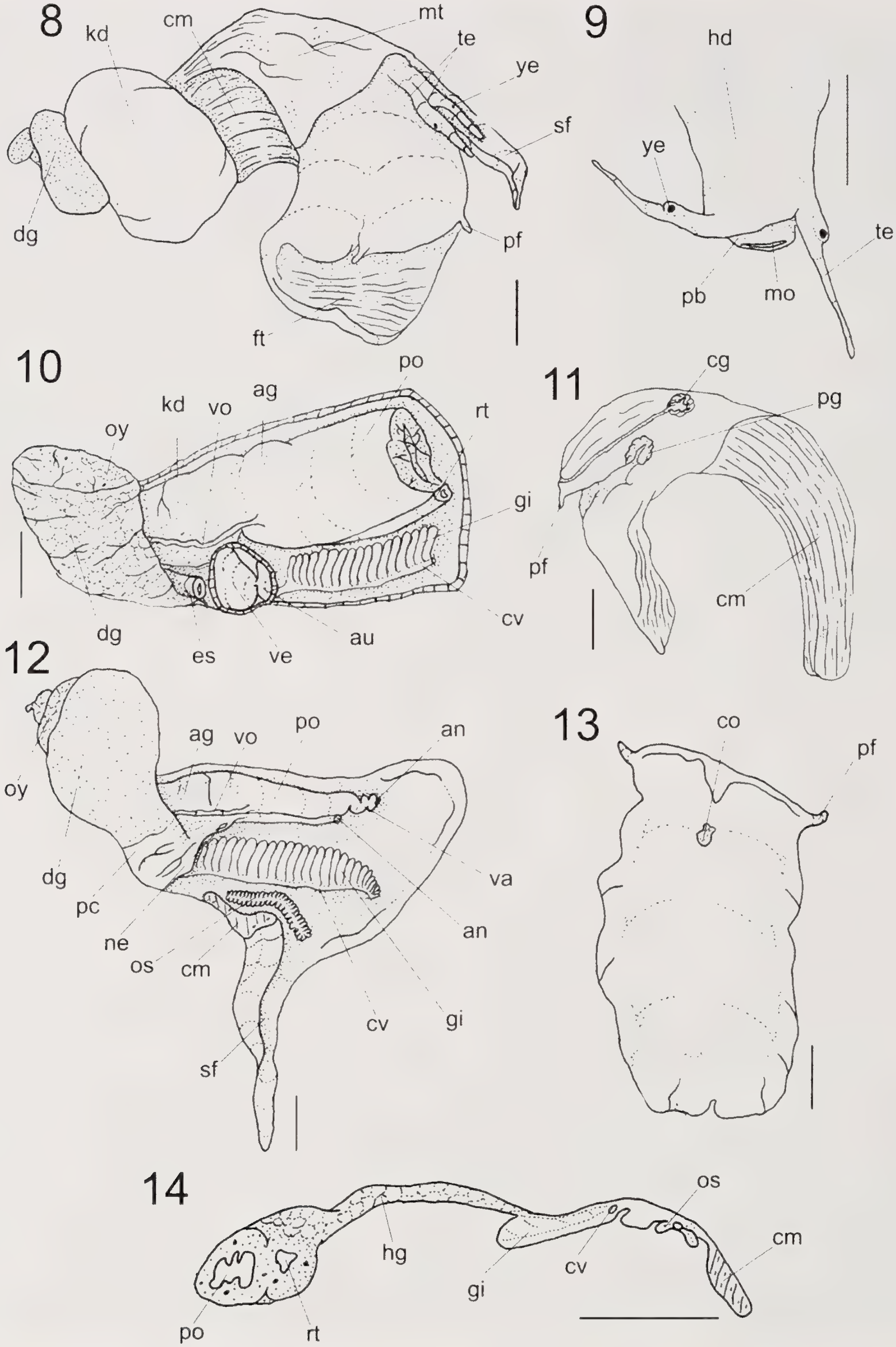
Description: SHELL (Figures 1, 3, 4). Fusiform, twice as long as wide, with 7–8 convex whorls, light gray to cream. Protoconch wide, smooth, dome-shaped, white, with three whorls; transition indistinct. Teleoconch sculpture consisting of 5–8 thin spiral cords along entire surface of all whorls (twice as many on body whorl); space between cords equals three to four times their width, becoming more closely spaced near suture; spiral cords crossed by wide axial ribs (width ~1/10 of whorl width) bearing rounded nodules at middle level on earlier whorls, and on upper portion of body whorl; axial ribs becoming less prominent toward suture and basal portion of body whorl; depression between ribs as wide as ribs. Spire angle ~30°. Aperture elliptical, twice as long as wide, white, glossy; length ~1/2 of shell length. Siphonal canal short, broad, dorsally recurved. Anal notch present, but not well-marked. Outer lip thick, lirate, with thickened outer edge. Columella straight, without folds.

HEAD-FOOT (Figures 8, 9, 11, 13). Head protruded, tentacles elongated and narrow, twice as long as head; eyes located on small protuberances at mid level of tentacle, clearly separating basal broad and distal narrow portions. Rhynchostome as transverse slit, located in middle region of ventral surface of head (Figure 9, 15). Foot large, occupying whole body whorl (retracted), bearing pair of small propodeal expansions; pedal gland located in central region of foot (Figure 11), forming groove, extending from dorsum of foot (propodium) to sole. Cement gland of females rounded, located in anterior region of mesopodium, inner space wide, duct long (Figure 11). Cement gland orifice located on median line of anterior sole region (Figure 13). Opercular pad elliptical, ~80% as wide as dorsal surface of foot; attachment with operculum occupying ~70% of foot area. Penis originated on right lateral region, posterior to cephalic base, at level of mantle edge. Columellar muscle wide and broad, 1½ whorl long. Haemocoel long and thin, extending dorsally along center of foot and columellar muscle (Figure 8, 11).

OPERCULUM (Figure 2). Small, oval, corneous, pale brown, located close to edge of foot; occupying 1/2 of apertural area. Nucleus terminal, inferior. Outer surface with normal concentric growth lines, forming undulations. Scar oval, occupying ~⅔ of inner surface.



Figures 1–7. *Engoniophos unicinctus*, MZSP 77798 ♀, shell, operculum and radula. **1.** Shell, apertural and dorsal views (L = 18.7 mm). **2.** Operculum, inner and outer views. Scale bar = 2 mm. **3–4.** Protoconch and first teleoconch whorls. **3.** Lateral view. Scale bar = 0.5 mm. **4.** Apical view. Scale bar = 1mm. **5–7.** SEMs of radula. **5.** Middle portion of radula. Scale bar = 30 μm. **6.** Detail of central teeth. Scale bar = 10 μm. **7.** Detail of lateral teeth. Scale bar = 10 μm.



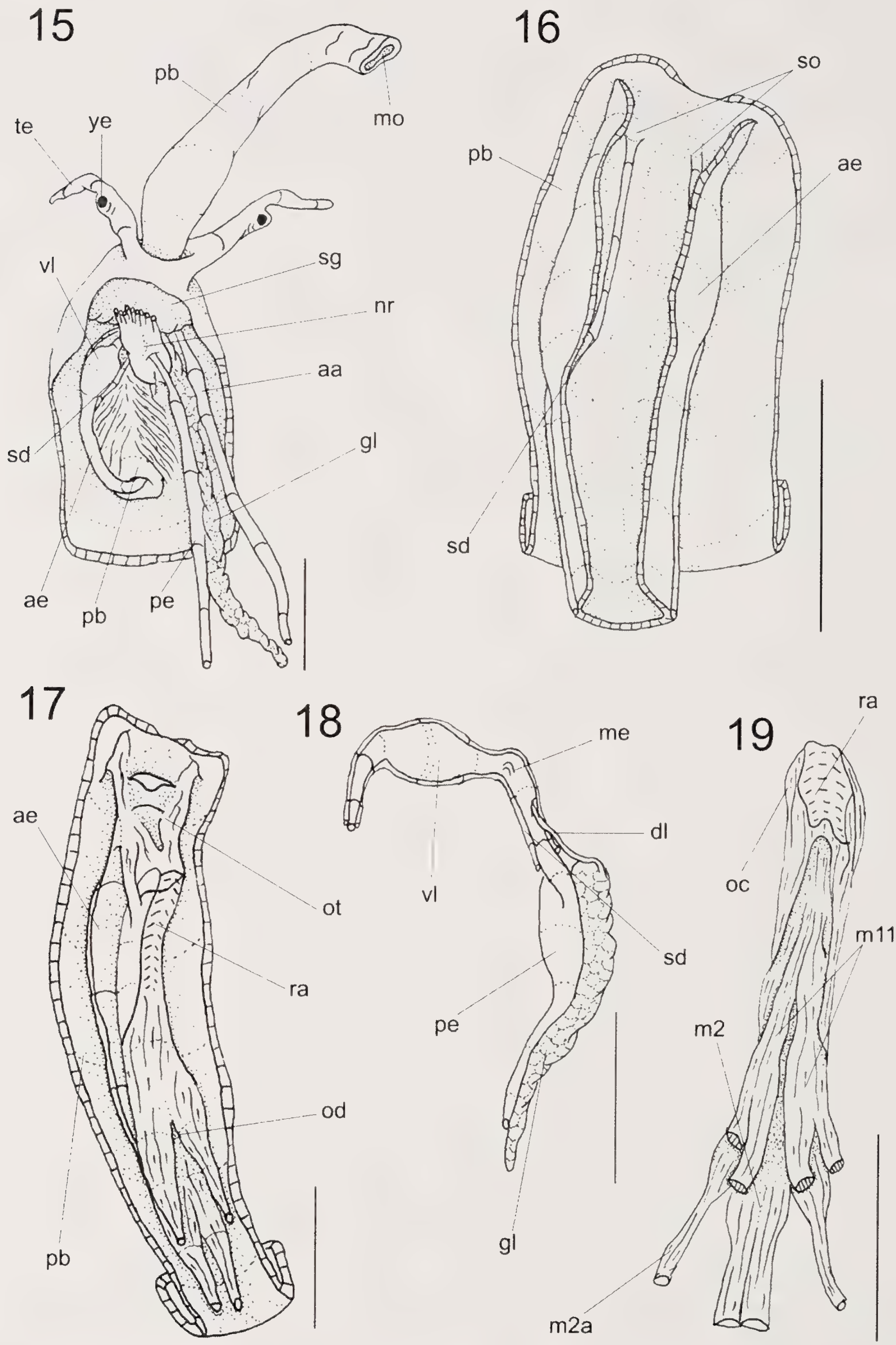
Figures 8–14. *Engoniophos unicinctus*, detailed anatomy. **8.** Complete specimen extracted from shell (operculum removed), anterior-right view. **9.** Detail of head, dorsal view. **10.** Reno-pericardial region, ventral view, some adjacent structures also shown. **11.** Foot of female, sagital section. **12.** Pallial cavity roof, ventral view, and coiled visceral mass. 13. Sole of foot, female, showing propodial expansions and cement gland opening. **14.** Pallial cavity roof, transverse section at middle level of osphradium. Scale bars = 2 mm.

MANTLE CAVITY ORGANS (Figures 10, 12, 14). Mantle cavity covering ~1 whorl. Siphon width ~1/2 of mantle cavity width, length ~2/3 of mantle cavity length. Right base of siphon high, width ~twice of mantle edge width; left base low. Osphradium long and narrow, elliptical, length ~1/3 of pallial cavity length, width ~1/6 of its width. Osphradial filaments short, width similar to mantle edge. Ctenidial vein (efferent branchial vessel) with uniformly narrow along its length. Gill elliptic, occupying ~80% of length and ~1/4 of width of pallial cavity. Anterior end of gill rounded, ending gradually, inserted directly into pallial cavity. Gill filaments relatively uniform in size along its entire length. Posterior end of gill rounded, located in posterior region of mantle cavity close to pericardium. Gill filaments height ~1/3 of pallial cavity height, apex rounded, at middle portion, tilted to right; right and left edges of filament straight; space between gill and right pallial organs about twice of gill width. Hypobranchial gland inconspicuous. Right side of pallial cavity almost entirely filled by gonoducts. Rectum long and thin, with ~1/2 of pallial cavity length. Anus sessile, distance between anus and mantle border 1/3 of total pallial cavity length. Anal gland absent.

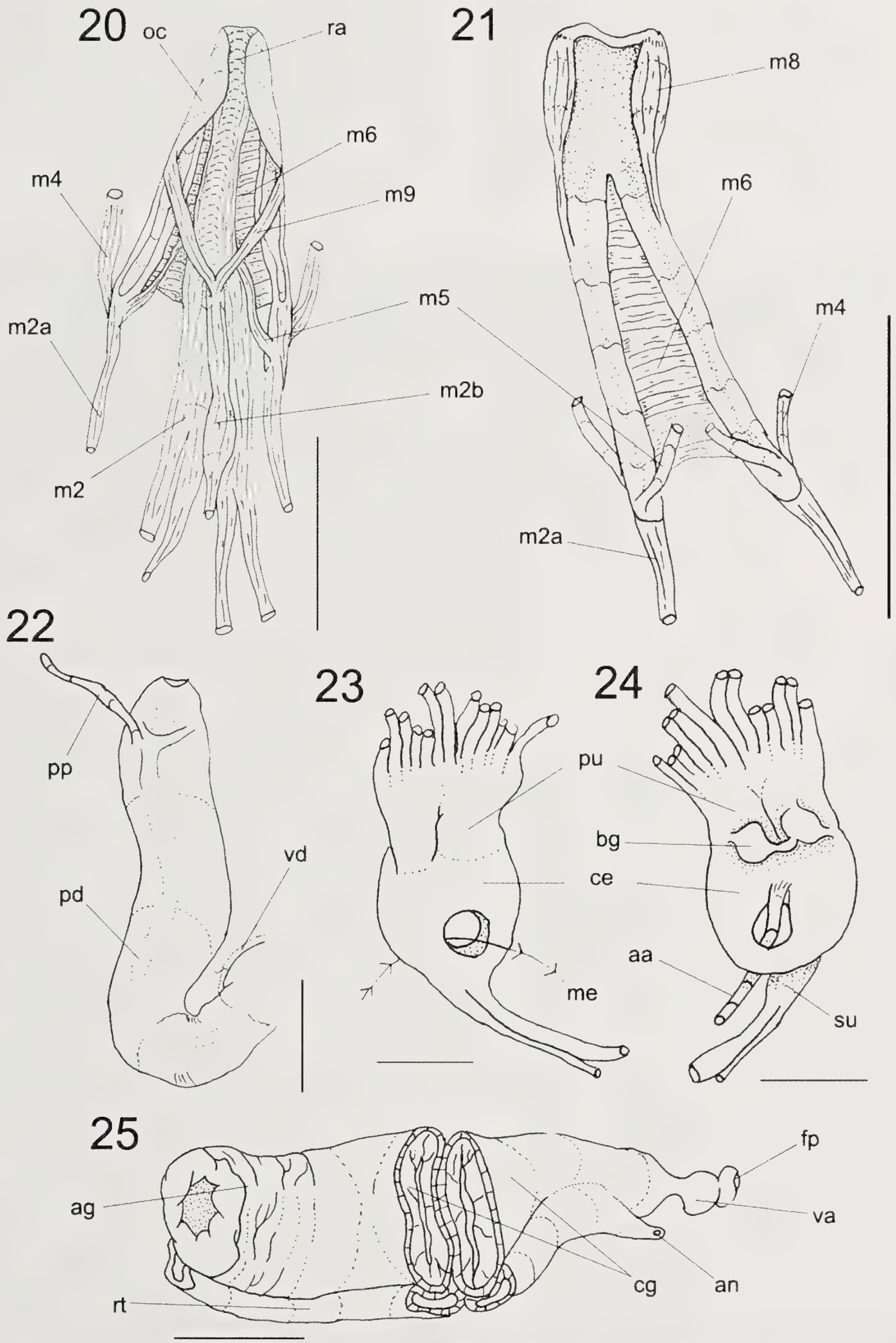
VISCERAL MASS (Figures 8, 10, 12). Extending ~3 whorls posteriorly to pallial cavity. Digestive gland dark beige, occupying ~80% of visceral mass volume, encircling stomach. Gonad orange with small black spots, located on columellar surface, posterior to stomach. Seminal vesicle of males located in anterior portion of gonad, ~½ of its size. Kidney occupying ~1/3 of visceral mass volume, located on right side of anterior visceral end. Stomach not seen in detail.

CIRCULATORY AND EXCRETORY SYSTEMS (Figure 10, 12). Reno-pericardial region occupying 1/3 whorl, oval, on right margin of last whorl of visceral mass, adjacent to mantle cavity. Pericardium occupying 1/3 of reno-pericardial region, posterior to gill; situated on left anterior margin of visceral mass. Auricle reniform, anterior to ventricle; with three connections: on upper right side with kidney, on anterior right side with gill, and on posterior left side with ventricle. Ventricle four times size of auricle, with common aorta on left posterior margin. Aortas wide, located along left-posterior region of ventricle. Kidney occupying 1/5 of pallial cavity volume, renal lobe single, solid, with glandular transverse folds along its ventral surface; efferent renal vessel located at its right portion. Nephridial gland not seen in detail. Nephrostome a small, transverse slit, located in anterior region of membrane between kidney and pallial cavity.

DIGESTIVE SYSTEM (Figures 9, 15–21). Mouth longitudinal, narrow, located on center proboscis tip. Proboscis long, straight and thin, occupying ~80% of hemocoel volume; not completely retractable. Rhinchodeal wall thin, involving ~1/3 of proboscis. Retractor muscles covering ~1/3 of proboscis; several thin retractors muscles originated on dorsal surface of foot, inserted into posterior end surface of proboscis. Odontophore and buccal mass muscles: **mj**, thin pairs of perioral muscles connected on both sides, dorsal and ventral, surrounding odontophore cartilages; **m1**, jugal muscles, several small muscle fibers connecting buccal mass to adjacent inner surface of proboscis; **m2**, pair of strong retractor muscles of buccal mass, originating on inner surface of proboscis, running along entire odontophore, inserting into anterior region of odontophore cartilages; **m2a**, pair of retractor muscles of buccal mass, originating on dorsal surface of haemocoel, inserting at end of posterior margin of odontophore cartilages; **m2b**, ventral single, thin muscle auxiliary of **m2**, originating on ventral medial fibers of **m2**, detaching from it in region just posterior to **m6**; **m3**, long, ~80 % of odontophore length, cylindrical muscle forming outer wall of odontophore, with transverse fibers; **m4**, pairs of strong radular dorsal tensor muscles covering almost entire surface of posterior portion of odontophore cartilages, inserting into subradular membrane; **m5,** pair of auxiliary dorsal tensor muscles of radula, originating inside edges of cartilage, adjacent to insertion of **m4**; **m6**, horizontal muscle, thick, connecting ventral edges of cartilages, running almost along its entire length; **m8**, pair of small elliptical muscles, length ~1/3 of odontophore cartilage length, originating at anterior end of odontophore cartilages, running along ventral surface of odontophore, inserting on anterior ventral surface of cartilages; **m11**, pair of ventral tensor muscles of radula, elongated, about 1/2 of total odontophore length, originating at ventral-posterior end of cartilages, crossing ventrally entire odontophore, inserting into ventral posterior surface of radula. Additional odontophore structures: **br**, subradular membrane, thin, translucent, along entire length of radular ribbon, covering inner surface of odontophore cartilages; **oc**, odontophore cartilages, about 3 times as long as wide, inner ventral surface concave, ~1/4 of anterior end fused with each other, ~1/3 of anterior region, concave, involving radular ribbon; **rs**, radular sac thin-walled, cylindrical, located at posterior end of radula. Radular teeth (Figures 5, 6, 7): rachidian tooth wide, comb-like, occupying about half of radular width; base curved, width ~3× its length; ~9 triangular, sharp pointed cusps of similar size, except for some lateral reduction; lateral tooth hook-like, bicuspid, base broad (equivalent to rachidian base width), obliquely disposed; external lateral cusp widely curved inwards, about as long as base; inner cusp approximately half size of main lateral cusp. Salivary glands (Figure 15) small, located at anterior portion of haemocoel, occupying ~1/8 of haemocoel volume, entirely involving nerve ring, middle esophagus and anterior portion of proboscis. Salivary ducts very narrow, except for short proximal region running completely attached to anterior esophagus wall and, more anteriorly, inside dorsal folds of buccal cavity (Figure 16); opening very small (Figure 16: **so**), in anterior-middle region of dorsal folds of buccal cavity. Valve of Leiblein (Figures 15, 18: **vl**) large, about 1/8 of odontophore volume, located in medium esophagus anterior to nervous ring, anterior region with transverse white band bearing long cilia, middle and posterior regions white, corresponding to inner gland



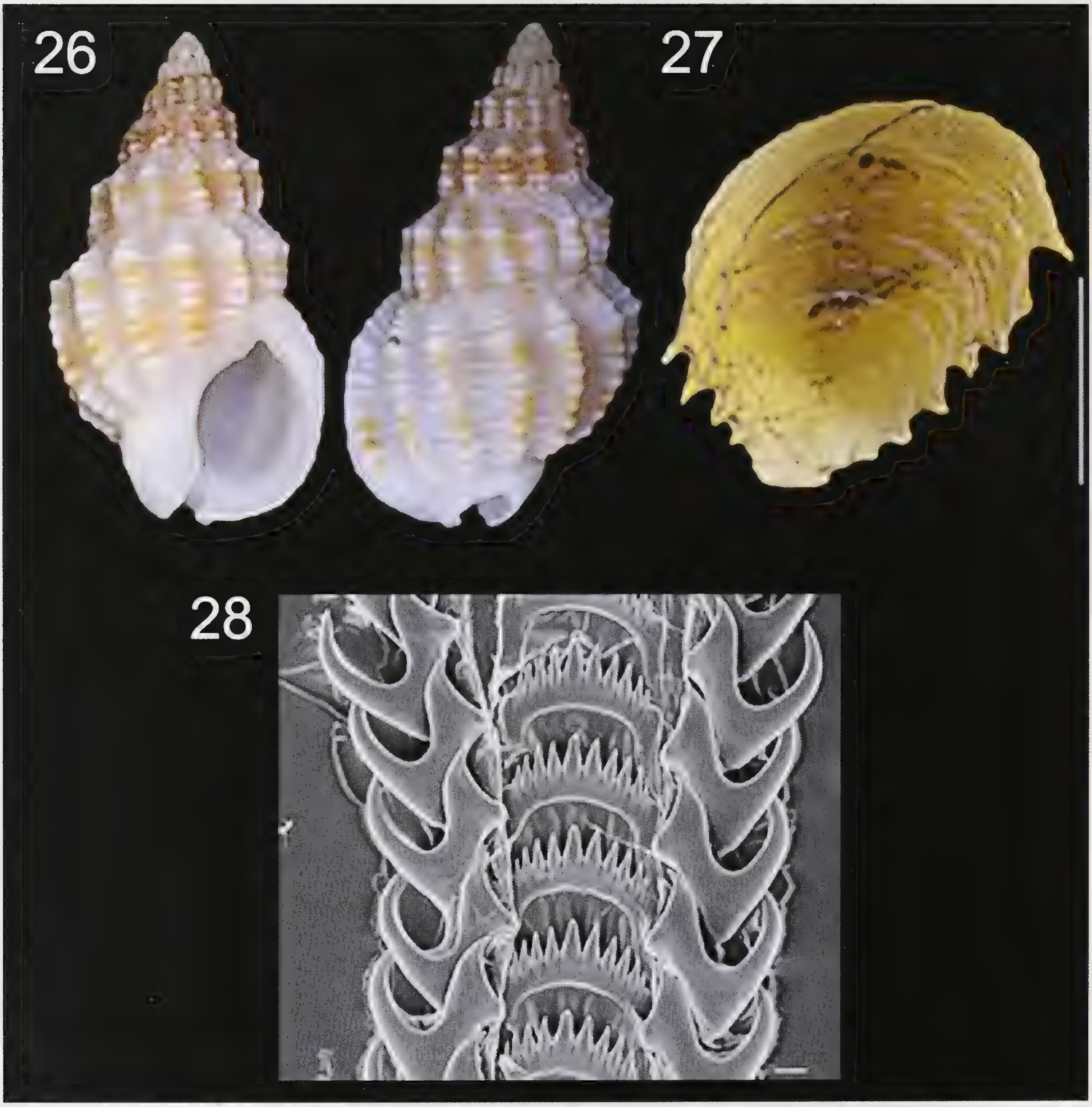
Figures 15–19. *Engoniophos unicinctus.* Detailed anatomy. **15.** Head and haemocoel, ventral view, foot and columellar muscle removed. **16.** Proboscis and anterior esophagus opened longitudinally, showing salivary ducts and their apertures. **17.** Extended proboscis opened longitudinally, ventral view, odontophore as in situ. **18.** Mid and anterior region of posterior esophagus and associated structures, showing valve and gland of Leiblein. **19.** Odontophore, dorsal view, superficial layer of membrane removed. Scale bars = 2 mm.



Figures 20–25. *Engoniophos unicinctus.* Detailed of anatomy. **20.** Odontophore, dorsal view, superficial muscles dissected. **21.** Odontophore cartilages, dorsal view, some adjacent muscles shown. **22.** Penis, ventral view, penis duct shown by translucency. **23–24.** Nerve ring, ventral and dorsal views. **25.** Pallial oviduct, ventral view, transversely sectioned at its middle level, some adjacent structures also shown. Scale bars = 2 mm.

occupying most of inner surface; bypass absent. Gland of Leiblein narrow and elongated (Figures 15, 18: **gl**), ~twice as long as middle esophagus, becoming gradually narrower posteriorly; duct of gland of Leiblein straight, long and very narrow, length ~1/2 of medium esophagus length, width ~1/6 of medium esophagus width. Accessory salivary glands absent. Anterior esophagus broader; walls muscular, with several dorsal internal longitudinal folds, occupying entire length of proboscis. Middle esophagus slender, short, diameter and length approximately half those of anterior esophagus. Posterior esophagus narrow, straight, about as long as anterior esophagus; anterior region broad, differentiation between middle and posterior esophagus clear with a thin duct. Stomach not seen in detail.

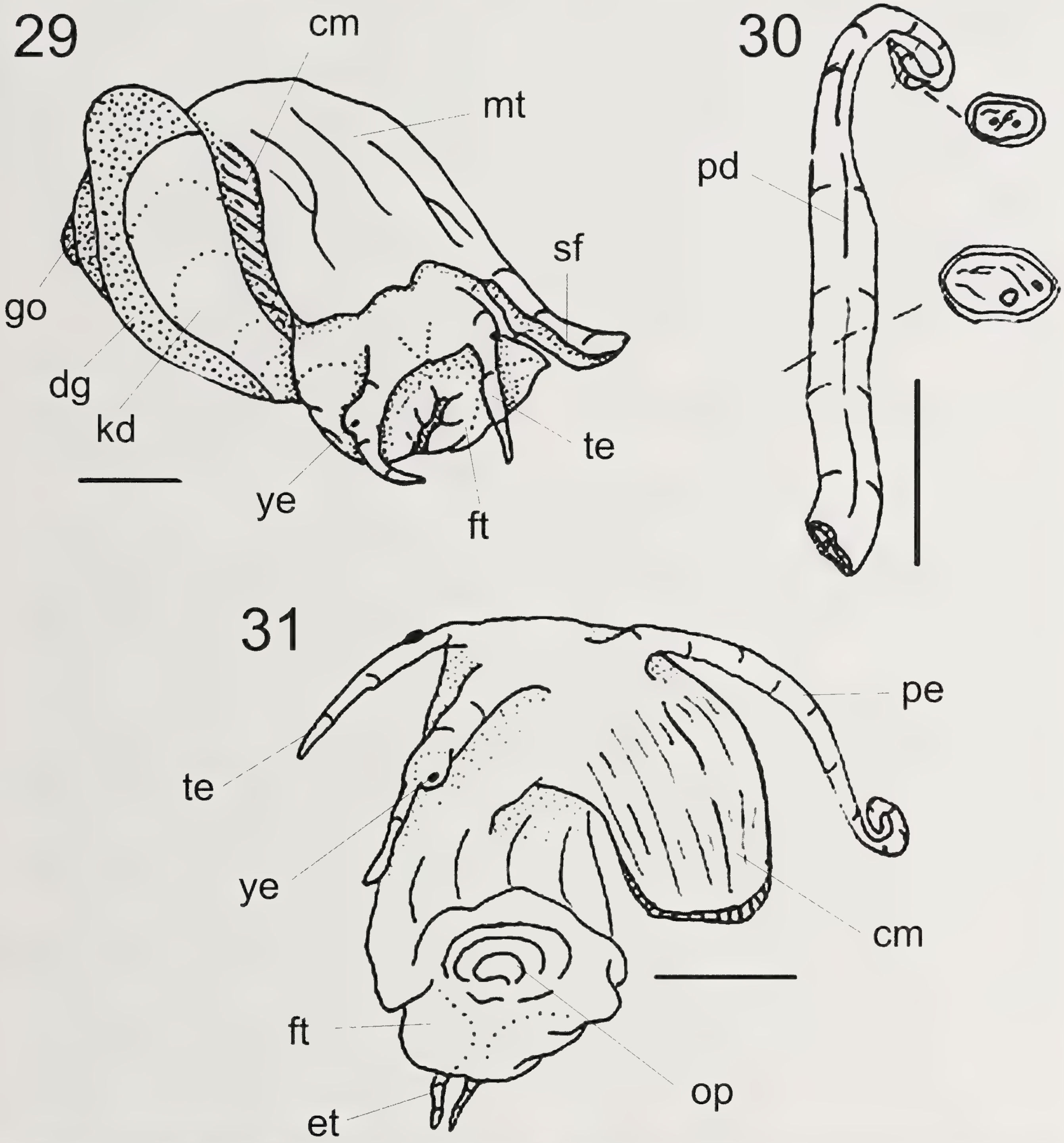
Reproductive System, Male (Figure 22). Vas deferens narrow, simple, straight, running along ventral surface of kidney up to pallial cavity. Prostate totally closed



Figures 26–28. Hard structures of some nassarids for comparison. **26.** *Nassarius albus* MZSP: 109759 shell, apertural and dorsal views. **27.** Operculum of *Nassarius arcularia plicatus* MZSP: 99863 outer view, scale bar = 2 mm. **28.** Radula of *Nassarius arcularia plicatus*, SEM, MZSP: 99863, detail of central and lateral teeth. Scale bar = 20 μm.

(tubular), running through right mantle edge, at ~2/3 of total pallial cavity length. Vas deferens anterior to prostate, straight, running immersed into integument of dorsum, next to mantle border and penis base. Penis large, length ~1/2 of total head-foot length, dorso-ventrally flattened; base curved, apical region pointed. Penial duct straight, running through center of penis, closed (tubular). Penial papilla long, slender, subterminal, located at anterior left region of penis. Penial aperture apical, far from papilla.

Reproductive System, Female (Figures 10, 12, 25). Visceral oviduct narrow, straight, running along ventral surface of



Figures 29–31. Anatomy of *Nassarius vibex*. **29.** Complete specimen extracted from shell (operculum removed), right-anterior view. **30.** Penis, ventral view, transverse section at indicated levels also shown. **31.** Head-foot, dorsal view, showing metapodial tentacles. Scale bars = 2 mm.

kidney in first whorl of visceral mass, located in front of pallial cavity. Posterior region of pallial oviduct protruding into kidney, occupying almost entire length of pallial cavity and 1/3 of its width. Albumen gland posterior, whitish, thick-walled, occupying ~1/5 of pallial oviduct volume. Capsule gland ~4/5 of oviduct volume, elongated, orange, thick-walled. Vaginal atrium anterior to capsule gland occupying ~1/7 of oviduct volume; sinuous, walls thick, muscular, female genital pore narrow, protruded, papilla-like, with thick edges. Bursa copulatrix absent.

Central Nervous System (Figures 25, 26). Nerve ring located in ventral basal proboscis region (Figure 15: **nr**), occupying ~1/12 of haemocoel volume, highly concentrated. Ganglia mostly fused, hard to distinguish from each other, somewhat asymmetrical. Pairs of pleural and cerebral ganglia fully fused with each other. Sub-esophageal ganglion about half of cerebro-pleural ganglion size, shortly and broadly connected to right cerebral ganglion. Pair of buccal ganglia small, located close to posterior edge of cerebral ganglia. Esophageal aperture small, occupying about 1/9 of ventral surface of nerve ring. Statocysts not seen.

Shell Measurements (length × width in mm): MZSP 77798; 2♂ 20.7 × 10.4; 17.5 × 9.0; 2♀ 13.9 × 6.1; 18.7 × 9.5.

Habitat: Muddy and sandy bottoms, intertidal.

Material Examined: MZSP 77798; 2♂, 2♀, Venezuela: Isla Margarita; Playa Bella Vista, 10°56' N, 63°50' W, 3–4 m depth (Simone col., 02/ii/1995).

DISCUSSION

Engoniophos unicinctus has a clear conchological resemblance to some representatives of Nassariidae, e.g., *Tritia alba* (Say, 1826) (Figure 26), in having a small shell with a poorly developed parietal callus, a high spire, short siphonal canal, weak anal notch, and uniform sculpture throughout the shell surface. Moreover, there is also a resemblance in radular configuration. The radula of *E. unicinctus* shows lateral teeth bearing two similarly sized cusps, lacking the smaller intermediate teeth present in *Buccinum undatum* Linnaeus, 1758, type species of Buccinidae (Fretter and Graham, 1962: 171, fig. 105E). On the other hand, the species in the nassariid genus *Buccinanops* also bears intermediate cusps in lateral teeth. It also shows rachidian teeth with a larger number of cusps, as in *Nassarius arcularia plicatus* (Röding, 1798), a subspecies of the type species of Nassariidae (Figure 28). Such characteristics led Faber (2004) to argue that *E. unicinctus* would be better placed in Nassariidae, following Bandel's (1984) suggestion, instead of being allocated in Buccinidae, as proposed by certain authors in more traditional classifications (e.g., Cernohorsky, 1984; Miloslavich, 1999; Reyes, 2007).

Engoniophos unicinctus presents some anatomical differences from those of typical nassariids, for example, the operculum (Figure 2) lacking marginal serrations commonly found in nassariines (Figure 27), but these are also absent in dorsanines/buccinanopsines. The head of nassariids is generally well developed (Figure 29), while in *E. unicinctus* it is proportionally much smaller and simpler, with the tentacles inserted directly into the dorsum (Figure 8: **te**). The penis is short and broad, with a long and slender papilla in *E. unicinctus* (Figure 22), while in other nassariids it is normally long and slender, lacking papillae (Figure 30). The epipodial tentacles (Figure 31), either singly or in pairs, are a traditional character and a diagnostic anatomical feature of Nassariidae (Simone and Pastorino, 2014). This feature is not found in *E. unicinctus*, which only bears a pair of propodeal (anterior) expansions (Figure 13), also commonly found in other nassariids, but no tentacles. Last but not least, recent molecular analyses, place *E. unicinctus* within the Nassariidae (Galindo et al., 2016).

The morphological similarities above mentioned in common with nassariids and the aforementioned recent findings in the literature so far indicate that *E. unicinctus*, in fact, belongs to Nassariidae. This conclusion adds anatomical argumentation to the already known conchological and radular similarities, and further corroborates the familiar placement, and its positioning within Buccinoidea proposed by Galindo et. al (2016).

ACKNOWLEDGMENTS

The authors are grateful to Lara Guimarães (MZSP) for helping with the SEM examination. This work was partially supported by a doctoral grant by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, proc. No 159448/2012-3).

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Mericella zhangsupingae, a new cancellariid species from the South China Sea (Gastropoda: Cancellariidae)

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ABSTRACT

A new western Pacific species belonging to the family Cancellariidae is described from off Dongsha Islands, South China Sea, at bathyal depths of 500–600 m. *Mericella zhangsupingae* new species is most similar to *Mericella bozzettii* Petit and Harasewych, 1993 in shell size and proportion. However, the new species can be separated from that species in having a larger, depressed protoconch, more convex teleoconch whorl, much weaker sculpture, and more sinuous outer lip. The new species represents the first member of genus *Mericella* discovered from western Pacific.

Additional Keywords: Volutoidea, Dongsha Islands, China, protoconch

INTRODUCTION

The genus *Mericella* was originally established by Thiele (1929), as a subgenus of *Cancellaria*, to accommodate a single species previously treated as *Cancellaria* (*Merica*) *jucunda* Thiele, 1925. To date, three species have been recognized in the genus, including *Mericella jucunda* (Thiele, 1925) from off Tanzania, *Mericella paschalis* (Thiele, 1925) from off Tanzania and Mozambique, and *Mericella bozzettii* Petit and Harasewych, 1993 from off Somalia. Olsson and Bayer (1972) proposed the generic name *Gerdiella* to include three cancellariid species from bathyal depths (516–897 m) of the Florida Straits and the Caribbean Sea. In that publication, they recognized that *Gerdiella* was related to, and possibly congeneric with, *Mericella*, but would differ by shell size and geographical distribution. Verhecken and Bozzetti (2006) compared the two genera based on conchological characters, and found no reason for further generic separation, although recognizing some degree of difference (e.g. spire height, suture form, relatively aperture height). However, a significnt distinction between the two genera was overlooked by Verhecken and Bozzetti (2006). *Mericella* species have a smooth protoconch, while *Gerdiella* species have axial ribs on the protoconch. In addition, some microscopic spiral threads were observed on the protoconch of *Gerdiella alvesi* Lima, Barros, and Petit, 2007. Verhecken (2002) stated that protoconch characters are of no diagnostic importance at the generic level. This opinion was not followed by Lima et al. (2007), who regarded *Gerdiella* as a distinct genus endemic to the western and southern Atlantic Ocean.

In this paper we describe a western Pacific species belonging to the Cancellariidae and assign it to the genus *Mericella* based on its smooth protoconch and geographic proximity to other species of *Mericella*. The finding extends the distribution of *Mericella* from East African waters to the western Pacific.

MATERIALS AND METHODS

Specimens were trawled by fishermen from bathyal depths (500–600 m) off Dongsha Islands, South China Sea (see Figure 1). Shells were observed using a light microscope and protoconch characters by scanning electron microscope (SEM). All specimens have been deposited at the Marine Biology Museum of Chinese Academy of Sciences (MBMCAS). The following abbreviations are used in the text: MBM, Marine Biological Museum, Qingdao, China; USNM, National Museum of National History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851

Genus *Mericella* Thiele, 1929

Type Species: *Cancellaria jucunda* Thiele, 1925 (off Dar es Salaam, Tanzania).

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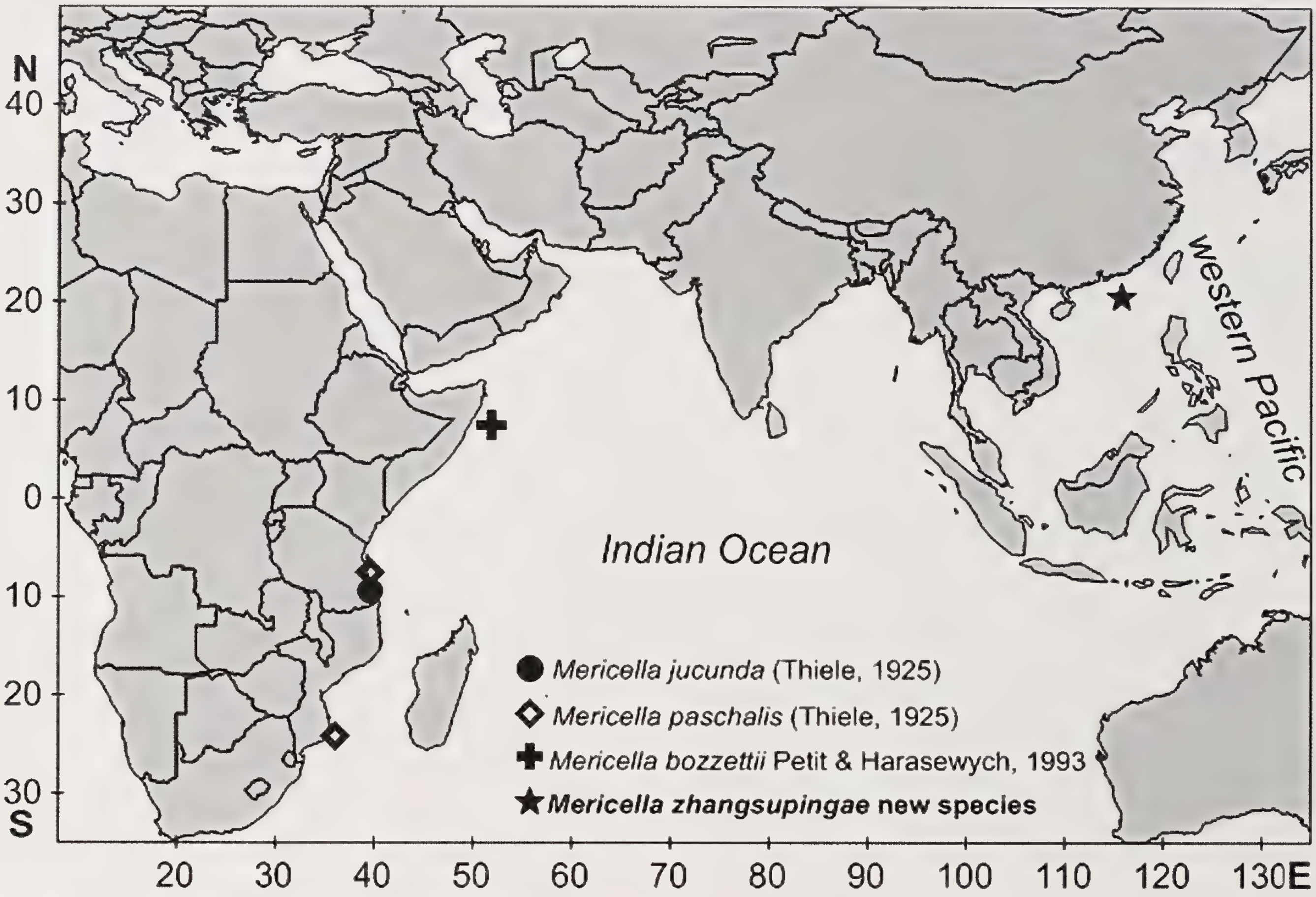


Figure 1. Geographic distribution of known *Mericella* species.

Mericella zhangsupingae **new species**
(Figures 1–12)

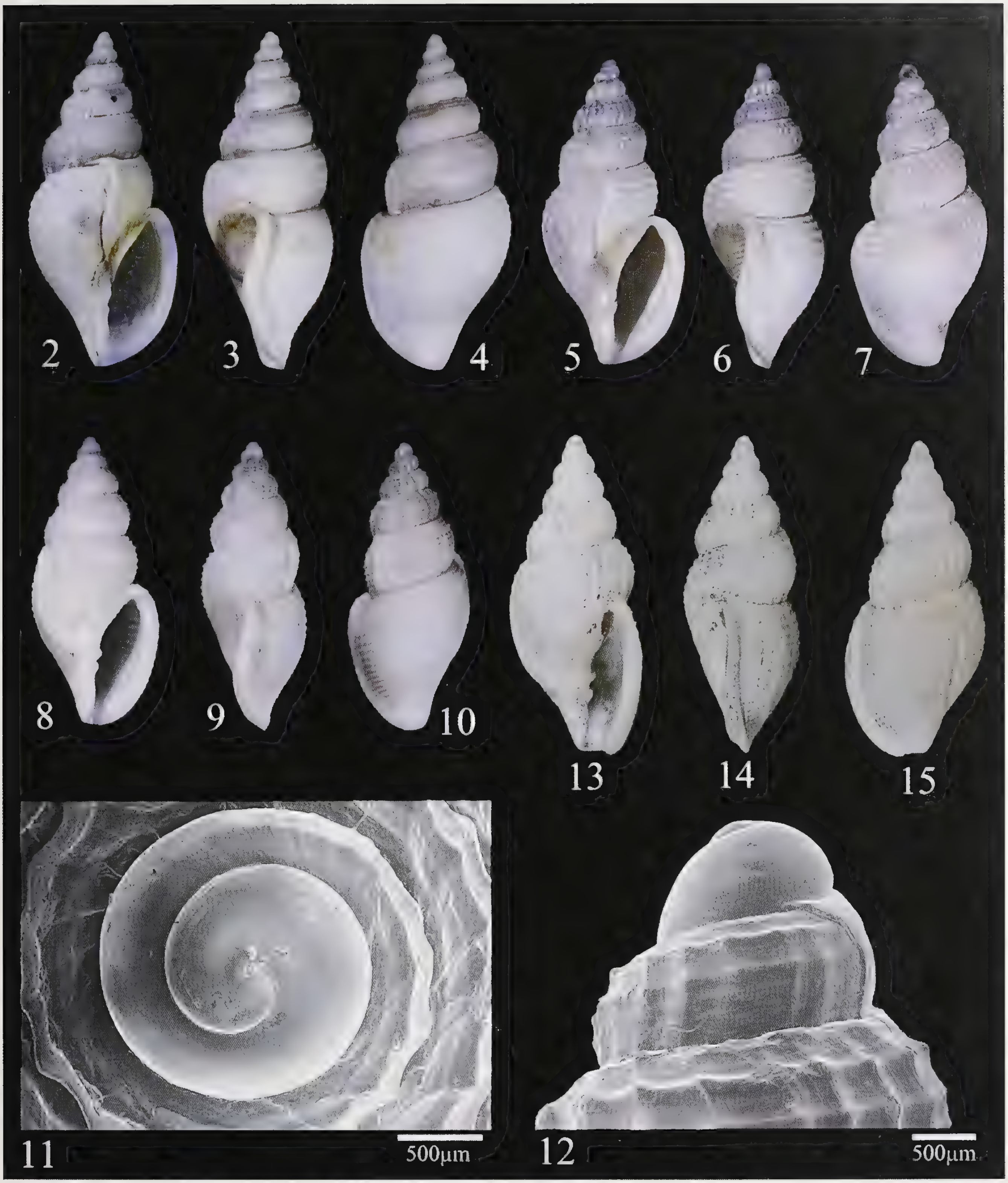
Description: Shell (Figures 2–12) large for genus, up to 31.5 mm, solid, elongated, with a tall spire, conical, protoconch rounded, aperture narrow. Protoconch (Figures 11–12) with two smooth, glassy whorls, large, maximum diameter nearly 2 mm, indicating planktotrophic larval development. Transition to teleoconch distinct, marked by numerous weak axial incremental processes. Protoconch forms smooth keel prior to transition to teleoconch. Teleoconch with up to five roundly convex whorls. Suture constricted, narrow, deep. First teleoconch whorl with four weak initial spiral cords, becoming five on second whorl, eight on penultimate whorl and ca. 30 on body whorl, occasionally with intercalated spiral threads. Axial sculpture of regularly spaced, sinuate, opisthocline ribs, 17 on first teleoconch whorl, 22 on second whorl, forming sharp nodules and cancellated appearance at intersections with spiral cords. Axial ribs and nodules becoming weak and smoother toward penultimate and body whorl. Incremental lines distinct, dense, forming conspicuous axial ridges between spiral interspaces. Varices up to seven in number, very weak on spire whorls, distinct on body whorl. Aperture narrowly elongate, elliptical, deflected from coiling axis by 18° (in holotype). Outer lip thickened, with about 20 obsolete denticles along entire length of the flaring, strongly sinuate outer lip; columellar lip with two developed folds. Radula and soft parts unknown.

Type Material: Holotype, MBM286508 (height 31.5 mm; width 13.8 mm); Paratypes 1–2, MBM286509, all from the type locality.

Type Locality: Off Dongsha Islands, South China Sea, 500–600 m.

Etymology: This new species is named after Prof. Suping Zhang in recognition of her contribution to gastropod taxonomy in China.

Comparative Remarks: Based on its elongate shell with a smooth protoconch and a flaring, sinuate outer lip, we assign this new cancellariid species to genus *Mericella*. *Mericella zhangsupingae* new species is most similar to *Mericella bozzettii* Petit and Harasewych, 1993 (Figures 13–15) in shell size and proportion, but differs in having a larger, lower, more globose protoconch, more convex teleoconch whorls, much weaker axial sculpture, and



Figures 2–15. Shells of *Mericella* species. **2–12.** *Mericella zhangsupingae* new species. **2–4.** Holotype, MBM286508, 31.5 mm. **5–7.** Paratype 1, MBM286509, 26.6 mm. **8–10.** Paratype 2, MBM286509, 23.2 mm. **11–12**. Protoconch of paratype 2. **13–15**. Holotype *Mericella bozzettii* Petit and Harasewych, 1993, USNM 860315, 28.7 mm.

more sinuous outer lip. In addition, spiral sculpture is dominant in *Mericella zhangsupingae*, whereas the axial sculpture is dominant in *Mericella bozzettii*. *Mericella zhangsupingae* new species can be clearly distinguished from the other two congeners, *Mericella jucunda* (Thiele, 1925) and *Mericella paschalis* (Thiele, 1925), by its larger, thicker shell with roundly convex teleoconch whorls, and a white color. Previously, all members of genus *Mericella* were only known from off East Africa (see Figure 1). The finding of *Mericella zhangsupingae* new species extends the distribution of the genus to the western Pacific Ocean.

ACKNOWLEDGMENTS

We would like to express our sincere thanks to Drs. M.G. Harasewych and José H. Leal for valuable comments and meticulous editing. This research was financially supported by the National Natural Science Foundation of China (31750002, 41376167).

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A newly discovered Paleocene species of *Boreocomitas* (Gastropoda: Pseudomelatomidae) from eastern Hokkaido, Japan, with implications for the biogeography of the Paleocene Bering Strait

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ABSTRACT

Two species of the gastropod family Pseudomelatomidae, genus *Boreocomitas,* including the new species *B. inouei*, are described from the Paleocene (upper Selandian to lowest Thanetian) Katsuhira Formation in eastern Hokkaido, Japan. These species represent the first Paleocene record of *Boreocomitas*. The paper discusses also the new recognition of species of *Boreocomitas* in Paleocene deposits of western Greenland and Denmark. Occurrences of some taxa, including this genus, are suggestive of faunal exchanges between the northern Pacific and the North Atlantic/Artic regions from the middle Paleocene (Selandian) to late Eocene. These exchanges could have resulted from direct marine connections between both areas via the Bering Strait.

Additional Keywords: Paleocene, gastropod, *Boreocomitas*, new species, palaeogeography

INTRODUCTION

Two species of a Paleocene bathyal gastropod genus including a new species are reported from eastern Hokkaido, Japan. These species are here assigned to the pseudomelatomid gastropod genus *Boreocomitas*. The deep-sea gastropod genus *Boreocomitas* was proposed by Hickman (1976) as an extinct subgenus of *Comitas* Finlay, 1926, based on specimens from the Cowlitz and Keasey formations in Oregon, western USA. Recent data show that the age of the Cowlitz Formation is middle to late Eocene and that of the Keasey Formation is late Eocene to earliest Oligocene (Prothero, 2001). *Boreocomitas* has also been recorded from the upper Eocene Kovachinskaya Formation in western Kamchatka (Gladenkov et al., 1991).

Many well-preserved molluscan fossils have been described from the upper Selandian to the lowest Thanetian Katsuhira Formation in eastern Hokkaido, northern Japan (Figure 1; Amano and Jenkins, 2014, 2017; Amano and Oleinik, 2014; Amano et al., 2015a, b, 2016, 2018). These fossils occur mainly in small calcareous concretions (about 30 cm in diameter) with plant debris, considered to be wood-fall communities (Amano et al., 2016a, 2018). From the locality at Katsuhira along the Urahoro River, two species of *Boreocomitas* including a new one have been recovered. In this paper, we describe these species and discuss their paleobiogeographical significance.

MATERIALS AND METHODS

Three specimens of *Boreocomitas inouei* new species and one specimen of *Boreocomitas* species were obtained from carbonate concretions (20 cm in diameter) with many bored wood fragments included in dark gray mudstones of the Katsuhira Formation. These concretions are exposed along the Urahoro River, 44 m south from the mouth of the Kokatsuhirazawa River, Urahoro Town, eastern Hokkaido (Figure 1; 42°59'10" N, 143°37'38" E). Rocks in the direct proximity to the locality contain dinoflagellate fossils indicating a late Selandian to earliest Thanetian age (Amano et al., 2018). These species were associated with 22 species of mollusks (Table 1) and one species of echinoid. Among them, *Myrtea ezoensis* (Nagao, 1938), and *Thyasira oliveri* Amano and Jenkins, 2018, were proposed as chemosymbiotic bivalves. As mentioned by Amano et al. (2018), the paleobathymetry of the Katsuhira Formation can be estimated as 200 to 500 m in depth. From these occurrences of mollusks, it is possible to consider the two species of *Boreocomitas* as members of the deep-sea wood-fall community.

All specimens of *Boreocomitas* are catalogued in the University Museum of the University of Tokyo (UMUT). The associated fauna is stored at Joetsu University of Education (JUE). Classification at family level follows

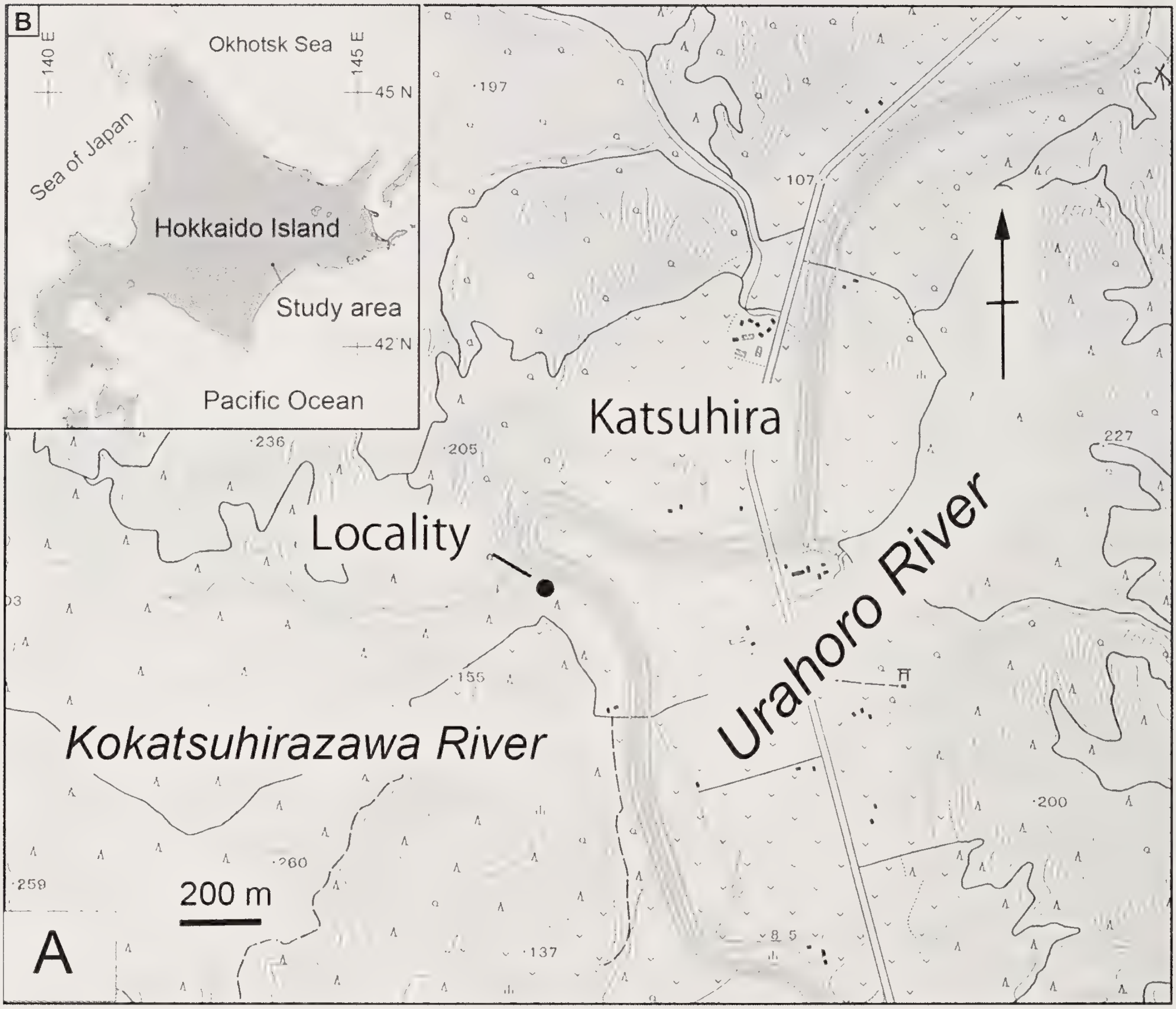


Figure 1. Map showing the locality yielding the two species of *Boreocomitas* discussed.

the current taxonomy of Conoidea by Bouchet et al. (2011, 2017).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Fleming, 1822
Family Pseudomelatomidae Morrison, 1966

Remarks: *Boreocomitas* was originally proposed as a subgenus of the genus *Comitas* Finlay, 1926, and placed in Turriculinae Powell, 1942, of Turridae H. Adams and A. Adams, 1853 by Hickman (1976). Family Pseudomelatomidae including the genus *Comitas* is characterized by a smooth paucispiral protoconch.

Genus *Boreocomitas* Hickman, 1976

Type Species: *Comitas* (*Boreocomitas*) *oregonensis* Hickman, 1976

Remarks: *Boreocomitas* is characterized by having a medium to moderately large-sized fusiform shell with axial nodes on the keel and fine spiral threads, which are less prominent on its wide shoulder than anterior ward. Its anal sinus is broad and moderately deep on the shoulder. According to Hickman (1976), "the protoconch is missing or worn on all specimens examined, but it is apparently paucispiral". The genus *Comitas* Finlay, 1926, has a more slender shell, a narrower shoulder, a longer anterior canal and weaker nodes on the periphery than in *Boreocomitas*. It can be judged that these differences are enough to separate the two taxa as distinct genera. Although the

Table 1. Mollusks associated species with *Boreocomitas inouei* new species.

Species
Leionucula yotsukurensis (Hirayama)
Acila (*Truncacila*) *hokkaidoensis* (Nagao)
Ezonuculana aff. *obsoleta* Tashiro
Malletia poronaica (Yokoyama)
Menneroctenia plena Kalishevich
Pseudoneilonella? sp.
Tindaria paleocenica Amano and Jenkins
Propeamussium yubarense (Yabe and Nagao)
Limaria sp.
Myrtea ezoensis (Nagao)*
Thyasira oliveri Amano and Jenkins*
Astarte sp.
Cidarina? sp.
Naticidae gen. et sp. indet.
Kangilioptera sp.
Urahorosphaera kanekoi Amano and Oleinik
Admete katsauhiraensis Amano, Oleonik and Jenkins
Acteocina sp.
Retusa sp.
Biplica paleocenica Amano and Jenkins
Striodentalium sp.
Laevidentalium sp.

* Chemosymbiotic species.

pseudomelatomid genus *Nekewis* Stewart, 1927, resembles *Boreocomitas*, *Nekewis* can be distinguished from *Boreocomitas* by having a long and straight anterior canal with a fasciole and shallow anal sinus. Wenz (1938) mistakenly considered *Nekewis* to be a synonym of the raphitomid genus *Clinura* Bellardi, 1875. *Clinura* is very similar to *Boreocomitas* in having biconic general outline with distinct axial nodes on its periphery. However, *Clinura* has a protoconch that is narrowly conical and diagonally cancellate. Its diagonally cancellate protoconch demonstrates that *Clinura* belongs in Raphitomidae Bellardi, 1875. *Clinura* also has an anal sinus whose apex is located near the suture on the shoulder slope.

Boreocomitas inouei new species
(Figures 2, 3, 4)

Diagnosis: Moderate-sized, short, biconic *Boreocomitas* species consisting of five and half whorls and at least one smooth paucispiral protoconch. Surface sculptured with 23 spiral cords on base, nine on keel and six above wide shoulder, and fine sinuous growth lines on last whorl. Apex of anal sinus located at midpoint of shoulder.

Description: Shell moderate-sized, attaining 20.4 mm in height, fusiform, consisting of 5.5 teleoconch whorls and one protoconch whorl. Apical angle ranging from 59° to 73°. Protoconch smooth, paucispiral, and with large diameter ($d = 1.6$ mm in paratype UMUT CM 32942). Last whorl very large, occupying about 74% of shell height in holotype; spire low; subsutural band very weak; shoulder slope broad and gently concave. Surface of penultimate whorl sculptured with one fine spiral cord below keel, six on keel, shoulder slope smooth, without growth lines, and 21 axial nodes on keel; keel of last whorl with 22 axial nodes, 23 spiral cords on base, nine on keel, and six very weak fine cords just above keel and five very faint on shoulder below subsutural band; among spiral cords on last whorl, two cords below keel stronger than other cords. Anal sinus moderately deep, its apex located at midpoint of shoulder slope on last whorl and just below subsutural band on penultimate whorl. Aperture pyriform; outer lip very thin; inner lip covered by thin, narrow callus. Anterior canal short, slightly broken on anteriormost part, but having slight siphonal fasciole.

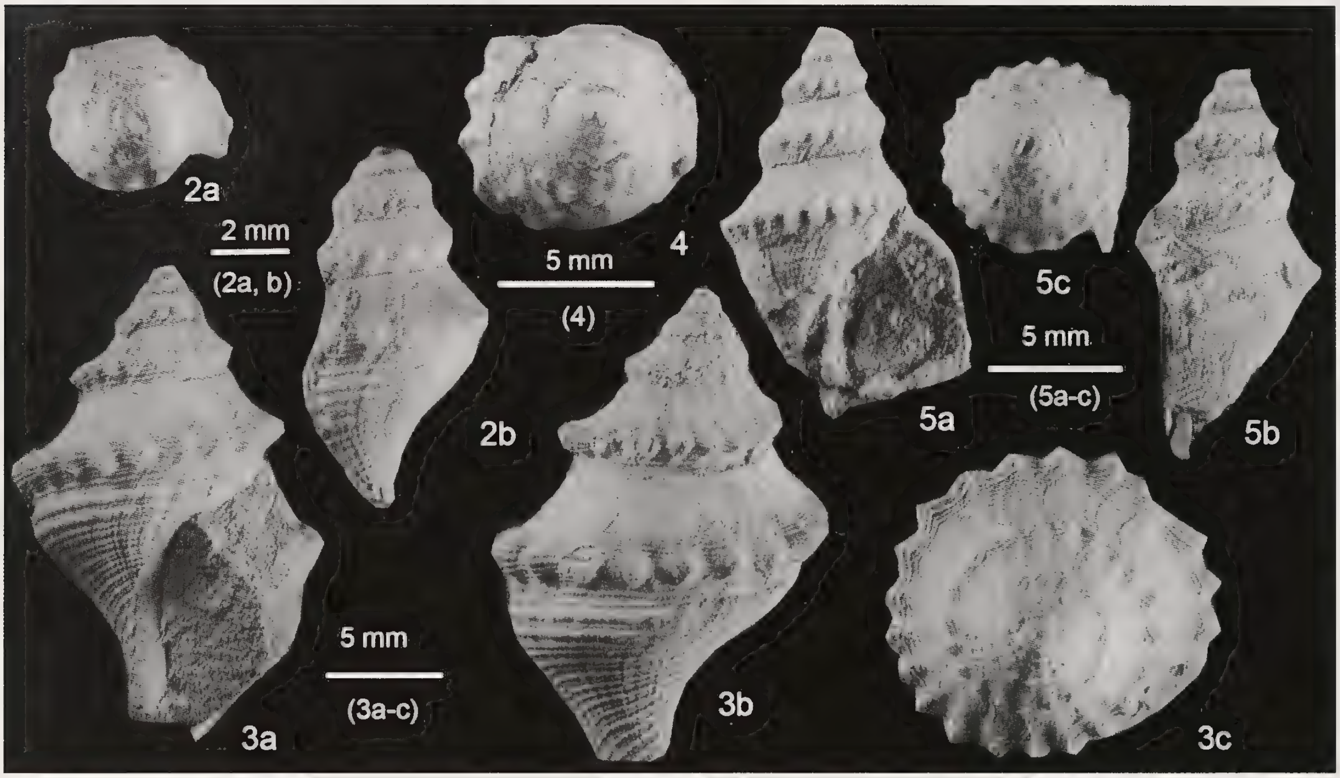
Type Material: Holotype, UMUT CM 32793 (shell height, 20.4 mm+; diameter, 13.5 mm); Paratype, UMUT CM 32794 (shell height, 9.0 mm; diameter, 5.9 mm); Paratype, UMUT CM 32942 (diameter, 7.5 mm+).

Type Locality: Cliff along Urahoro River, 44 m south from mouth of Kokatsuhirazawa River, Urahoro Town, eastern Hokkaido.

Remarks: This is the first record of *Boreocomitas* in the Paleocene and from the northwestern Pacific region. *Boreocomitas inouei* new species is similar to *Boreocomitas biconica* (Hickman, 1976) from the middle to upper Eocene Cowlitz Formation in northwestern Oregon in having a similar size (shell height of *B. biconica*, 20.0 mm), a relatively low spire and a similar number of nodes on the last whorl (20 in *B. biconica*). However, the present new species has higher ratio of diameter (D)/shell height (H) than the *B. biconica* species ($D/H = 0.66$ for *B. inouei*; 0.53 in *B. biconica*). Also, unlike *B. biconica*, the present species has a spiral cord below the periphery and no beaded subsutural cords.

Some previously identified species belonging to the now invalid genus *Pleurotoma* Lamarck, 1799, are now allocated to other genera. Among them, *Pleurotoma* (*Pseudotoma*) *brevior* von Koenen, 1885 (p. 35–36, pl. 2, figs. 5a–c), was described from the Selandian of Copenhagen, Denmark. Later, this species was re-described as *Genotia brevior* by Ravn (1939, p. 93–94, pl. 4, fig. 11a–b). Judging from the size, outline, sculpture and smooth protoconch, *P. brevior* can be confidently allocated to *Boreocomitas*. *Boreocomitas brevior* **new combination** differs from *B. inouei* new species in having a more slender, larger shell (ca. 30 mm in height), with fewer nodes on the axial keel (18 to 19 in *B. brevior*) and distinct spiral cords on the shoulder slope, and with more numerous protoconch whorls (3.5 in *B. brevior*).

The genus *Clinura* Bellardi, 1875, has a similar shell outline to *Boreocomitas*, with similar, moderately deep anal sinus and many nodes on its keel. Among the species of *Clinura*, *Clinura* sp. 1 from the Sonja Lens of the Selandian Agatdal Formation in the western part of Greenland (Nûgssuaq) was illustrated by Kollmann and Peel (1983, p. 97–98, fig. 220). This species is very similar to the present new species in having a short biconic outline, apex of the anal sinus located at the midpoint of the broad shoulder slope, and very fine spiral cords above



Figures 2–5. *Boreocomitas* species from the Katsuhira Formation. **2–4.** *Boreocomitas inouei* new species. **2.** Paratype, UMUT CM 32794; 2a. Apical view; 2b. Lateral view showing deep anal sinus of growth lines above shoulder slope. **3.** Holotype, UMUT CM 32793; 3a. Apertural view; 3b. Abapertural view; 3c. Apical view. **4.** Paratype, UMUT CM 32942, Apical view. **5.** *Boreocomitas* sp., UMUT CM 32943; 5a. Apertural view; 5b. Side view; 5c. Apical view.

the keel. This species also has a smooth paucispiral protoconch, which warrants its allocation to *Boreocomitas*, not in *Clinura*. This species can be distinguished from *B. inouei* new species by its larger shell (ca. 40 mm in height), less numerous axial nodes, and by having only one spiral cord below the keel on the last whorl.

Etymology: The new species is named for Kiyokazu Inoue (Obihiro), who collected the holotype.

Distribution: Known only from the type locality, in the upper Selandian to lowest Thanetian Katsuhira Formation, Urahoro Town, eastern Hokkaido.

Boreocomitas species
(Figure 5)

Description: Shell small, 13.1 mm in height, fusiform, consisting of 5 teleoconch whorls; protoconch missing. Apical angle 47°. Last whorl large, occupying about 69% of shell height; spire high; subsutural band very weak; shoulder slope broad and gently concave. Surface of penultimate whorl sculptured with four fine spiral cords below keel, three on keel, shoulder slope smooth, and 21 axial nodes on keel; keel of last whorl with 20 axial nodes, 12 spiral cords on base, three on keel, and no cord on shoulder below subsutural band. Anal sinus moderately deep, its apex located at midpoint of shoulder slope on last whorl and just below subsutural band on penultimate whorl. Aperture pyriform; outer lip very thin; inner lip covered by thin, narrow callus. Anterior canal short.

Remarks: This species is similar to *Boreocomitas inouei* new species as above described. However, *Boreocomitas* species differs from *B. inouei* by having a slender form, a higher spire, no spiral cord on the shoulder. *Boreocomitas oregonensis* (Hickman, 1976), the type species of the genus, is similar to *Boreocomitas* species in having a rather higher spire. However, the type species has some distinct spiral threads on its shoulder.

Distribution: Known only from the type locality of *Boreocomitas inouei* new speices, in the upper Selandian to lowest Thanetian Katsuhira Formation, Urahoro Town, eastern Hokkaido.

DISCUSSION

The described species possibly lived in a wood-fall community of upper bathyal depths. When Hickman (1976) proposed *Boreocomitas*, this genus appeared to be confined mainly to the middle Eocene to lower Oligocene deposits in Oregon. As noted above, Gladenkov et al. (1991) described and illustrated *Comitas* (*Boreocomitas*) sp. from the upper Eocene Kovachinskaya Formation in western Kamchatka. However, that shell is poorly preserved, with weak nodes on the keel and a narrow shoulder. It is uncertain whether this species can be classified in *Boreocomitas*. Our study shows that *Boreocomitas* dates back to the Selandian and it had a broad distribution including Denmark, western Greenland and eastern Hokkaido.

The aporrhaid gastropod *Kangilioptera* Rosenkranz, 1970 shows the same geographical pattern to *Boreocomitas*. *Kangilioptera* has been recorded from the upper Danian Kangilia Formation in western Greenland, the Selandian Kerteminde Marl in Denmark and the upper Selandian to lowest Thanetian Katsuhira Formation in eastern Hokkaido (Rosenkranz, 1970; Kollmann and Peel, 1983; Amano and Jenkins, 2014; Schnetler and Nielsen, 2018) (Table 2).

The astartid bivalve *Astarte paleocenica* Amano and Jenkins in Amano et al., 2018 from the Katsuhira Formation is similar to *A. parvula* Kalishevich in Kalishevich et al., 1981, from the Danian Krasnoyarskaya Formation in southeastern Sakhalin and *A. trigonula* Koenen, 1885, from the Selandian Lellinge Greensand (see also Amano et al. 2018; Schnetler, 2001).

The bivalve genus *Conchocele* Gabb, 1866, has its earliest confirmed occurrences in the latest Cretaceous (Maastrichtian) of Antarctica, the Danian of western Greenland, and the Thanetian of Spitsbergen (Rosenkranz, 1970; Little et al. 2015; Hryniewicz et al., 2016, 2017). In Spitsbergen, the genus survived to the late Eocene–early Oligocene (Thiedig et al., 1980). There are so far no confirmed records of *Conchocele* from the Cretaceous and Paleocene of the northern Pacific area. However, some publications suggest it could have been present in the Pacific during the Late Cretaceous. *Conchocele cretacea* has been recorded from the Upper Cretaceous deposits from Vancouver Island area (Whiteaves 1874, p. 11–12, figs. 2, 2a). *Thyasira cretacea* (= *Conchocele cretacea*) has also been recorded from the Coniacian(?) Funks Formation of Sacramento Valley area in California (Anderson, 1958). Therefore, the absence of *Conchocele* in the Upper Cretaceous and Paleocene of northern Pacific area might be just an artifact of the fossil record. The genus became very common in the northern Pacific region after the Paleocene (Hickman, 2015; Hryniewicz et al., 2017). This distribution pattern shows that *Conchocele* populations could have interchanged between the northern Pacific and the North Atlantic/Arctic regions at least by the late Eocene, or probably earlier.

Moreover, the oldest record of the deep-sea arcid bivalve genus *Bentharca* Verrill and Bush, 1898, has been found in the upper Selandian to lowest Thanetian Katsuhira Formation in eastern Hokkaido (Amano et al., 2015). As pointed by Amano et al. (2015), *Barbatia* (*Acar*) *hennigi* Heinberg, 1978, from the Maastrichtian to Danian deposits in Denmark is possibly an ancestor of this genus.

Adding to *Boreocomitas*, the four deep-sea mollusks above mentioned occur in both northern Pacific and North Atlantic/Arctic, indicating the sea connection between both areas during the Paleocene, although most paleontologists believe that the Arctic was isolated from the Pacific from the Albian to the latest Miocene (Marincovich et al., 1990, 2002; Thiede et al., 1990; Marincovich, 1993; Marincovich and Gladenkov, 1999; Beard and Dawson, 1999). Deep-sea genera commonly have broad geographic distribution (e.g. Amano et al. 2015a, b; Amano and Jenkins 2017), and similarities between the fauna of the Paleocene Katsuhira Formation from Hokkaido and that of the North Atlantic/Arctic Paleocene mollusk faunas could be partially caused by that. However, an alternative explanation is that the Bering Strait was to some extent open and connected northern Pacific and Arctic oceans, allowing for faunal interchange between both areas during the Selandian to late Eocene time. When Brikiatis (2014) reviewed the early Cenozoic paleogeography around the Arctic region based on the land mammals and flora, he showed no land bridge around the Arctic Ocean during the Selandian in his Figure 8. Gleason et al. (2009) also reconstructed the early Eocene paleogeographic map without any land bridge surrounding the Arctic Ocean, based on the

Table 2. Taxa of Paleocene faunas shared between the Northwestern Pacific, Arctic and Northern Atlantic regions.

Region	NW. Pacific		Arctic/ N.Atlantic			
	E. Hokkaido	SE. Sakhalin	Ellesmere Is.	Spitsbergen Is.	W. Greenland	Denmark
Taxa Age	L. Selandian– E. Thanetian	Danian	Paleocene	Selandian	Danian– Selandian	Danian– Selandian
Bentharca	+					+?
Small *Astarte*	+	+				+
Thyasira	+	+				+
Conchocele				+	+	
Kangilioptera	+				+	+
Drepanocheilus		+	+		+	+
Aporrhaidae				+		
Boreocomitas	+				+	+
Reference	This study	Kalishevich (1981)	Marincovich and Zinsmeister (1991)	Hryniewicz et al. (2016)	Rosenkranz (1970), Kollmann and Peel (1983)	Ravn (1939), Heinberg (1999), Schnetler and Nielsen (2018)

examination of Nd-Sr isotopes in fossil fish debris from Lomonosov Ridge. Although these data support our hypothesis on the Paleogene temporary opening of the Bering Strait, more data are needed to confirm it.

ACKNOWLEDGMENTS

We acknowledge Alan Beu (GNS Science) and Geerat J. Vermeij (UC Davis) for providing comments to an earlier version of the manuscript. We thank Carole S. Hickman (UC Berkeley) for her information on the type specimens of *Boreocomitas* species. We thank Anton E. Oleinik (Florida Atlantic University) and Kai I. Schnetler (Denmark) for their information on fossil species from the Paleogene in Kamchatka and Denmark. We also express many thanks to Kiyokazu Inoue (Obihoro in eastern Hokkaido) who found the holotype and kindly donated *Boreocomitas* specimen. This study was supported by a Grant-in-aid for Scientific Research from the Japan Society for Promotion of Science (C, 17K05691, 2017–2019) to KA and RGJ. Financial support to KH was provided by the Polish National Science Centre (NCN) research grant 2014/15/B/ST10/04886 "The influence of Paleocene/Eocene Thermal Maximum on oceanic chemosynthesis-based ecosystems".

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Three new species of the genus *Humboldtiana* (Gastropoda: Pulmonata: Humboldtianidae) from Mexico

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ABSTRACT

Three new species of the genus *Humboldtiana* are described. The presence of a mantle mottled with dark spots allocates *H. paquimei* from Chihuahua to the subgenus *Gymnopallax*. On the other hand, the embryonic whorls, a smooth and granular sculpture distributed over the shell surface, allocate *H. wixarika* from Jalisco and *H. aurea* from Chihuahua to the subgenus *Humboldtiana* s.s. The newly described species are distinguished from other species of the genus by the combination of shell and anatomical characters and by their geographic distribution.

Additional Keywords: Taxonomy, land snail, neotropical region

INTRODUCTION

The land snail genus *Humboldtiana* von Ihering 1892 (see Pilsbry, 1927) is comprised by more than 50 species patchily distributed from the southwestern United States to central Mexico (Thompson, 2011). With the exception of three "widely distributed species", *H. buffoniana*, *H. nuevoleonis*, and *H. durangoensis*, most of the species are microendemic and known only from the type locality. The classification followed herein was proposed by Thompson (2011). It recognizes six subgenera based on shell and reproductive anatomy: *Polyomphala* Thompson and Brewer, 2000; *Gymnopallax* Thompson, 2006; *Clydonacme* Thompson, 2006; *Aglotrochus* Thompson, 2006; *Oreades* Thompson and Brewer, 2000; and *Humboldtiana* Thompson and Brewer, 2000. The subgenus *Polyomphala* includes species with depressed shells with nodular tubercles and dart bulbs exposed; the subgenus *Gymnopallax* is composed of species with mottled mantle with dark gray spot, and shell apex usually decollated; the subgenus *Clydonacme* includes species with an embryonic shell sculpture consisting of wavy transverse striations and granular sculpture restricted to the first postembryonic whorl; the subgenus *Aglotrochus* comprises species that completely lack the granular sculpture; species in the subgenus *Oreades* do not have the dart apparatus; and the subgenus *Humboldtiana* is composed of species with embryonic whorls present (not decollated) and a smooth and granular sculpture distributed over the entire shell surface. Despite the presence of a more or less conserved pattern that suggests morphostatic radiation (Gittenberger, 1991), it is difficult to find morphological synapomorphies for the entire genus owing to the fact that the granular sculpture is absent in certain species (Thompson and Brewer, 2000; Thompson, 2006). Nevertheless, the molecular phylogeny clearly supports the monophyly of the genera, although not the monophyly of the subgenera (Mejía and Zúñiga, 2007). Despite of this, we adhere to the current classification until a new review of the genus is available. Authorities for the new species are as follows: *Humboldtiana wixarika* new species Mejía, López, and Reyes-Gómez; *Humboldtiana aurea* new species Mejía and López; and *Humboldtiana paquimei* new species Mejía and López.

MATERIALS AND METHODS

Despite being medium- to large-sized land snails, the species of the genus *Humboldtiana* are very elusive and hard to collect. In fact, with selected exceptions noted, most of the species previously named have been described based on very few individuals. For this reason, the descriptions of new species herein are based on the holotype and one or two paratypes only. Shell description and morphological measurements were performed according to Thompson and Brewer (2000). In all cases, the first measurement (or counts, for the number of whorls) is from the holotype and the measurements in parentheses are from paratypes 1 and 2, respectively. The types of the newly described species are deposited at Colección Nacional de Moluscos (CNMO), Instituto de Biología, UNAM, Ciudad de México. Color photographs of the currently described species shells are available at https://osf.io/3cswm.

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SYSTEMATICS

Family Humboldtianidae Pilsbry, 1939

Genus *Humboldtiana* von Ihering, 1892

Humboldtiana wixarika new species Mejía, López, and Reyes-Gómez

(Figures 1–4, 13)

Diagnosis: Medium-sized *Humboldtiana* with pale-brown shell bearing three equal-sized dark brown bands clearly visible on internal shell surface. Presence of short verge composed by four lobes and penis with two thick longitudinal fleshy columns distinguish this species from other species in subgenus *Humboldtiana*, where dart glands are separated from dart sacs by distance equal to or longer than glands length.

Description: Shell (Figures 1–4) globose, outer lip not reflected, pale brown, with three chestnut to dark-brown bands of same size, first band often lighter in color toward end of embryonic whorl, 4 whorls (4.1, 4.0). Embryonic shell caramel in color, with 1.7 whorls (1.8, 1.7), first whorl without sculpture, then with almost imperceptible growth lines. Sculpture of rest of shell consisting of white growth lines more evident toward shell aperture and randomly distributed small oval granules absent toward aperture. Umbilicus completely covered by basal portion of

Figures 1–4. *Humboldtiana wixarika* new species. Holotype, CNMO 756. 1) Apertural view 2) Apical view 3) Oblique basal view 4) Detail of embryonic whorls.

peristome. Parietal callus thin, transparent to white. Shell height 37 mm (36, 38); shell diameter 39 mm (43, 45); aperture height 28 mm (33, 29); aperture diameter 26 mm (25, 29).

REPRODUCTIVE ANATOMY (Figure 13): Penis short 8 mm (6.5, 7.2), bulbous to globose, tapering at distal end, penis lumen with two thick columns, short verge extending to first third of penis and composed of four lobes. Penis retractor muscle 14 mm long (14, 15). Epiphallus long, cylindrical, measuring 38 mm (46, 34). Flagellum short, 51 mm in length (44, 59), near 0.85 times (1.18, 0.67) the combined length of penis plus epiphallus. Atrium short, 1.28 mm (2.27, 1.65). Lower vagina short and slightly shorter than half penis size, 3.76 mm (3.76, 3.40), extending to region of dart sacs; four dart sacs approximately of same size: ds1 (2.41 mm), ds2 (2.33 mm), ds3 (2.70 mm), and ds4 (2.07 mm) (3.14, 3.02, 4.00, 3.38) (2.53, 2.17, 3.40, 2.56). Median vagina short, bearing four dart glands forming a ring, dart glands reaching a maximum height of 2.91 mm (3.24, 3.31) and separated from dart sacs by distance of 2.55 mm (2.8, 2.11). Spermathecal duct 81 mm length (128, 114), spermatheca with caecum of 11 mm length (8, 8) adhering to the albumen gland, elongated and sac-shaped, with a length of 11 mm (10, 7).

Type Material: Holotype: CNMO 7561; collected 29 August 2017 by José María Reyes Gómez; **Paratypes:** CNMO 7562 (2); same data as the holotype. All from type locality.

Type Locality: Jalisco, km 29 Carretera Bolaños, Tuxpan, 11.1 km northwest of Bolaños, Jalisco, 2454 m altitude (21°54′04″ N, 103°51′33″ W). The individuals were collected on the ground in a pine-oak forest.

Distribution: Known only from type locality.

Remarks: The subgenus *Humboldtiana* comprises a very disparate group of species where the embryonic whorls are smooth (Thompson, 2006). In this subgenus, three groups of species have been recognized, the *Humboldtiana buffoniana* species group in which the dart glands are located just above the dart sacs, the *Humboldtiana bicincta* species group where the dart sac apparatus is reduced, and the *Humboldtiana texana* species group where the dart glands are separated from the dart sacs by a distance equal or higher than the length of the dart sacs and the epiphallic chamber is absent (Thompson and Brewer, 2000). *Humboldtiana wixarika* new species belongs to the *Humboldtiana texana* species group. By having a short verge with four digitiform lobes, this species is similar to *H. fasciata* (Burch and Thompson, 1957) from the state of Hidalgo, Mexico, but in contrast to *H. fasciata*, *H. wixarika* presents two thick columns in the interior of the penis instead seven longitudinal folds. Besides, this latter feature, the verge, and the median vagina in *H. wixarika* are smaller than in *H. fasciata*. On the other hand, the shape of the penis of *H. wixarika* is similar to that of *H. balanites* from the state of Chihuahua, Mexico, but in this last species, the verge is multilobed and its size is almost the size of the penis, in opposition to *H. wixarika*, where the verge is short. Additionally, although in both species the atrium is short, it is quite evident in *H. wixarika*, while in *H. balanites* it is barely distinguishable.

Etymology: The specific epithet, a noun in apposition, is dedicated to the Wixárika people, better known by their Spanish name, Huicholes, a brave people that reject succumbing to the pressures of the modern world.

Humboldtiana aurea new species Mejía and López

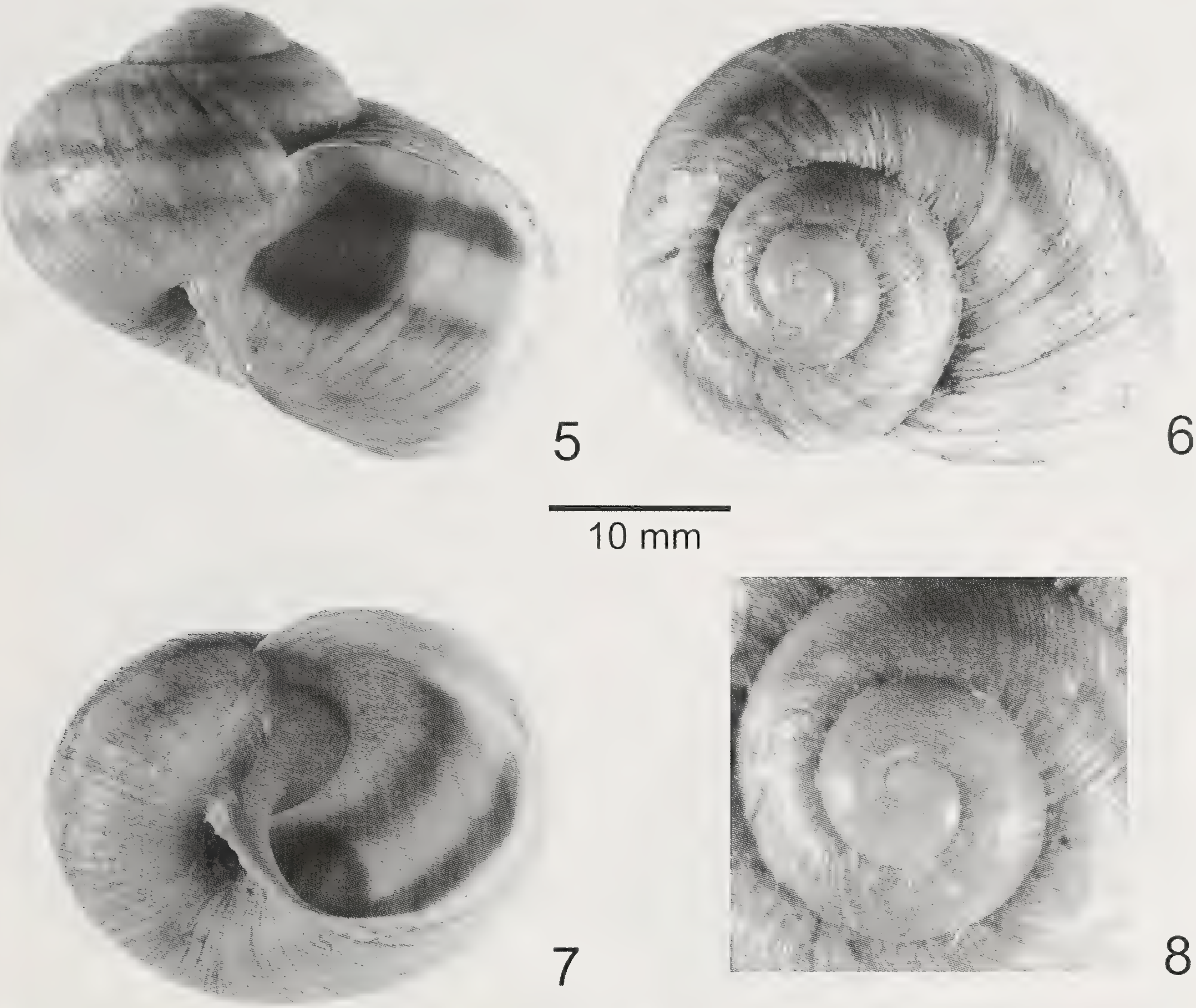
(Figures 5–8, 14)

Diagnosis: Medium-sized *Humboldtiana* with thin and fragile shell. The new species is similar to other species in the *Humboldtiana texana* species complex by having protruding dart bulbs at the base of the dart sacs while differing from the rest of the species in the group by possessing four sub-equal dart sacs and lacking a caecum on the spermathecal duct. The description is based on the holotype and two paratypes.

Description: SHELL (Figures 5–8) small, subglobose and thin, outer lip slightly thickened, pale-brown to golden with three clearly defined dark-brown bands, in certain specimens bands fade toward the aperture, with first and second band of same width, third band narrower, 4.1 whorls (3.2, 3.2). Embryonic shell with 1.2 whorls (1.1, 1.3), paler than rest of shell. First whorl without sculpture, remainder of whorls with few, weak growth lines. Remainder of shell sculptured with growth lines and small ovate granules absent on umbilicus. Umbilicus partially covered by basal portion of peristome. Callus thin, transparent. Shell height 25 mm (25, 23); shell diameter 29 mm (31, 28); aperture height 19 mm (17, 16), aperture diameter 19 mm (18, 18).

REPRODUCTIVE ANATOMY (Figure 14): Penis short and globose 7.61 mm (6.94, 7.98), penis with verge extending half penis length, composed of three skirts of tissue, one of them with three digitiform processes. Penis retractor muscle 5 mm (5.77, 5.2). Epiphallus short and cylindrical 20 mm (19.2, 20.0). Flagellum short 36 mm (38, 32), nearly 1.2 times (0.68, 0.87) the combined length of penis plus epiphallus. Atrium abbreviated and barely distinguishable. Lower vagina 5.82 mm (4.29, 5.32), extending to region of dart sacs; four sub-equal dart sacs ds1 (3.22 mm), ds2 (3.73 mm), ds3 (2.81 mm) and ds4 (2.30 mm) (2.39, 2.47, 1.98, 1.68) (2.35, 2.95, 2.81, 2.56). Dart bulbs embedded in vagina wall, forming conspicuous bulges. Median vagina abbreviated, bearing ring of four dart glands, dart glands reaching maximum height of 3.80 mm (3.05–3.39) and separated from dart sacs by distance of 1.83 mm length (2.86–2.81). Spermathecal duct short, 47mm (37–50) and without a caecum. Spermatheca elongated and sac-shaped, 9 mm length (7.54–9.81).

Type Material: Holotype: CNMO 7563; collected 9 August 2007 by Omar Mejía. **Paratypes:** CNMO 7564 (2); same data as the holotype. All from type locality.



Figures 5–8. *Humboldtiana aurea* new species. Holotype, CNMO 7563. 5) Apertural view 6) Apical view 7) Oblique basal view 8) Detail of embryonic whorls.

Type Locality: Chihuahua, El Oro, municipality of Casas Grandes, near the border with the State of Sonora, 67 km southwest of Nuevo Casas Grandes, Chihuahua, 2054 m altitude (30°09′ 35″ N, 108°33′56″ W). The specimens were collected on the rocks next to a small waterfall, where the predominant vegetation is an oak-pine forest.

Distribution: Only known from the type locality.

Remarks: *Humboldtiana aurea* new species belongs to the *H. texana* species group based on its dart glands separated from the dart sacs. Two other species of the group had been described from the state of Chihuahua, *H. balanites* (Thompson, 2006) and *H. corruga* (Thompson and Mejía, 2006). *Humboldtiana aurea* is similar to *H. balanites* as both have a thin shell, an abbreviated atrium, and bulges on the dart sac caused by the underlying dart bulbs; nevertheless, the light shell color with dark-brown bands of *H. aurea* contrasts with the dark-brown ground color with black bands of *H. balanites*. In addition, *H. balanites* has a multilobed verge, a long flagellum two times longer than the combined length of the penis plus epiphallus, a spermathecal duct that is twice the length of that present in *H. aurea* and, last but not least, *H. balanites* presents a short caecum in the spermathecal duct that is absent in *H. aurea*. On the other hand, *H. aurea* resembles *H. corruga* in size, but the shells of *H. corruga* are darker in color. The reproductive anatomies of *H. corruga* and *H. aurea* are similar in that both species have darts that protrude at the basis of the dart sacs, and both also have a short flagellum that is of same size as the combined length of the penis plus epiphallus; nevertheless, *H. corruga* differs from *H. aurea* by having a slenderer atrium, larger penis, dart sacs of the same size, a globular spermatheca, and a spermathecal duct that with a caecum.

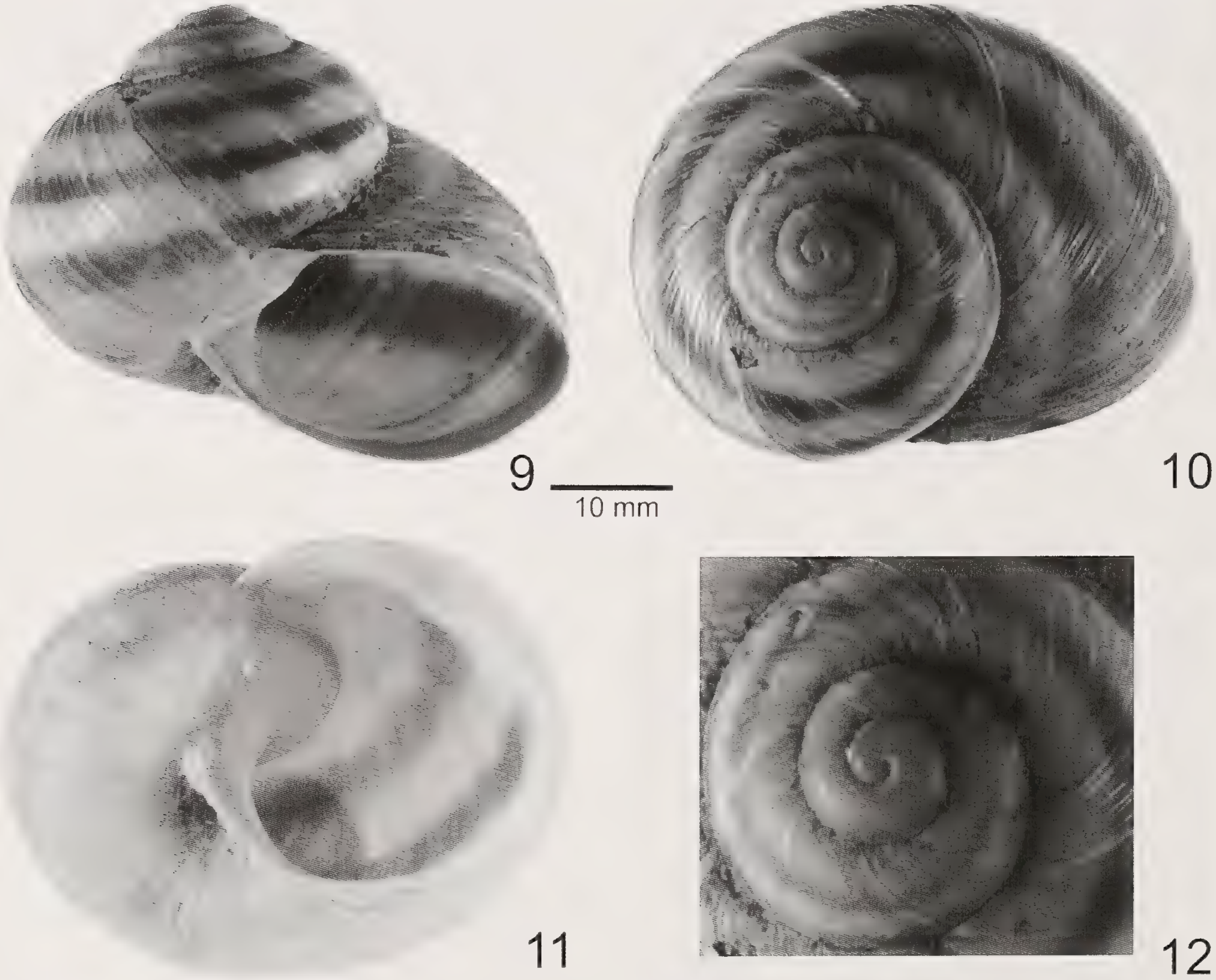
Etymology: The specific epithet, *aurea*, alludes to the name of the type locality, “El Oro” (“The Gold”) where the species was collected.

***Humboldtiana paquimei* new species Mejía and López** (Figures 9–12, 15)

Diagnosis: Medium-sized *Humboldtiana*. The new species has a similar shell to *H. regula* (Thompson, 2006), but differs in reproductive anatomy particularly on the verge, the length of the epiphallus and the spermathecal duct. The description is based on the holotype and one paratype.

Description: Shell (Figures 9–12) large, external lip not reflected, background color pale-brown, becoming darker toward aperture. Three well-defined chestnut- to dark-brown bands, third one wider than first and second. 4.1 Whorls (4.1). Embryonic shell lighter than remainder of shell, with 1.2 (1.4) whorls and with sculpture of weak wavy striations. Sculpture of second whorl with small granules; remainder of shell with striations and white streaks. Umbilicus almost completely covered by basal portion of peristome. Callus very thin, transparent. Shell height 37 mm (31); shell diameter 38 mm (33); aperture height 25 mm (21); aperture diameter 23 mm (20).

Reproductive Anatomy (Figure 15): Penis short 7.91 mm (7.24), slender at base and swollen in middle; short and stout verge of approximately one-third penis length and consisting of two tissue folds with digitiform processes. Penis retractor muscle 3.04 mm long (7.71). Epiphalus long, cylindrical and stout, measuring 34 mm (29), four times penis length. Flagellum short 60 mm in length (62), nearly 1.4 times (1.7) combined length of penis plus epiphallus. Atrium short and barely perceptible. Lower vagina of almost same length as penis, measuring 6.13 mm (5.68) and extending to region of dart sacs; four dart sacs of different sizes, ds1 largest, remainder decreasing in size,



Figures 9–12. *Humboldtiana paquimei* new species. Holotype, CNMO 7565. 9) Apertural view 10) Apical view 11) Oblique basal view 12) Detail of embryonic whorls.

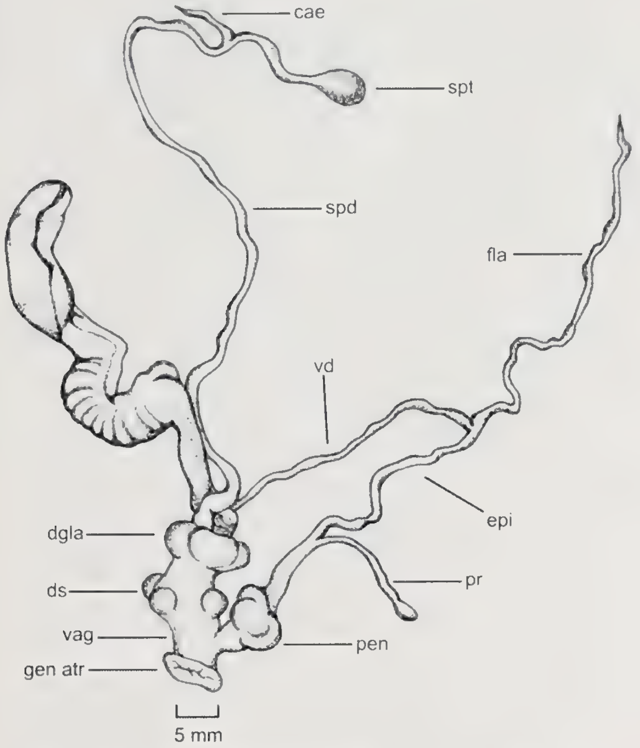


Figure 13. Reproductive anatomy of *Humboldtiana wixarika* new species. Abbreviations. **cae** :spermathecal caecum; **dgla:** dart glands;**ds;** dart sacs; **epi:** epiphallus; **fla:** flagellum; **gen atr;** genital atrium **pen:** penis; **pr:** penis retractor; **spd:** spermathecal duct; **spt:** spermatheca; **vag:** vagina; **vd:** vas deferens.

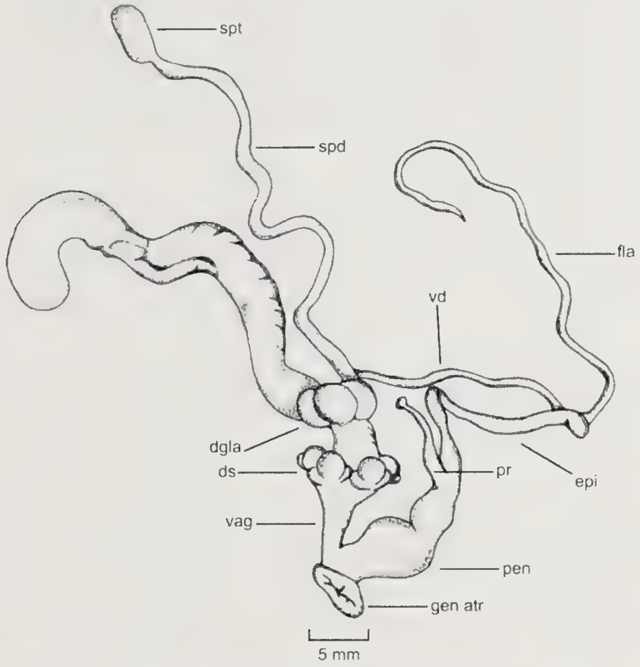


Figure 14. Reproductive anatomy of *Humboldtiana aurea* new species. Abbreviations. **dgla:** dart glands;**ds;** dart sacs; **epi:** epiphallus; **fla:** flagellum; **gen atr**; genital atrium **pen:** penis; **pr:** penis retractor; **spd:** spermathecal duct; **spt:** spermatheca; **vag:** vagina; **vd:** vas deferens.

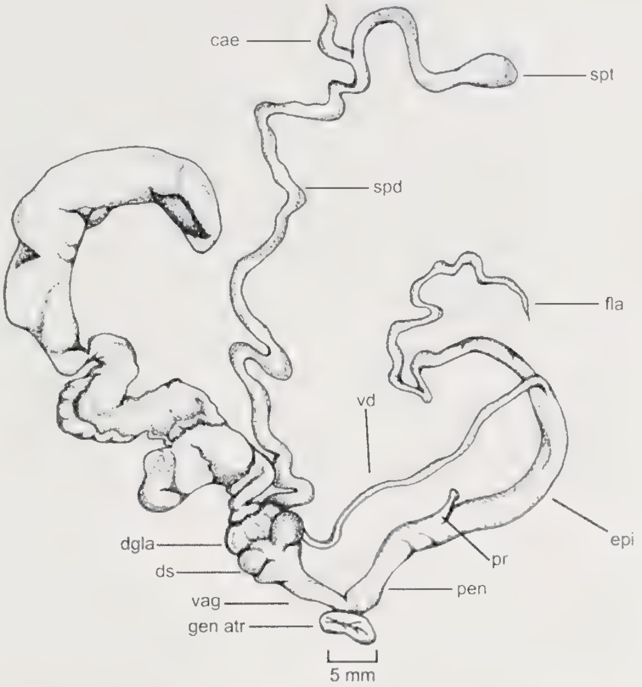


Figure 15. Reproductive anatomy of *Humboldtiana paquimei* new species. Abbreviations. **cae** :spermathecal caecum; **dgla:** dart glands;**ds;** dart sacs; **epi:** epiphallus; **fla:** flagellum; **gen atr;** genital atrium **pen:** penis; **pr:** penis retractor; **spd:** spermathecal duct; **spt:** spermatheca; **vag:** vagina; **vd:** vas deferens.

ds1 (4.12 mm), ds2 (3.51 mm), ds3 (3.02 mm) and ds4 (3.77 mm) (4.25, 4.08, 3.0, 3.5). Median vagina bearing four dart glands that form ring just above dart sacs and with maximum height of (3.07mm) (3.02). Spermathecal duct long, measuring 112 mm (103), bearing short caecum of 8 mm length (6). Spermatheca sac-shaped, adhered to albumen gland, measuring 7 mm (10).

Type Material: Holotype: CNMO 7565; collected 9 August 2007 by Omar Mejía; **Paratype:** CNMO 7566 (1); same data as the holotype. All from type locality.

Type Locality: Chihuahua, bridge over Río Piedras Verdes. Approximately 1 km Southeast of El Willy, municipality of Casas Grandes, Chihuahua, 1829 m altitude (30°10'29" N, 108°18'40" W). Individuals were collected on the south wall of the canyon that surround the Piedras Verdes river, the predominant vegetation is an oak-pine forest.

Distribution: Only known from the type locality.

Remarks: The wavy sculpture of the embryonic whorl and the granular sculpture restricted to the first post-embryonic assigns the new species to the subgenus *Clydonacme*, a taxon so far limited to the State of Chihuahua that comprises six currently recognized species (Thompson, 2006). The shell of the new species is similar to *H. regula* (Thompson, 2006), but differs in three reproductive traits. In *H. paquimei*, the verge is stout and consisting of two tissue folds, in contrast to *H. regula*, where the verge is composed of a thin skirt of tissue. In

H. paquimei, the epiphallus is four times larger than the penis, and in *H. regula*, the epiphallus is twice the length of the penis. Last but not least, in *H. paquimei*, the spermathecal duct plus the spermatheca is three times longer than in *H. regula*. Two shells deposited at the Florida Museum of Natural History (UF 185700 and UF103138) may be *H. paquimei* based on geographical proximity. These two specimens unfortunately lack reproductive anatomy and were excluded from the description.

Etymology: Paquimé was an ancient culture that developed in northwestern Mexico between the years 700 and 1475. The maximum expression of this culture is found in the municipality of Casas Grandes, Chihuahua. The name of the new species honors this culture and the archaeological zone of Paquimé, Intangible Cultural Heritage of Humanity since 1998.

ACKNOWLEDGMENTS

We are grateful to César Guzmán for taking the photographs, to Alejandra Rocha-Gómez for the illustrations of the reproductive anatomy, to John Slapcinsky at University of Florida Museum of Zoology who provided some photos *of H. regula* and two anonymous reviewers for their comments. This work was partially funded by Conacyt project number 165990. This work is dedicated to the memory of Prof. Fred G. Thompson.

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