CONTENTS

Jose H. Leal
Celebrating a long life: *The Nautilus* turns 120! .......................... 1

Nikolaus Malchus
Amended description of the areoid bivalve *Philobrya brattstromi*
Soot-Ryen, 1957, from Chile .................................................. 8

Claude Vilvens
Javier Sellanes
Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea:
Calliolomatidae) and *Margarettes huloti* new species (Gastropoda:
Trochoidea: Trochidae) from a methane seep area off Chile ............... 15

Fred G. Thompson
A new land snail of the genus *Humboldtiana* (Gastropoda: Pulmonata:
Humboldtianidae) from Nuevo León, Mexico .............................. 21

Fred G. Thompson
Omar Mejía
Two new land snails of the genus *Humboldtiana* (Gastropoda: Pulmonata:
Humboldtianidae) from Chihuahua, Mexico .............................. 25

W. Wyatt Oswald
Mollusks in a Holocene lake-sediment core from the Arctic Foothills of
northern Alaska ................................................................. 30

Michelle L. Boudreaux
Linda J. Walters
*Mytilopsis charrauana* (Bivalvia: Mytilidae): a new, invasive bivalve in
Mosquito Lagoon, Florida ..................................................... 34

Notice ..................................................................................... 37
Celebrating a long life: The Nautilus turns 120!

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The Nautilus is turning 120 years this year and I feel extremely honored and lucky to be writing this note to celebrate the occasion! The Nautilus is the one of the two oldest English-language malacological journals, second only to the Journal of Conchology in longevity in this category. My goal is to briefly showcase, particularly to readers from younger generations, some highlights of the journal’s evolution and of the work of its editors.

AN INAUSPICIOUS BEGINNING?

The Nautilus started in Philadelphia in July, 1886, as The Conchologists’ Exchange (TCE). William D. Averell (1853-1928), a shell trader from Chestnut Hill, Philadelphia, created TCE as a small publication aimed at "giving information of vital interest to the student of Mollusca" (Averell, 1886a).

In November of that same year Averell (1886b) observed: "It is our desire that each number shall be an improvement upon its predecessor... It is inevitable that new discoveries will continue to be made in our chosen field of research from now until the end of time, as vast areas have yet to be fully explored and their treasures described; and, again numerous species are rapidly becoming extinct, while others are scarcely known or have never had the light of discovery cast upon them." Averell’s words proved to be mostly prophetic in the long run. But the immediate future of TCE was uncertain. Starting in May, 1888, after 21 months of publication, the periodical went out of circulation for one year.

Former editor R. Tucker Abbott in his dedication of the 100th volume (1986) of the journal observed that "The Nautilus had a very auspicious beginning... Volume 1, number 1, was merely a postcard sent out to 500 people announcing that the annual subscription price... would be all of 25 cents." The first two volumes each consisted of a few pages published monthly in a duodecimo (12 mo) size (16.5x14 cm). The contents of TCE covered specimen exchange notices for collectors, short articles about collecting and preservation of mollusks, news, and brief narratives of field trips, sometimes to distant and exotic places such as Tampa, Florida.

PILSBRY TO THE RESCUE

Young conchologist and TCE contributor Henry Augustus Pilsbry (1862-1957) (Figure 1) was hired as conservator of the Conchological Section of the Academy of Natural Sciences of Philadelphia (ANSP) in 1888, a few weeks after he turned 25. After a year’s lapse and following negotiations between Pilsbry and Averell, in May, 1889, TCE became The Nautilus (volume 3, number 1), with Pilsbry as its editor. The journal size was adjusted to crown octavo (about 19x13 cm).

In his first number Pilsbry changed the physical format of the journal from double-column to single-column. In addition, he prominently displayed, starting on page 2, a brief technical article by W. H. Dall (1889) on the anatomy of the gastropod Trochus infundibulum. Dall’s paper, which differed considerably in style and content from the average note and exchange notice previously published in TCE, marked the beginning of Pilsbry’s shift in orientation of the journal. That change gave The Nautilus a new lease on life.

In all likelihood, Pilsbry assumed from the start that the reorganization of TCE as the more science-oriented The Nautilus was the natural thing to do. In the very first sentence of the Introduction to volume 3 (Pilsbry, 1889) the 26 year-old editor observed: "The publishers of The Nautilus feel that no explanation of their [objective] in offering this journal to the scientific public is necessary."

On the same page, he indicated that it was his wish to have malacological papers concentrated in a few specialized periodicals rather than in "the pages of innumerable [general science] journals." By "establishing journals devoted to special branches of science" such as malacology, it would be possible to "limit by some means the number of publications in which a certain subject is likely to be treated upon."

Possibly anticipating a decline in interest from subscribers, Pilsbry proposed that, upon the transition from TCE to The Nautilus, "All subscribers... will be allowed one insertion of twenty-five words in the Exchange Column, free of charge." The appeal to a diverse audience was epitomized in a brick-colored, promotional 15.2x8.2 cm flyer (Figure 2) published sometime in the early 1890s. The flyer professed: "Its scope is broad, including..."
articles on recent and fossil shells. Notes showing the drift of opinion on conchological subjects, are a valuable feature. In addition, the footer of the flyer announced: "Exchange column free to subscribers." The subscription price was $1.00 per year, $1.12 to foreign countries.

W. D. Averell remained as business manager of The Nautilus after the transition until the end of 1890. According to Baker (1958b), "His [Pilsbry's] one year's association with William D. Averell as its business manager was none too happy and, at the end of one volume, Averell was replaced by ... Charles W. Johnson ..." In a brief obituary of Averell, Pilsbry (1928) remarked: "He was deeply interested in conchology, but made no permanent collection. He was chiefly known as a dealer in shells and in connection with his little journal, which proved to be highly useful for bringing together the conchologists and collectors of the late '80s."

Pilsbry's tenure as editor of The Nautilus equaled in length and paralleled his long and productive career as a scientist (see Baker, 1958a); he edited the new version of the "little journal" between 1888 and 1957, a 69-year editorial stint probably unmatched in duration in the world of malacological publications. Pilsbry unquestionably consolidated the reputation of The Nautilus as a cutting-edge publication dealing with the many facets of 20th Century malacology. Pilsbry's biographers commented about his fortitude and love for The Nautilus to the very end. Daughter Elizabeth Pilsbry (1958) observed: "Of Father, at nearly 95, one truly may say: 'He died young.'"

EARLY BUSINESS MANAGEMENT

Pilsbry was aided for most of his career as editor of The Nautilus by Charles Willison Johnson (1863-1932) (Figure 2). Johnson was curator at the Wagner Free Institute.

Figure 1. Henry Augustus Pilsbry, 1862-1957, editor 1889-1957. Photo The Nautilus archives.

Figure 2. Promotional flyer, circa early 1890s. Note emphasis on scientific aspects combined with appeals to the non-professional audience of the journal. The line drawing portrays North American land snail Volutivna denotatum (Ferussac, 1821). The same drawing appeared earlier, as Helix palliata Say, in Bimney (1857), Bimney and Bland (1869), and Teator (1890).

THE NAUTILUS

A MONTHLY DEVO TED TO THE INTERESTS OF CONCH OLOGISTS.

EDITORS AND PUBLISHERS:
H. A. PILSBRY { Conservator Conchological Section, Academy Natural Sciences, Philadelphia.
C. W. JOHNSON { Curator of the Wagner Free Institute of Science, Philadelphia.

$1.00 per Year. $1.12 to Foreign Countries.
10 cts. a Copy.

The Nautilus is the only magazine in America devoted to the study of Mollusks. Its scope is broad, including articles on recent and fossil shells, often illustrated; on the anatomy and classification of mollusca; and papers of popular interest dealing with experiences of collectors in the field. Notes on current publications at home and abroad, showing the drift of opinion on conchological subjects, are a valuable feature. Indispensable to the Conchologist and Paleontologist.

Exchange column free to subscribers.
LIFE AFTER PILSBRY

After Pilsbry's death in December, 1957, Baker published a memorial issue (volume 71, number 3) appropriately named "The Pilsbry Nautilus". In that issue, Baker (1958b) observed: "At least twice, during September and October, 1957, Dr. Pilsbry implored me to make sure that The Nautilus would continue, and solemnly promised that it would."

And continue it did. Beginning in April, 1958, with volume 71, number 4, The Nautilus was edited by a triumvirate of malacologists led by Baker, now editor-in-chief of the journal. Baker outlined the operations plan for the journal following Pilsbry's death: Charles B. Wurtz (1916-1982) (Figure 6) from Philadelphia, and Robert Tucker Abbott (1919-1995) (Figure 7), newly hired to fill the Pilsbry Chair of Malacology at the ANSP, "will join the staff as junior editors with the understanding that, if at any future time either should cease to be a resident of the Philadelphia area, this would be considered as a tendered resignation" (Baker, 1958b).

R. Tucker Abbott was initially in charge of marine mollusks. Wurtz was responsible for mailing issues and became editor for fresh water mollusks and ecology, and Bernadine B. Baker ("Mrs. Horace B. B.") tended to the finances and subscriptions. Baker added: "Since the Bakers and The Nautilus can afford but one bank account, checks may be made out as usual." Between April, 1958, (volume 71, number 4) and April, 1972, (volume 85, number 4), The Nautilus was subtitled "The Pilsbry Quarterly devoted to the Interests of Conchologists." Between July, 1936 (volume 50, number 1) and April, 1972 (Volume 85, number 4), text on the second cover indicated that The Nautilus was "...the official [ ...an official ...] in the latter part of that period] organ of the American Malacological Union (now American Malacological Society)."

Baker was editor-in-chief until 1965, and served as Editor Emeritus until the time of his death in 1971. Abbott and Wurtz (1971) reminisced: "For 40 years he gave unstintingly of his time as business manager and editor of The Nautilus."

TUCKER'S TENURE

R. Tucker Abbott had been acting editor of The Nautilus since H. B. Baker had his first flurry of health complications in 1968. He left ANSP in that year to occupy the newly created Dr. Pont Chair of Malacology and serve as assistant director of the Delaware Museum of Natural History. Upon Baker's death in March, 1971, he formally became editor-in-chief of the journal, helped by Charles Wurtz and with Mrs. Baker as business manager.

Tucker edited The Nautilus from 1968 through 1985, making several changes in the format and editorial policy that basically shaped the journal as we know it today. Most of these improvements took place in July, 1972, with the publication of volume 86, number 1. This was a very hectic time in Tucker's life; among his many activi-
ties then were the preparation of the trend-setting and classic second edition of his American Seashells and the grand opening of the Hall of Shells at the Delaware Museum in May, 1972 (Harasewych, 1997). Tucker made many changes in the appearance of the journal. The size changed from crown octavo to 26.5x20.5 cm. He added a gray protective cover (each number in the preceding 85 years started with a contents

Figure 6. Charles B. Wurtz (1916–1982) at the AMU meeting at Haverford College in 1959. Photo from the American Malacological Society archives.


page of the same stock as the regular pages). An outline of a slightly stylized nautilus shell in cross-section became the logo (Figure 8), and the journal subtitle became “A quarterly devoted to malacology and the interests of conchologists”.

Another advance introduced in the same number was the addition of an editorial committee composed of 13 professionals representing a wide swath of American malacology. These were Arthur H. Clarke, Jr., William J. Clench, William K. Emerson, Morris K. Jacobson, Aurèle La Rocque, James H. McLean, Arthur S. Merrill, Donald R. Moore, Joseph Rosewater, G. Alan Solem, David H. Stansbery, Ruth D. Turner, and Gilbert L Voss.

Last but not least, he shifted the publication of the first number of each volume from July to January beginning with volume 57 (1973); volumes now match calendar years.

Tucker’s tenure as editor-in-chief spanned 17 years, not counting his years as co-editor under H. B. Baker. Tucker left the Delaware Museum in 1978 and, in his own words, “moved The Nautilus, now under the jurisdiction of my American Malacologists, Inc., to Melbourne, Florida, where it has been published for the last six years [1979–1985, actually seven years]” (Abbott, 1986). In that period, Tucker’s wife Cecelia was the journal’s business manager.

**THE HARASEWYCH YEARS**

In 1984 Tucker invited Miroslav George (Jerry) Harasewych (born in 1949) (Figure 9), a former student
and, at the time, a Research Fellow at the National Institute of Mental Health, to join the editorial staff of The Nautilus and to assist in various aspects of the production of the journal. Following the publication of volume 100 of The Nautilus, Abbott retired as editor, to be succeeded by Harasewych, then a newly appointed Curator of Marine Molluscs at the Smithsonian's National Museum of Natural History. During its first hundred volumes, The Nautilus was "owned" by the editor. To comply with the Smithsonian's requirement "to avoid the potential for an appearance of a conflict of interest," ownership of The Nautilus passed from American Malacologists to Trophion Corporation, a non-profit corporation established for the purpose during Harasewych's tenure as Editor.

Beginning with volume 101 (January 1987), Harasewych became editor-in-chief while Abbott continued as associate editor until his death in 1995. Harasewych again altered the format and contributed a new cover and logo, designed and illustrated by Hal Lewis Design, Inc., of Philadelphia; this is the design still in use today, including Lewis's beautiful line drawing of a live Nautilus pompilius on the cover, a nice improvement over the previous layout.

In addition, Jerry further added to the professional spin imparted by Tucker. He remarked (Harasewych, 1987) in the opening of volume 101, "The Nautilus will continue to meet ever higher standards in the publication of papers on all aspects of the biology and systematics of mollusks." At that time I was second-year graduate student at the Rosenstiel School in Miami and wondered how hard it would be from then on to have a manuscript accepted by the journal.

THE PRESENT

Jerry was editor until the baton was passed to me in May, 1998 (volume 111, number 3), after a brief stint as managing editor from February, 1997 (volume 110, number 2), to February, 1998 (volume 111, number 2). Tina Yorgey was managing editor between March, 2001 (volume 115, number 1) and December, 2006 (volume 119, number 4).

With the acquisition of The Nautilus by The Bailey-Matthews Shell Museum in 1998, the journal became for the first time owned by an academic organization. Tucker's role as founding director of the museum until his death in November, 1995, was ultimately instrumental in the transfer of The Nautilus to the organization.

The Nautilus results from a cooperative effort between its staff, authors, reviewers, and subscribers. With your help and support of future generations, I am certain that the journal will thrive for at least another 120 years.

ACKNOWLEDGMENTS

Baseline biographical data for this note was gleaned from the massive work by Coan, Kabat, and Petit (2006). For key information I am grateful to Paul Callomon, M.G.
Harasewych, Alan Kabat, Harry G. Lee, and Richard E. Petit. M.G. Harasewych, Linda Kramer, Kimberly Nealon, and Richard E. Petit critically reviewed the manuscript.

LITERATURE CITED


Amended description of the arcoid bivalve *Philobrya brattstromi*
Soot-Ryen, 1957, from Chile

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ABSTRACT
Cross-checking of the original material and labels for *Philobrya brattstromi* with the data from Soot-Ryen's publications (1957, 1959) confirms that that author had designated a holotype and five paratypes by 1953. All species other than those from station M24 and determined in the same year are thus excluded from the type series. The correct height of the holotype is 5.5 mm and not 15 mm as originally indicated by Soot-Ryen (1957) or 5.8 mm as he indicated subsequently (Soot-Ryen, 1959). The prodissoconch of *P. brattstromi* is devoid of sculptural elements (also at high magnifications) except for a raised, round-crested shell margin as already described by Soot-Ryen. However, it also has an incipient dorso-central boss and well-developed anterior and posterior wings. The mean length is 627 μm; the L/H ratio of 1.5 is high when compared to eleven congeners for which such measurements are available. Prominent morphological features of the postlarval shell are: (1) well-developed posterior G1 teeth which considerably increase in length antero-ventrally to a elongated ligament and that disintegrate ventrally into pustules; (2) four to five posterior tooth-like folds on the inner margin (previously described by Soot-Ryen), which correspond in number with ribs on the outer surface of valve; (3) a non-flaky periostracum. The shell microstructure is linear to complex crossed-lamelar with an inner prismatic layer. The additional presence of a (vestigial?) outer prismatic layer dorsal to the ligament area, the posterior disintegration of G1 teeth and the presence of a dorso-central boss on the prodissoconch resemble these states in the Limopsidae. However, it remains questionable whether these traits are inherited or convergent.

MATERIALS AND METHODS
The material includes five lots from the invertebrate collection of the Swedish Museum of Natural History in Stockholm (SMNH). The type series from the collection site “station M24” (SMNH 35894) consists of the holotype with articulated valves (AV) and five paratypes (one disarticulated LV and RV, and three AV). Eight specimens are from station M17 (SMNH 74831) (5 AV, 1 LV, 2 RV fragments), two soft parts (no shell) from station M48 (SMNH 74832), two AV from station M92 (SMNH 74833), and one AV from station M103 (SMNH 74834) (Table 1). Specimens from stations M21 and M27 mentioned in Soot-Ryen (1959) are not in the collection. Material from station M48 found in the collection is not mentioned in the list of stations in Soot-Ryen (1959: 6). One of the labels from SMNH 74834 indicates station M104; this latter, however, is not mentioned in the list of stations (1959). However, all other data on the label are identical with those given for station M103 in that list (Soot-Ryen 1959; 6) (Table 1). All specimens were preserved in ethanol, many of them with the periostracum preserved to a large extent.

INTRODUCTION
*Philobrya brattstromi* Soot-Ryen, 1957, belongs to a small but rather successful arcoid family, the Philobyidae, which radiated into about 85 extant species since the Eocene; about 45 of these species are currently included in the type genus *Philobrya* (Linse, 2004, pers. comm.). All descriptive and phylogenetic work on Philobyidae emphasizes the importance of prodissoconch and postlarval hinge characters (e.g., Bernard, 1897; Dell, 1964; Hayami and Kase, 1993; Malchus and Waren, 2005; Tevesz, 1977). However, until now, details of these characters and of the shell microstructure of *Philobrya brattstromi* have not been examined using a high-resolution microscope such as a scanning electron microscope (SEM) and are therefore still poorly known (compare with Soot-Ryen, 1957, 1959: pl. 1, fig. 6; Ramovino, 1968: pl. 5, figs. 2 and 4). In addition, Soot-Ryen’s original publications cast doubts about the identity of the holotype and thus also about the composition of the type series. The present contribution, therefore, aims to re-describe the main shell features in a modern interpretational context and to clarify the type status of the specimens.
Table 1. Data for the five lots of *P. brattstromi* from the Swedish Museum of Natural History (SMNH).

<table>
<thead>
<tr>
<th>SMNH number</th>
<th>Station</th>
<th>Date</th>
<th>Locality</th>
<th>Depth, substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>3894</td>
<td>M24</td>
<td>16 Dec. 1948</td>
<td>Seno Beluncavi, S of Isla Guar, 41°44' S, 72°45' W</td>
<td>70 m, sand with shells</td>
</tr>
<tr>
<td>74831</td>
<td>M17</td>
<td>14 Dec. 1948</td>
<td>Golfo de Ancud, Canal Callmuro, 41°46' S, 72°06' W</td>
<td>30 m, grey sand and small stones</td>
</tr>
<tr>
<td>74832</td>
<td>M48</td>
<td>3 Feb. 1949</td>
<td>Seno Beluncavi, bay of Puerto Monti, 41°28' S, 72°56' W</td>
<td>50 m, ?</td>
</tr>
<tr>
<td>74833</td>
<td>M92</td>
<td>3 May 1949</td>
<td>Golfo de Ancud, Bahia Bto, 41°53' S, 73°10' W</td>
<td>45 m, sand with dead algae</td>
</tr>
<tr>
<td>74834</td>
<td>M103 (M104?)</td>
<td>5 May 1949</td>
<td>Canal Chacao, N of Punta Soledad, 41°48' S, 73°31' W</td>
<td>40 m, stones and polychaete tubes</td>
</tr>
</tbody>
</table>

This material is deposited in the British Antarctic Survey, Cambridge, UK, accessible through ongoing collaborative work with Katrin Linse on Southern Ocean philobryids and the Swedish Museum of Natural History, Stockholm, Sweden, examined during a research stay; in addition, I examined the type series of *P. meleagrina* (Museum national d'Histoire naturelle, Paris) and *P. obstdah* (Zoological Museum, Oslo).

Specimens of *Philobyra brattstromi* were studied and shell dimensions (length and height) measured using a binocular microscope (×40 magnification). In addition, the holotype was photographed and measured under a Leica MZ FL IlS stereo microscope equipped with a Planapno objective and a DC 500 digital camera. Both valves of a disarticulated paratype and five specimens from lot SMNH 74831 were examined and measured under SEM. For this, the specimens were cleaned in 70% ethanol and some specimens also cleaned with commercial bleach for dissolution of the periostracum. Specimens were mounted on aluminum stubs with adhesive carbon pads and sputter-coated with gold. The microstructure was described from broken shells of a disarticulated paratype and one specimen from station M17 (SMNH 74831).

The lengths of the larval and postlarval shells were measured as the longest anterior–posterior distance parallel to the straight hinge axis of the prodissococho and the height as the longest dorso-ventral distance perpendicular to that axis (Figures 1, 2). Measurements of the adult shell under light microscopy include the periostracum; specimens measured under SEM lack the periostracum. Holotype dimensions were also determined using the long axis of the shell (with periostracum) and the longest extension perpendicular to the long axis (Figure 1). This orientation appears to be equivalent to the axes used by Soot-Ryen (1959). The umbral angle is defined as the angle enclosed by the tangents to the postero-dorsal and antero-dorsal shell margins of the postlarval shell (Figure 1).

**Historical Background**

Tron Soot-Ryen was entrusted with the identification of the bivalve fauna obtained during the Lund University Chile Expedition 1948–1949. The original labels accompanying the Museum material indicate that Soot-Ryen had established a holotype and paratypes and had determined all specimens now present in the collection by 1953. However, this is not evident from his original publication (Soot-Ryen, 1957), which provides only of a brief preliminary diagnosis, making reference to the type locality and to a shell length of 15 mm, supposedly of the holotype. A more complete account of the taxon with a taxonomic discussion and a list of collection sites was published in 1958. The description (called “diagnosis” therein) is identical to that from 1957 except that the shell length of the now explicitly named holotype changed to 5.8 mm (Soot-Ryen, 1959: 22–23, pl. 1, fig. 6). This value matches the measurements obtained here (with a slight deviation) whereas none of the collection specimens is as large as 15 mm. Interestingly, Soot-Ryen (1957: 3) cited a length of 5.8 mm for *Lyssidia elegantula*, which directly follows the diagnosis of *Philobyra brattstromi* in that paper. This value changed to 15 mm.
Figures 1–11. Definitions, terms, and general shell features. Scale bars = 1 mm (where not indicated otherwise). 1. Outline of an adult shell (left valve) indicating shell axes for measurements. 2. Outline of a left valve prodissoconch (from exterior) superimposed on a dark circular background with specimen outline and circle sharing central point (see Figure 3). The size of such circle is defined as the minimum size at which the shell contour becomes enclosed and the center of both shell and circle coincide. The acute angle (<90°) between dorsal and posterior shell margins (quadrants I and II) is typical of many philobryid species (Malchus and Waren, 2005, fig. 5). 3. Prodissoconchs of right valve (top) and left valve of an articulated specimen (SMNH 74531). 4–6. Left valve, prodissoconch, and right valve of holotype (SMNH 3894) (photos taken with optical microscope). 7–8. Left valve (left) and right valve of two specimens (SMNH 74531). 9. Left valve of paratype (SMNH 3894). 10. Close-up of hinge of specimen in Figure 7 (SMNH 74531). 11. Detail of most ventral part of posterior G1 teeth of Figure 9 showing disintegration of teeth into pustules (SMNH 3894).
in Soot-Ryen (1959: 36) suggesting that the dimensions of the two species were exchanged in the first publication. This interpretation is supported by the fact that the author described no other species with exactly that size in 1957.

SYSTEMATICS

Order Arcoida Stoliczka, 1871
Family Philobryidae Bernard, 1897

Description: Small (<10 mm), brooding, with large prodissoconch (length 240–1200 μm), postlarval shell more or less obliquely oval (antero-dorsal/postero-ventral axis = long axis). Primary tooth series (generation 1 teeth, G1) functional throughout adult life or reduced to pulsates in larger adults and then unlikely functional (e.g., Philobrya sublacis); primary, “larval” ligament (I.1) within primary resilifier throughout adult life; with or without a reduced number of generation 2 teeth (G2); disjunct fibrous adult ligament (sensu Waller, 1990) lacking and thus adult ligament not duplilvinear, fibrous ligament sublayer between LV and RV continuous, i.e., without lamellar bridge (corroborating a communication by Waller, 1989, to Carter, 1990; 195). (Description after Bernard, 1897; Dell, 1964; Hain and Arnaud, 1992; Keen, 1993; Tevesz, 1977; own observations; based also on Malcluls and Warén, 2005; Morton, 1978; Prezant, 1990).

Discussion: Recent studies leave little doubt that the postlarval first generation of hinge teeth and the ligament/resilifier of philobryids are holomorphous with the larval to early postlarval hinge teeth and larval ligament/resilifier of planktotrophic Pteriomorphia. Similarly, the second generation of hinge teeth (e.g., Lissarca) is holomorphous with the adult tooth series as found in the majority of arcoid bivalves (Malcluls, 2004a, b; Malcluls and Warén, 2005; Prezant, 1990; and references therein). The maintenance of functional G1 teeth and primary ligament, the reduction of G2 teeth and the lack of a duplilvinear adult ligament are deemed to indicate paedomorphic evolution (Malcluls and Warén, 2005; Morton, 1978; Waller, 1990).

Genus Philobrya Carpenter, 1872

Description: G2 teeth lacking, ligament and resilial groove posteriorly elongated, many or most species teardrop-shaped with a pointed umbo capped by prodissoconch, umbonal angle from 90° to 120° (between antero-dorsal and postero-dorsal shell margins; Figure 1), anterior adductor muscle scar lacking. Periostracum not always flaky. (After Tevesz, 1977; this study.)

Discussion: The periostracum is not always flaky as diagnosed by Keen (1969: N270). Philobrya differs from Adiacura by its more mytilid-like shape, anterior position of its umbo, and a posteriorly elongated ligament and groove. Both genera differ from Lissarca by their lack of G2 teeth (Dell, 1990: figs. 41-45, 49, 54, 58). Nicol (1966: 28) correctly described the hinge of Adiacura but incorrectly included Philobrya wandalensis in that genus based on hinge similarities. More in line with the results presented herein, Dell (1990: 26-27) assumed that this similarity is superficial even though he interpreted the "vertical striae" as ligament pits rather than G1 teeth. In fact, the similarity is not superficial but may reflect a primitive trait (Dell, 1990: fig. 57 of a Daecrydia hinge; Malcluls and Warén, 2005: figs. 1-2 of various Limopsidace; among many others). For this reason, Nicol's concepts of Philobrya and Adiacura are not accepted herein.

Philobrya brattstromi Soot-Ryen, 1957

Philobrya brattstromi n. sp.: Soot-Ryen, 1957: 2.
Philobrya brattstromi Soot-Ryen, 1957: Banorino, 1968: p. 198, pl. 1, figs. 5–6, pl. 5, figs. 2 and 4.

Type Series: By original designation, the type series includes only the specimens from station M24 (SMNH 3894) even though the author determined all specimens of the collection in the same year (International Commission on Zoological Nomenclature [1999]: Articles 72.4.1 and 72.4.6.).

Holotype: The holotype and paratypes were designated by the author. The holotype is complete with a rather well preserved prodissoconch, articulated and closed shell with a protruding byssus and an almost entire, transparent, and non-flaky periostracum. The periostracum extends up to about 0.9 mm beyond the shell and forms 11 larger radial ridges with hairy bristles (Figures 4–6).

This specimen corresponds with the figure given by Soot-Ryen (1959, pl. 1, fig. 6) (except that the RV was found broken antero-centrally). However, the dimensions found here only coincide with those of Soot-Ryen (1959), if measurements (1) include the periostracum, (2) his "length" refers to the longest dorsal-ventral axis (height in the present terminology), and (3) his "height" (length here) is measured perpendicular to that dorsal-ventral axis. Thus measured, the shell is 4.1×3.5×2.1 mm (length x height x width) versus 4.5×3.5×2.3 mm given by Soot-Ryen. Using the straight larval hinge as a reference (as is done throughout here), dimensions are 4.2×4.9 mm (L×H) (Figure 1).

Year of Publication: Although the preliminary diagnosis of P. brattstromi from 1957 is rather rudimentary, that publication appears to fulfill the requirements of the International Commission of Zoological Nomenclature (1999; particularly Articles 11, 13) and 1957 should be considered as the valid year of publication.

Original Description (Soot-Ryen, 1957: 2): “Shell small, oblique ovate, white, with faint radiating ribs. Periostracum yellow with 9 to 13 ribs formed by protruding hairs over the ribs of the shell, continuing beyond the shell margin. Shell with numerous fine pittings inside the pallial line. Anterior margin very short with rounded dor-
Figures 12-23. Prodissoconch, central hinge, and microstructure of postlarval shell. 12. Central hinge of left valve (SMNH 74831; see Figures 7, 10). 13. Central hinge of left valve of paratype (SMNH 3894; see Figure 9). 14-15. Central hinge of right valve of paratype, posteriorly broken. Note lack of tooth that would fit in the depression of the opposite valve (Figure 13). Figure 15 shows the round-crested, raised margin of the prodissoconch (SMNH 3894). 16. Prodissoconch of left valve of paratype (same as Figures 9, 11, 13, SMNH 3894). 17. Right-valve prodissoconch, same specimen as Figure 3 (SMNH 74831). 18-19. Dorsal-ventral fracture surface showing central portion of right valve paratype with pores. 19. Detail showing outer cross-lamellar, middle complex cross-lamellar, and inner prismatic (same specimen as Figures 14-15) (SMNH 3894). 20-23. Dorsal-ventral fracture surfaces of a specimen from SMNH 74831. 20. Middle of the shell with pores penetrating each other. 21. Fracture near ventral shell margin, showing low penetration angle (about 35°) of pores with respect to inner shell margin (to the right). 22. Fracture through umbonal area. 23. Detail of Figure 22, showing complex cross-lamellar structure covered by very thin outer prismatic shell layer (white arrows).
sal angle, linearly descending to the rounded ventral margin which continues to a rounded posterodorsal angle. Dorsal margin slightly convex or straight. Prodissocochoen with raised margins and without visible sculpture. Hinge with anterior tooth-like projection corresponding to a depression in the other valve. From the anterior part of the prodissocochoen a rather broad, cross-lined part extends backwards below the resilium, which starts below the middle of the prodissocochoen and continues backwards and inwards to the middle of the hinge plate. Above and behind the ligament the cross-lining continues to the end of the hinge plate, before which there are 4 to 5 oblique, tooth-like folds in the margin. Adductor scar placed considerably within the pallial line in the posterodental part. Mantle margin with brownish pigment, but lacks eyes. Length 15 mm. (Should read 5.8 mm, see above).

Amended Shell Description: The prodissocochoen is moderately elevated with a round-crested rim and steep ramp towards the postlarval shell, the surface is smooth, except for posterodorsal and anterodorsal wings marked by growth increments and a small dorsocentral bump-like elevation (boss); mean prodissocochoen size is 627×415 μm (L×H) (5 specimens), with a L/H ratio of 1.5 (Figures 2–3, 12–13, 15–17).

Postlarval G1 teeth ("cross-lining" of Soot-Ryen) well developed; ventral to the long ligament and groove, the teeth of the posterior row grow considerably in length, then the row tapers and teeth disintegrate into irregular pustules (Figures 10–11). The "anterior tooth-like projection" mentioned by Soot-Ryen does not correspond to a depression in the other valve; instead, both valves show a depression directly ventral to the anterior row of G1 teeth (Figures 12–14). The posterodorsal radial folds on the inner shell margin correspond to an equal number of radial ribs on the outer surface, which are slightly more prominent than the other radial ribs (Figures 7–9).

Most of the shell has a linear crossed-lamellar structure (CL), further internally the structure is also complex CL (CCL): the innermost layer is prismatic (P) with up to 10 μm thickness (Figures 18–19). An outer prismatic layer 1 μm thick was only observed in a zone dorsal to the ligament (Figures 22–23). Numerous, mainly straight shell pores ("fine pittings" of Soot-Ryen) penetrate the inner (depositional) surface but not all extend to the outer shell surface, some occur in the prodissocochoen. Pores are distributed almost homogenously over the depositional surface within the pallial line. Diameters range from 1.5 to 2.5 μm within the shell, the funnel-like entrances have inner diameters of 2 to 4 μm. Penetration angles are mostly perpendicular to the (inner) central shell surface but about 35° near the shell margins; ramifications were not observed but pores occasionally penetrate each other (Figures 18–21). Adult shell size is up to about 5.6 mm (L×H).

Discussion: Philobrya brattstromi is an easily recognized species given the combination of (1) a smooth prodissocochoen with incipient dorso-central boss, well developed anterior and posterior wings, and mean length of 627 μm and relatively high L/H ratio of about 1.5, (2) well developed posterior G1 teeth reaching far ventrally, enhancing in length anteroventral to the ligament and disintegrating into pustules, (3) the number of posterior radial ridges which correspond in number with folds on the inner shell margin which is otherwise smooth, and (4) a non-flaky periostreaum.

Most of the other shell characters described here are either typical of the family Philobryidae or of the genus Philobrya (see respective descriptions, above), and shell pores are characteristic for probably all Arcoida (Taylor, Kennedy and Hall, 1971; Malchus and Warén, 2005; Waller, 1980). Similarly, an approximately homogenous distribution of pores appears to be common for most arcoids even though they occur concentrated in radial rows in some (or all) Adacarea species.

Accordingly, it is significant that characters such as the presence of an incipient dorso-central boss, the disintegration of G1 teeth and the presence of remnants of an outer prismatic layer are similar to those in Limopsidae (Carter, 1990: 194; Malchus and Warén, 2005). G1 disintegration is also common in other species of Philobrya and although a small dorso-central boss appears to be rare in this genus, this feature appears to develop into a prominent cone in the philobyrid genera Cratis and Cosa (e.g. Hayami and Kase, 1993). The distribution of these characters is consistent with the generally assumed ancestor-descendent relationship between Limopsidae and Philobryidae. However, the boss and tooth disintegration are not characters demonstrating relationship conclusively, as similar structures are also known from unrelated groups (Malchus and Warén, 2005, for a recent discussion) and microstructure details are still needed for other Philobryidae.

ACKNOWLEDGMENTS

I thank Anders Warén for logistic and scientific support during my stay at the Swedish Museum of Natural History, Stockholm, and Alan Ben (GNS Science, NZ), Diego Zelaya (MNCN, La Plata, Argentina) and two anonymous reviewers for their constructive comments. Financial support through the European Commissions' "Access to Research Infrastructure" (High Lat Resources, HIPRI-CT-2001-00125) and the Spanish Ministerio de Educación y Ciencias y Generalitat de Catalunya (Ramón y Cajal Research Contract) is highly appreciated.

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Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea: Calliostomatidae) and *Margarites huloti* new species (Gastropoda: Trochoidea: Trochidae) from a methane seep area off Chile

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ABSTRACT

Two new species of Trochoidea are described from a methane seep area off central Chile (~36°S). *Otukaia crustulum* new species is compared with similar calliostomatid species such as *Otukaia kihizuchien* (Otuka, 1939), *O. altimini* Dell, 1990, and *Calliostoma jacobeliene* McLean, 1970. The new species is separated from these similar species by convex whorls bearing a prominent abapical cord and an almost invisible adapical cord, and five spiral cords on the base. *Margarites huloti* new species from the same locality is compared with similar margarite species, such as *M. shinuai* Okutani, Tsuchiya and Fujikura, 1982, *M. salmonata* (Carpenter, 1864), and *Solariella tauceina* Dall, 1910, and with calliostomatid species such as *Calliostoma malvesianum* (von Martens, 1851), *C. magallenesi* Caldini and Guimarães-Prado, 1999 and *C. koreae* McLean, 1970. The new species differs mainly by the size of its shell, elevated spire, rather thick spiral cords on the whorls, numerous low spiral cords on the base and the narrow, funnel-shaped umbilicus.

INTRODUCTION

The deep-sea malaco fauna of Chile is still scarcely known. The bathyal (>200 m water depth) mollusks associated with the deep-sea shrimp fisheries off central Chile (31° to 35°S) were described by McLean and Andrade (1982). Among the 15 species observed, four belonged to the Trochoidea (sensu Bouche et al., 2005), two of them belonging to the genus *Otukaia* (*O. chilena* Rehder, 1971) and *O. delhi* (McLean and Andrade, 1982) and two to the genus *Bathybembix* (*B. macdonaldi* Dall, 1890) and *B. hamboleti* Rehder, 1971.

The diversity of the Trochoidea from the coast of northern Chile (15° to 31°S) was subsequently studied by Veliz and Vásquez (2000). Their study covered the intertidal to the slope area, and among the 11 species reported, the same four species indicated by McLean and Andrade (1982) were mentioned for the bathyal region. Vilvens (2002) described *Zetela alphensis* from 800 m depth from off Chiloe, farther south (~40°S).

Forcelli (2000) cited 27 species of Trochoidea for the Magellanic province, but almost always without considering their distributional range (except for *Calliostoma fonkii* (Philippi, 1860) (Figures 8–9), clearly reported for the Pacific side of the Magellanic province); some of these species are in fact described from or reported for the southwestern Pacific (e.g., *Calliostoma consinulilis* (E. A. Smith, 1881)).

In relation to the shallow-water malaco fauna of Chile, *Calliostoma fonkii* (Philippi, 1860) has been known from moderately shallow-water north to Peru and the Galapagos Islands (Keen, 1971). Several fossil species of the genus *Calliostoma* have been found in Miocene sediments of the Aranuco Peninsula (~35°S), none with geological ranges extending to the Recent (Nielsen et al., 2004).

Recent dredge hauls taken 75 km NW off the Bay of Concepción have allowed the location of a previously unknown habitat at bathyal depths along the Chilean coast, a methane seep area (Sellanes et al., 2004) named Concepción Methane Seep Area or CMSA (Sellanes and Krylova, 2005). At methane-seep areas, as well as in other marine reducing environments, chemically reduced fluids are utilized as an energy source by free-living and endosymbiotic chemosynthetic bacteria in the synthesis of organic carbon (Paull et al., 1984). Furthermore, microbially-mediated oxidation of methane within the sediments facilitates production of carbonates that act as cement, ultimately giving rise to reefs of carbonate-cemented mud. A diverse community benefits both from the food sources originating from chemosynthesis and from the shelter and substrate provided by the reefs (Sibuet and Ohn, 1988).
About 30 species of mollusks have been recorded at the CMSA. Part of this assemblage is composed by several recently described species of chemosymbiotic bivalves (Holmes et al., 2005; Oliver and Sellanes, 2005; Sellanes and Krylova, 2005), and non-chemosymbiotic accompanying species (Sellanes, unpublished data). Among gastropods, five species of Trochoidea have been recorded, including Batillamphibix macdonaldi, Otukaia chileana, Zizela alphonoi, and the two unnamed species proposed herein. In this paper we describe a species of Otukaia and a species of Margaretia that have been collected at the CMSA.

MATERIALS AND METHODS

Material in the present study consists of specimens obtained living (lv) from the dredgings of R/V Vidal Gómez in various stations (stn) of the CMSA.

Abbreviations used for measurements are: H: shell height; W: shell width; HA: aperture height; TW: number of teleoconch whorls. Spiral cords of teleoconch of the shells are labelled as P1, P2, etc., for primary cords (P1 is the most adapical) and S1, S2, etc., for secondary cords (S1 is the most adapical).

Type specimens are deposited at National History Museum of Chile, Santiago (MNHNCL) and Instituut royal des Sciences naturelles de Belgique, Bruxelles, Belgium (IRSNB).

SYSTEMATICS

We follow herein the suprageneric classification of Marshall (1995) and Bouchet et al. (2005) for Calliostoma, Otukaia, and other related genera. Other authors, however, use the classification of Hickman and McLean (1990) where Calliostomatinae is considered as a subfamily of Trochidae.

Superfamily Trochoidea Rafinesque, 1815
Family Calliostomatidae Thiele, 1924
Subfamily Calliostomatinae Thiele, 1924
Tribe Calliostomatini Thiele, 1924
Genus Otukaia Ikee, 1942

Type Species: Calliostoma kilizeichisn Otuka, 1939 (by original designation); Recent, off Japan.

Otukaia crustulinum new species
(Figures 1–5)

Description: Shell of medium size for genus (height up to 15.6 mm, width up to 14.4 mm), conical to weakly coeloconidal in shape; spire high, as broad as large, height about 2.4 to 3.5 times higher than aperture; umbilicus closed in adult shell.

Protoconch damaged on all available specimens, about 450 μm in diameter, probably encompassing 1 whorl, too eroded to state presence and shape of terminal varix.

Teleoconch of up to 6 moderately convex whorls, bearing 3 spiral granular cords, adapical one the weakest, only poorly visible on last whorls; prolocine ribs on first 3 whorls connecting beads on spiral cords and very thin, axial lamellate threads between cords of the base. Suture visible, impressed, not channeled. First whorl of teleoconch convex, sculptured by 2 primary cords; P2 appearing immediately, granular; P1 appearing a quarter of whorl later, subgranular, weaker than P2; prolocine axial ribs in the intervals between cords, connecting beads of cords; interval between ribs 1.5 times larger than width of ribs. On second whorl, beads of P2 becoming thicker and sharp, isolated but connected by cord; beads of P1 axially elongated; P3 partly emerging from suture, granular; interval between axial ribs becoming 2 times larger than width of ribs; area between P2 and P3 concave. On third whorl, P1 is closer to suture, distance between beads of about 1.5 times width of beads; P2 the strongest, beads becoming axially elongated, distance between beads decrease to size of beads; P3 clearly visible, weakest, with small sharp beads. On fourth whorl, P2 closer to second apical whorl than with beads less sharp, axially very elongated, and closely packed; beads of P1 becoming weaker, separated by interval 3 times larger than beads; axial ribs becoming obsolete. On fifth whorl, P1 becoming obsolete, almost disappearing; P2 thick, beads reducing to axial prosocline ribs. On last whorl, P1 virtually invisible; P2 very thick, producing carina; P3 much weaker, with small beads. Aperture subquadrate; interior of outer lip with fine corresponding to external cords, producing strong angle at the rim; inner lip curved, projecting over umbilical area. Columnella slightly curved, slightly oblique, without tooth. Base weakly convex, with 5 spiral cords; 2 innermost cords granular, interspace between cords similar in size to cords; 3 outermost cords subgranular, distance between cords two times larger than cords; very thin axial lamellate threads between cords, stronger in umbilical area. Color of teleoconch brownish-beige, tips of beads of spiral cords lighter in color.

Type Locality: Central Chile, 36°21.91’ S, 73°43.21’ W, 43–728 m, South Pacific Ocean.

Type Material: Holotype MNHNCL (2016.9) (lv), AGOR Vidal Gómez, stn AGT 13, from type locality, 15.6 × 14.4 mm; Paratype IRSNB 30514.56 S (lv), 10.4 × 11.0 mm.

Etymology: Of a cake (Latin), with reference to the shape of the shell whorls, which invoke the image of a baked cake. The genus-group name Otukaia was erected by Ikee without definition of its etymology and without reference to its gender. We assume that the name is neutral.

Remarks: Absence of complete protoconchs in specimens from the type series prevents a definitive allocation of the new species in the Calliostomatidae. Provisional placement in this family, however, is prompted by the general shell shape, open umbilicus in the immature specimen, and similarities in the axial sculpture of the
Figures 1-9. *Otukaia* and *Calliostoma* species. 1-5. *Otukaia crustulum* new species, Central Chile. 1-3. Holotype MNHNCL 201649, 15.6 x 14.4 mm. 4-5. Paratype IRSNB 30514, 10.4 x 11.0 mm. 6, 8. *Calliostoma jacquelinae* McLean, 1970. C.Vilvens coll., Galapagos Islands. 12.0 x 13.0 mm. 7, 9. *Calliostoma fonkii* (Philippi, 1860), C.Vilvens coll., northern Chile. 16.0 x 14.5 mm.

Early teleoconch whorls with other calliostomatids. Further studies including more complete specimens may reveal that the new species belongs in the *Chilodontidae*, tribe Calliotropini.

Among Calliostomatidae, the genus *Otukaia* Ikobe, 1942, seems to be the most adequate to include the new species. *Otukaia crustulum* new species weakly resembles *O. kileiziebisu* (Ohtuka, 1939) from Japan (200-1000 m; Sasaki, 2000: pl.37, fig.108), but the median spiral cord P2 of this species is much thinner and the base bears more cords. The new species may also be compared to *O. eltanini* Dell, 1990, from the Pacific-Antarctic Ridge (915-1153 m; Dell, 1990: fig.168); this species, however, bears 4 primary, evenly distributed spiral cords on the last whorl, with 2 strong adapical cords, and 21 spiral cords on the base. *Otukaia crustulum* new species is rather similar to *Calliostoma jacquelinae* McLean, 1970, (Figures 6, 8) from the Galapagos Islands (150-350 m). Both species have a prominent abapical cord, but this latter species differs by having a strong, granular, subsutural primary cord P1, about 8 low smooth spiral cords between P1, and many more (about 30) narrow, smooth spiral cords on the base.

Family Trochidae Rafinesque, 1815
Subfamily Margaritinae Stoliczka, 1868
Tribe Margaritini Stoliczka, 1868
Genus *Margarites* Gray, 1847
Table 1. *Margarites huloti*. Shells measurements in mm for the largest specimens (n = 4). Abbreviations are: H: shell height; W: shell width; HA: aperture height; TW: number of teleoconch whorls.

<table>
<thead>
<tr>
<th>Character</th>
<th>TW (cm)</th>
<th>H (cm)</th>
<th>W (cm)</th>
<th>HA (cm)</th>
<th>HW</th>
<th>H/HA</th>
</tr>
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<tbody>
<tr>
<td>Mean</td>
<td>4.55</td>
<td>11.45</td>
<td>12.50</td>
<td>4.95</td>
<td>0.91</td>
<td>2.31</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.38</td>
<td>1.10</td>
<td>0.82</td>
<td>0.27</td>
<td>0.44</td>
<td>0.16</td>
</tr>
</tbody>
</table>

**Type species:** *Turbo helicus* Phipps, 1774, by original designation; Recent, northern Atlantic Ocean.

*Margarites huloti* new species (Figures 10–17)

**Description:** Shell of medium size for the genus (height up to 12.5 mm, width up to 13.4 mm), cyrtocoenoidal in shape; spire moderately high, height about 0.9 times width and 2.0–2.4 times aperture height (Table 1); umbilicus narrow and deep. Protoconch about 550 μm wide, about 1 whorl, smooth, with a thin terminal varix. Teleoconch of up to almost 5 convex whorls, bearing spiral cords; adapical cords granular, abapical cords smooth. Suture visible, impressed, not channeled. First whorl of teleoconch convex, sculptured by 6 smooth, weak, low, very close, similar in size and shape primary cords (from P2 to P7); weak irregular growth lines. On second whorl, cords becoming stronger except P2 still weak; PI appearing under suture, smooth; interval between cords of about half width of cords. On third whorl, S1 appearing, weak, weakly granular; cords evenly spaced; distance between cords similar in size to cords; area between cords concave, with prosocline thin growth lines. On last whorls, S1 clearly granular, with axially elongated beads; P2 becoming weakly granular, with horizontally elongated beads; other cords smooth; distance between cords of about 1.5 times width of cords; P5 emerging from suture only on last whorl, close to P7; S2 sometimes appearing at end of last whorl, thinner and subgranular. Aperture oval; interior of outer lip with thin hiral corresponding to the external cords; inner lip weakly curved, projecting over the umbilicus. Columella straight, slightly oblique, without tooth. Base nearly flat or very weakly convex, with 20 to 25 smooth spiral cords; three innermost broader than others; interspace between cords smaller than cords, smooth or with very weak axial threads. Umbilicus narrow, funnel shaped, diameter about 10% of shell diameter in largest specimens, with crowded axial lamellae and no spiral cord within. Colour of protoconch and teleoconch iridescent grey, last whorl lighter; base whitish grey. Operculum horny, multispiral with a short growing edge. Radula rhipidoglossate; formula ca. 20 + (1) + 6 + 1 + 6 + (1) + ca. 20. Rachidian and lateral teeth similar in size and shape, with large, oval base and serrated overhanging cusps. Lateromarginal plate present. Marginal teeth thin, with long shaft and serrated cutting edges.

**Type Locality:** Central Chile, 36°21.91' S, 73°43.21' W, 843–728 m, South Pacific Ocean.

**Type Material:** Holotype: MNHNCL 201650 (H). AGROR Vidal Gornáz, s.n. AGT 13, from type locality, 12.5 × 13.4 mm; paratypes: MNHNCL 201651 (5 H), IRSNB 30514 569 (1 H), all from type locality.

**Etymology:** Named after André Hulot, Belgian hydrobiologist, United Nations Development Programme, a scientist who initiated the marine science efforts in 1956 at the University of Concepción, Chile.

**Remarks:** *Margarites huloti* new species is superficially similar to another methane seep species *M. shikai* Okutani, Tsuchi and Fujikura, 1992 (Figures 18–19) from Japan. This latter species, however, has a more depressed shell, whorls more convex, more numerous and thinner spiral cords on whors, only with 6 in the new species; in addition, the rachidian and lateral teeth in the Japanese species have a more slender base (Okutani, Tsuchi and Fujikura, 1992: figs. 15–16).

The new species seems rather similar to *Margarites salmoarea* (Carpenter, 1864) from southern California, but the latter is much smaller for a similar number of whors, has less spiral cords on the base, and a broader umbilicus. *Margarites huloti* new species may also be compared to *Solariellae tomentula* Dall, 1919, from the Galápagos Islands. This latter species, however, has a smaller size for about the same number of whors and bears more convex whors with thinner spiral cords. The new species also resembles *Calliostoma undulatum* (von Martens, 1851) from the southwestern Atlantic, but the latter species differs from the new species by having a more depressed spire, less numerous spiral cords on whors, and lacks an open umbilicus. The new species weakly resembles *Calliostoma magalldii* Caldini and Guminaries-Prado, 1998, from the southwestern Atlantic, but shells of this latter species have no umbilicus, are pinkish white, and have whors and base bearing less numerous and thicker spiral cords. *Margarites huloti* new species may also be compared to *Calliostoma keean McLean*, 1970, from the central eastern Pacific, but this latter species is slightly larger, has a more horizontally elongated aperture, and thinner and more numerous granular spiral cords on whors.

**ACKNOWLEDGMENTS**

Our thanks to the officers and crew of R/V VIDAL CORNÁZ, for their skilful assistance at sea. Funding for ship time was provided by the Office of Naval Research.
(ONR). The Center for Oceanographic Research in the Eastern South Pacific (COPAS) and the Research Direction of the University of Concepción also provided partial support. We are very especially grateful to J. L. Van Goethem (Institut royal des Sciences naturelles de Belgique, Brussels) for his help with requisition of type loans. We also would like to thank H. Saito (National Museum of Science of Tokyo) for the loan of types from his institution. Last but not least, we are indebted to María Soledad Romero (Facultad de Ciencias del Mar, Universidad Católica del Norte), for help with the SEMs of the radula of Margarites hulotii.

LITERATURE CITED


A new land snail of the genus *Humboldtiana* (Gastropoda: Pulmonata: Humboldtianidae) from Nuevo León, Mexico

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**ABSTRACT**  
*Humboldtiana iversoni* new species is described from southern Nuevo León, Mexico. The species is most similar to *H. montezuma* Pilsbry, 1940, because of its reproductive system morphology and shell sculpture. The new species differs from *H. montezuma* by its smaller size, its color pattern and aspects of the structures of its reproductive system. It is unique within the genus because of its bulbous penis and its short, broadly conical vagina. Because of features of the dart apparatus in the female reproductive system *Humboldtiana inferior* Pilsbry, 1948, is recognized as a distinct species from *H. montezuma*, of which it was considered a subspecies formerly.

**INTRODUCTION**  
*Humboldtiana* is a genus of large helicoid land snails (Gastropoda, Pulmonata, Helicidae, Humboldtianidae). The genus is distributed from Texas and Chihuahua south to areas near Mexico City and central-western Veracruz. Approximately fifty species are recognized (Thompson, in press), and it is apparent that many more wait to be discovered. One such novelty was collected by John B. Iverson many years ago during herpetological investigations in northeastern Mexico. Repository institutions are: UF: Florida Museum of Natural History, University of Florida; ITCV: Instituto Tecnologico de Ciudad Victoria, Tamaulipas, Mexico.

**SYSTEMATICS**  
Family Humboldtianidae Pilsbry, 1939  
Genus Humboldtiana von Ihering, 1892  

*Humboldtiana iversoni* new species

**Description:** The shell (Figures 1–4) is small to medium for the genus, helicoid, up to about 35 mm wide, about 0.55–1.00 times as high as wide. The color pattern consists of three narrow brown bands (Figures 1, 3). The middle band is the most conspicuous. The bands are partially interrupted by white riblets on a tan or light-brown background color. The internal surface of aperture is tinged light tan in fresh specimens. The bands are barely distinguishable within the aperture. The suture is shallow, and descends abruptly to the aperture from the middle band to the lower band along the last eighth whorl. The whorls are weakly shouldered and nearly uniformly rounded. Adult shells have 4.0–4.6 whorls. The embryonic shell consists of 1.4–1.6 whorls. The first embryonic whorl is smooth, flat-topped, and 2.25 mm wide perpendicular to the initial suture. The following half whorl is covered with numerous very fine elliptical granules and has faint radial striations below the periphery. The post-embryonic whorls are sculptured with numerous close growth wrinkles and dense, fine, elongate granules that are aligned transversely (Figure 4). On the last 1.5 whorls the wrinkles become well-defined riblets that are about as wide as their interspaces. The riblets are continuous into the umbilicus. Transverse rows of granules are superimposed on and between the riblets. The aperture is nearly round in front view and is 0.76–0.82 times as wide as high in oblique view. The plane of the aperture lies at an angle of 37–43° to shell axis. The posterior corner is rather widely separated from the columellar margin. The parietal callus consists of a thin transparent glaze. The peristome is simple and blunt-edged. The basal-columellar edge is slightly reflected. The columellar lip is narrowly reflected to partially cover the umbilicus (Figure 2). Shell measurements in mm based on the holotype and the three paratypes are given in Table 1.

**Anatomy (Figures 5–6):** (Morphological terminology follows Thompson and Brewer, 2000.) The holotype is the only specimen that was available for study. It was preserved in the field in 70% ethanol, and was tightly contracted into the shell. The head-foot is dark gray. The mantle over the lung is uniform lighter gray. Reproductive system (Figure 5): The genital atrium is very short. The penis has a short narrow neck, and then it rapidly expands into a wide, bulbous orb that is wider than high length of penis 4.5 mm. The penis wall is very thin. Internally the wall has several longitudinal glandular folds in the neck. The penis has a very large verge that fills the upper half of the cavity and ends in four heavy...
lobes (Figure 6). The penis retractor muscle (pr) is short and stout; length 3.5 mm. It originates on the center of the mantle cavity about 1/8 of a whorl behind the mantle collar and inserts on the base of the epiphallus (epi) juxtaposed to the penis. It does not form a sheath around the epiphallus. The epiphallus is 11.5 mm long. It is moderately slender and uniformly wide throughout its length, being about the same diameter as the neck of the penis. It is lined internally with four longitudinal folds. The flagellum (flg) is 13 mm long. It is slightly longer than the epiphallus, is moderately stout, and bears four longitudinal folds internally. The vagina (vg) is short and stout with a broad conical base; total length of vagina 7.5 mm. The vagina bears four dart sacs (ds) of equal size. Dart bulbs are not evident externally. The dart glands (dgl) form around the vagina a robust ring that is juxtaposed to the dart sacs. The free vagina (vgf) is robust and is about 2.5 mm long. The spermathecal duct (spdt) is 27 mm long. It bears a cæcum (cae) 16 mm above it base. The cæcum is 9 mm long. The spermatheca is oval in shape and is relatively small for the genus. Measurements could not be made of the uterus (utr) or the albumen gland because of their state of preservation.

**Type Material:** Holotype, UF 130588; Paratypes, UF 367594 (2); ITCV (1); same data as the holotype; all collected by John B. Iverson, 18 June 1978, at type locality.

**Type Locality (Figure 7):** Nuevo León: Highway 68 at km post 116, Las Norias (24°11.0' N, 99°53.0' W), 3 km south of Antequitos; 1800 m altitude. Las Norias is about 50 km SE of Galeana on the highway to La Escondida and Doctor Arroyo. Specimens were found under limestone blocks on an open southeast facing grassy hillside with nearby scattered oaks (*Quercus* sp.) and clusters of Agave sp.

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Distribution: The species is known only from the type locality.

Etymology: This species is named for John B. Iverson, Earlham College, Richmond, Indiana, in acknowledgement for this and other novel species of mollusks collected by him in Mexico while conducting herpetological explorations.

Remarks: *Humboldtiana iversoni* belongs in the subgenus *Humboldtiana*, or at least, what is thought to be the subgenus *Humboldtiana*. The identity of the type species, *Helix humboldtiana* Pfeiffer, 1857, remains equivocal, and its type locality and range are unknown (Pilsbrv, 1927). It was described from “Mexico” without a specific locality. Fischer (1899) described and illustrated the anatomy of a specimen from Guanajuato that he identified as *H. humboldtiana*, but he did not describe or illustrate the shell, nor is it clear whether he meant the City of Guanajuato or the State of Guanajuato. For these reasons Pilsbrv (1927) expressed reservation concerning the identity of Fischer’s specimen. Notwithstanding the limitations concerning the identity of the type species, the subgenus is tentatively characterized as follows, because all other species described in the 19th Century and all species subsequently described from central and southern Mexico are known anatomically, and there is little reason to doubt that *H. humboldtiana* departs significantly from a common ground plan. This includes Fischer’s description. These species have in common the following characteristics: (1) The spermathecal duct has an appendix; (2) There are four dart sacs on the vagina; (3) Two dart bulbs are imbedded in the vaginal wall at the base of each sac and are not visible externally; (4) The four dart glands coalesce immediately above the dart sacs to form a ring around the vagina; and (5) The penis contains a verge internally, which is a papilla-like extension of the epiphallus into the penis chamber.

*Humboldtiana iversoni* belongs to a small group of species that includes *H. montezuma* Pilsbrv, 1940, and *H. inferior* Pilsbrv, 1948 (formerly *Humboldtiana montezuma inferior* Pilsbrv, 1948). The group is found in southeastern Nuevo León, *Humboldtiana montezuma* is found at 3080 m altitude at the summit of El Infernillo, a mountain near Pabliblo, south of Galeana; and *H. inferior* is found lower at about 1850 m altitude, near Pabliblo. The species have in common coarse postembryonic

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**Figures 5-6.** *Humboldtiana iversoni* new species. 5. Reproductive system. 6. Interior of penis.

**Figure 7.** Type locality of *Humboldtiana iversoni* new species at Las Lorias, Nuevo León, Mexico.
Humboldtiana ictersoni is unique within Humboldtiana because of the structure of the penis with its very large bulbous verge. Also, it is unusual because of the short, broadly conical lower vagina. Superficially the penis resembles that of H. tescola Thompson, 1967. In the latter species the inner wall of the penis bears heavy glandular folds that surround a short and relatively slender verge, and the penis retractor muscle inserts on the epiphallus (Thompson, 1967). Humboldtiana ictersoni differs from other members of the H. montezuma species-group by having a short, stout flagellum that is only slightly longer than the epiphallus, and by having the penis retractor muscle insert on the base of the epiphallus. Both H. montezuma and H. inferior have a long slender flagellum that is 1.3-1.6 times as long as the epiphallus, and the penis retractor inserts higher on the epiphallus (Pilsbry, 1948). Humboldtiana ictersoni is like H. montezuma by having four equal-sized dart sacs on the vagina. In H. inferior dart sacs ds2 and ds3 are reduced in size compared to ds1. Humboldtiana montezuma lacks bands, while H. inferior has three bands. In both H. montezuma and H. inferior the internal surface of the aperture is brown, in contrast to light tan-tinged aperture of H. ictersoni.

Humboldtiana inferior had been regarded as a subspecies of H. montezuma. Pilsbry (1948) states that the dart sacs of H. inferior are sub-equal in size, and his Fig. 1B shows that at least ds2 and ds3 are conspicuously smaller than is ds1. The reduced size of dart sacs ds2 and ds3 is a sufficient basis for recognizing Humboldtiana inferior as a separate species (see Thompson and Brewer, 2000).

ACKNOWLEDGMENTS
The anatomical drawings in Figures 5–6 were produced by Susan Trammell, Gainesville, Florida. Her excellent illustrations greatly enhance this paper. I am grateful to two anonymous reviewers whose comments improved this paper.

LITERATURE CITED


Two new land snails of the genus *Humboldtiana* (Gastropoda: Pulmonata: Humboldtianidae) from Chihuahua, Mexico

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ABSTRACT

*Humboldtiana corruga* new species and *Humboldtiana sylena* new species are described from Chihuahua. They are characterized by anatomical features as well as shell morphology.

INTRODUCTION

Snails of the genus *Humboldtiana* comprise some of the larger land snails in Mexico. In most cases the species occur in sparsely populated colonies, and they have irregular distribution patterns. Uniform distributions over areas larger than 1 km² are rare in what appear to be appropriate habitats. Instead, species occur in isolated colonies, with local endemism being the rule. This study describes two such species. Their descriptions are prompted by the need to round out phylogenetic studies (Mejía, in prep.). We use the following abbreviations for shell measurements: H: height; W: width; AH: aperture height; AW: aperture width. Repository institutions are: ITCV. Instituto Tecnológico de Ciudad Victoria, Tamaulipas, Mexico; UF. Florida Museum of Natural History, University of Florida, Gainesville, Florida.

SYSTEMATICS

Family Humboldtianidae Pilsbry, 1939  
Genus *Humboldtiana* von Ihering, 1892

*Humboldtiana corruga* new species

Diagnosis: This is a moderately large species that has smooth embryonic whorls. The globose shell is about as high as wide. It is sculptured with rugose growth wrinkles on the postembryonic shell, with dense granular sculpture aligned with the growth wrinkles. The color pattern consists of three narrow blackish bands of equal size on a dark brown ground color. The whorls are inflated and tend to take on a square appearance. The last whorl has a distinct shoulder and has a slightly channeled suture. The edge of the peristome is blunt and not reflected.

Description: The shell (Figures 1–5, Table 1) is medium in size, about 32 mm wide, globose in shape, about 1.02 times as high as wide. The color is lusterless dark brown with lighter brown streaks along the growth lines, and with three nearly equally narrow black bands. The bands are well defined, although they tend to be disrupted by transverse streaks on the lower half of the body whorl. The aperture is lighter brown and banded internally. The shell has up to 4.9 whorls. The 1.5 embryonic whorls protrude conspicuously above the following whorls. The first embryonic whorl is 5.8 mm wide transverse to the initial suture. The postembryonic whorls are inflated with a noticeable shoulder and a channeled suture which tends to give the whorls a squared appearance. The last half-whorl gradually descends to the aperture. The peristome inserts on the lower edge of the lower band. The embryonic whorls are smooth (Figures 3, 5). The postembryonic whorls are sculptured with coarse growth wrinkles and striations, which are continuous to the peristome and into the umbilicus. Numerous minute granules are superimposed on the growth wrinkles. The granular sculpture extends from the suture to the base, but it does not continue into the umbilicus. The aperture is wrinkled internally beneath the outer sculpture. The aperture is 1.3 times as high as wide and is about 0.73 times the height of the shell. It is prosocline at an angle of 18° to the shell axis (Figure 2). The peristome is blunt-edged, and is not reflected along the upper, outer, and basal lip, but it is broadly reflected along the columellar lip to partially cover the umbilical area (Figure 4).

Anatomy (Figures 11, 12): The anatomy of the holotype is described. The head-foot is gray above and on the sides bordering the sole. A lighter gray zone extends on the sides from the snout posterior to the mantle collar. The sole is very light gray. The mantle collar is light gray. The outer wall of the mantle cavity is light gray and is reticulated with narrow black lines.

The genital atrium (gen at) is slender, and is about a third the length of the penis (Figure 11). The penis is 14 mm long and is bulbous with a slight constriction near...
the apex at the insertion of the penis retractor muscle (pr). The penis has a verge that extends about half the length of the cavity. The verge is surrounded by a heavy pendulant curtain of glandular tissue (Figure 12). The lower wall of the penis bears a few small longitudinal folds below the curtain. The penis retractor muscle (pr) is 6 mm long, and is relatively short and moderately stout. It originated on the inner wall of the lung slightly behind the middle of the mantle collar, and inserts on the apex of the penis where it forms a narrow sheath around the base of the epiphallus. The epiphallus (epi) is slender, and is slightly longer than the penis. It is lined internally with four longitudinal folds. The slender flagellum (flg) is about as long as the combined length of the penis + epiphallus. The vagina is about 16 mm long. The lower vagina (vag) has a long slender neck, and bears four dart sacs of equal size (ds1, ds2, etc) each with a pair of dart bulbs (db) distinctly protruding at its base. The bulbs are embedded in the wall of the vagina and form conspicuous bulges in the wall. The dart glands (dgl) are widely separated from the dart sacs. The middle vagina (vagm) is about as long as the lower vagina, and is considerably stouter. The free vagina (vagf) is very short, and is barely visible above the dart glands. The spermatheca (spt) is small and globular. The spermathecal duct (sptd) is very long; the combined length of the spermatheca + duct is 65 mm. The duct bears a caecum (cae) at about a third of the distance below the spermatheca. The length of the uterus-prostate is about 40 mm.

Type Material: Holotype, UF 358872, collected by Omar Mejía, 25 August 2003; Paratype, ITCV (1 shell).

Table 1. *Humboldtiana corruga* new species. Measurements of the holotype and the paratype. Measurements of the paratype are incomplete because it has a fractured lip and apex. Abbreviations used are: H: height; W: width; AH: aperture height; AW: aperture width.

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both from the type locality. Measurements are given in Table 1.

**Type Locality:** Chihuahua, 0.5 km south and 0.3 km west of Norogachi. Chihuahua (27°15.9' N, 107°7.8' W), 2280 m altitude, open *Pinus-Quercus* woodland.

**Distribution:** Known definitely only from the type locality.

**Etymology:** The species name *corniga* derives from the Latin, co, meaning together or with, and *ruga*, meaning a wrinkle or fold. The name alludes to the coarse wrinkled sculpture on the shell.

**Remarks:** *Humboldtiana corniga* differs from other known species by its distinct anatomical features. *Humboldtiana corniga* is unique within the genus because of the following combination of anatomical characters. It has a long genital atrium. The penis has a moderately long verge, which is surrounded by a curtain of glandular tissue. The lower vagina has a long slender neck. The middle vagina is long and widely separates the dart sacs from the dart glands. The vagina bears four dart sacs of equal size, each of which is bordered by two dart bulbs. The spermathecal duct has a relatively long caecum that is located at about two-thirds of the distance from the base.

*Humboldtiana corniga* superficially is similar to another undescribed species from near San Ignacio Arareco, southeast of Creel, Chihuahua in that the shells are similar in size, and have similar color patterns (Thompson, in press). In *H. corniga* the umbilical perforation is more conspicuous, the aperture is proportionally higher, the suture is more deeply impressed and is channeled along the body whorl, the bands are narrower but better defined, and the bands are equal in width.

A very closely related form, which we tentatively identify as *Humboldtiana corniga*, comes from Baqueachi, Chihuahua (27°26.3' N, 107°30.3' W), 1940 m altitude (UF 359518). Baqueachi is about 8 km west of Norogachi. Our only available specimen has an immature shell. Its reproductive system is virtually identical to that of *H. corniga*, and its shell has similar sculpture.

**Diagnosis:** This species is distinguished by its large size, globose shape, and rotond whors with a distinct shoulder. The color is straw yellow with three well-defined black bands. The embryonic whors are smooth. The postembryonic sculpture consists of strong incremental striations and wrinkles. Granular sculpture is absent over the surface of the shell.

**Description:** The shell (Figures 6–10) is large, up to 36 mm wide. It is slightly depressed-globose, 0.88 times as high as wide, and is thin shelled, and is shiny. The color pattern is straw yellow with three distinct uninterrupted black bands with well-defined straight edges. The upper two bands are about equal in width. The lower band is narrower. The interior of the aperture is tan and shows the external bands. The umbilical perforation is narrowly rimate due to the reflected columnar margin of the peristome (Figure 9). The shell has 4.0 rotond whors that are noticeably shouldered with a deeply impressed suture. The body whorl descends to the aperture along the last quarter turn. The 1.5 embryonic whors are smooth (Figures 8, 10). The first embryonic whorl is 5.1 mm wide transverse to the initial suture. The post-embryonic whors are sculptured with relatively strong incremental striations and wrinkle which extend diminished from the suture to the umbilicus. Granular sculpture is absent on all parts of the shell. The rotond aperture is 0.80 times as high as wide and is 0.81 times the height of the shell. The upper lip inserts between the middle and the lower bands. The aperture is prosocline, lying at an angle of 33° to the shell axis. The peristome is blunt, narrowly but distinctly reflected along the upper, outer and basal lips, and is broadly reflected over the umbilical area.

**Anatomy (Figures 13, 14):** Only the holotype was available for dissection. The head-foot is very dark gray, almost black. The sole is a slightly lighter shade of gray. The mantle is light gray and is mottled with dark gray spots.

The genital atrium (gen at) is very short, almost nonexistent (Figure 13). The penis is bulbous with a slight constriction below the apex. The interior of the penis has a moderately slender verge that extends about half the length of the chamber and is surrounded by five heavy glandular folds (Figure 14). The neck of the penis is lined internally with 6-7 low narrow longitudinal folds. The penis retractor muscle (pr) is very short and stout. It originates on the inner lung wall immediately behind the middle of the mantle collar, inserts on the apex of the penis and forming a short sheath around the base of epiphallus. The epiphallus (epi) is relatively slender for the genus and tapers distally. It is 17 mm long and is almost twice the length of the penis. The interior of epiphallus is lined with four longitudinal folds. The flagellum (fig) is moderately long, and is about as long as the combined length of the penis + epiphallus. The interior of the flagellum is lined with four longitudinal folds. The vagina is 30 mm long. The lower vagina (vag) is short and tapers below to a narrow neck. It bears four dart sacs of equal size (ds1, ds2, etc.), each of which bears a pair of dart bulbs (db) along its base. The dart glands (dgl) form a well-developed lobed ring around the vagina. They are widely separated from the dart sacs by the middle vagina (vagm), which is slightly longer than the lower vagina. The free vagina (vagf) is very short. The spermathecal duct (sptd) is very long and lacks a caecum. The spermatheca (spt) is small and ovate in shape. The combined length of the spermatheca + duct is 65 mm. The length of the niterus-prostate (utr-pro) is 43 mm.

**Holotype:** UF 353714, collected by Omar Mejía, 31 August, 2003. Height: 32.0 mm; width: 36.2 mm; apert-
ture height: 26.0 mm; aperture width: 20.9 mm; whorls: 4.0.

**Type Locality:** Chihuahua, Corareachi, 4.4 km north, 0.4 km west of Baqueachi (27°28'45" N, 107°50'93" W); 2000 m altitude. Corareachi is a very small village, which is unnamed on the INEGI topographic map series 1: 50,000 (G13A32). The type locality is in a *Pinus-Quercus* forest in a grassy glen.

**Distribution:** Known only from the type locality.

**Etymology:** The species name *sylvatica* derives from the Latin word for woods or forest.

**Remarks:** Shell and anatomical features in *Humboldtiana sylvatica* are similar to those of an unnamed species from near Rancho Blanco, XNE of San Juanito, Chihuahua (Thompson, in press). Important shell and anatomical traits that the two species have in common separate them from other *Humboldtiana*. They share the following shell traits. The embryonic whorls are smooth. The postembryonic whorls are sculptured with coarse incremental striations and wrinkle. Granular sculpture is absent over the entire surface of the shell. The color pattern consists of three black bands on a lighter background.

In addition, they share the following anatomical traits. The outer wall of the lung is light gray and is mottled with numerous small darker-gray spots. The genital atrium is very short and almost non-existent. The bulboous penis has a moderately slender verge that is rounded in the lower half by heavy longitudinal glandular folds. The epiphallus is relatively slender. The flagellum is about as long as the combined length of the penis + epiphallus. The vagina bears four dart sacs of equal-size that are widely separated from the dart glands. The spermatic duct lacks a caecum.

Aside from size, the anatomies of the two species are very similar. The shells are distinguished by size and its color. The unnamed species from near Rancho Blanco has a shell that is up to 27 mm wide. Its ground color is light diaphanous brown with three dark brown bands that are interrupted by irregularly spaced alternating dark brown transverse bars and blotches. This contrasts strongly with color of *Humboldtiana sylvatica*, in which the straw yellow shell has with three distinct black bands that have discrete edges.

**ACKNOWLEDGMENTS**

The anatomical drawings comprising Figures 11–14 were rendered by Michael Falck, Gainesville, Florida.

**LITERATURE CITED**


Mollusks in a Holocene lake-sediment core from the Arctic Foothills of northern Alaska

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INTRODUCTION

Mollusk remains preserved in lake sediments have been analyzed in a variety of geographical regions and environmental settings. These faunal records provide insights into a range of issues, including (1) variations in mollusk community composition and diversity, (2) the current biogeography of freshwater gastropods and bivalves, and (3) past changes in the environment (e.g., Watts and Bright, 1968; Harris and Pip, 1973; Hu et al., 1996; Miller et al., 2000; Welter-Shultes and Richling, 2000; Jensen et al., 2002; Mouthon and Magny, 2004). This paper presents the first record of long-term changes in the mollusk community of a lake from northern Alaska.

STUDY AREA

Red Green Lake (informal name; 68°39.2' N, 149°24.6' W) is located north of the boreal treeline in the central Arctic Foothills of northern Alaska. The climate of this area is cold, with average January and July temperatures of 22°C and 11°C, respectively; it receives ~325 mm mean annual precipitation, most of which occurs during the summer months (Zhang et al., 1996). The lake is ~2 ha in area, with a maximum depth of 3.2 m, and pH of 8.2. Its ~50 ha watershed is dominated by prostrate-shrub tundra plant communities (Walker et al., 1994, 1998). The lake has a single outlet stream that flows west into the Itkillik River.

MATERIALS AND METHODS

A 25.5 cm sediment core was recovered from Red Green Lake in May 1997. Details of the coring operation and subsequent laboratory analyses of the core's organic content, chronology, and palynological record are described elsewhere (Oswald et al., 2003). After the preliminary sampling, the core was sectioned at 1 cm intervals and washed through a 500 μm screen. Mollusk remains were identified by T. J. Frest using a modern specimen collection and a variety of references (Burch, 1972, 1975, 1989; Clarke, 1973, 1981; Baxter, 1987; Turgeon, 1998). The mollusk data are expressed as the minimum number of individuals (MNI) per 20 cm². For bivalves, single right and left valves were counted separately, and the larger of those values was added to the number of paired valves to arrive at the MNI. For gastropods, only those specimens with intact apical whorls were included in the MNI value, as adults could yield a number of large fragments per individual. The specimens are deposited at the Quaternary Research Center, University of Washington, Seattle.

RESULTS

Six mollusk species (four bivalves, two gastropods) were present in a 70 cm interval of the core dating to ~8000-4000 calibrated 14C years before present (cal yr BP) (Figure 1). The fauna for this interval included Pisidium hiljeborgi, Pisidium nitidum, Pisidium rotundatum, Sphaerium nitidum, Lymnaea atkaensis, and Valvata sincera helicoida (Table 1). Mollusk diversity was low at any given level in this interval, with an average of 1.91 species per sample, and a range of 1-4 species per sample. P. hiljeborgi was the most abundant bivalve species, occurring in 46 samples between 8500 and 4100 cal yr BP, and reaching a peak abundance of 15 MNI at 6500 cal yr BP. The other Pisidium species were less common: P. nitidum was found in two samples (5900 and 5400 cal yr BP), and P. rotundatum was found in five samples between 7100 and 6400 cal yr BP. Sphaerium nitidum occurred in 13 samples between 7900 and 4600 cal yr BP, whereas L. atkaensis was encountered in 18 samples between 7900 and 5200 cal yr BP. V. sincera helicoida was the most abundant gastropod species, appearing in 23 samples between 8000 and 4100 cal yr BP, with highest MNI values at 8000-7700 and 6800-6100 cal yr BP.

DISCUSSION

The faunal community present in the mid-Holocene interval of the sediment core suggests that Red Green was
a shallow, oligotrophic lake between ~8000 and 4000 cal yr BP. In particular, *P. nitidum* and *P. rotundatum* are indicative of shallow lake depth, as they are common in water <1 m deep (Clarke, 1981; G.L. Mackie pers. comm.). *S. nitidum*, *P. ljiheborgi*, and *L. atkaeensis* can also occur in shallow water, and they are most common where oligotrophic conditions exist (Clarke, 1979, 1981; G.L. Mackie pers. comm.). *Valvata sincera helicoida* indicates that aquatic vegetation was present, as it is typically found with aquatic plants (Clarke, 1973). The interpretation of these species as indicators of shallow water depth is consistent with the findings of paleoecological studies in south-central Alaska (Hu et al., 1996) and in the northwestern corner of Canada’s Northwest Territories (Delorme et al., 1977).

The decline in mollusk abundance between ~5500 and 4000 cal yr BP suggests that the lake became deeper during that interval. That interpretation is consistent with other paleoenvironmental evidence from northern Alaska indicating an increase in effective moisture at that time. For example, the oxygen isotope record from Meli Lake, located in the Arctic Foothills, shows a shift to wetter conditions at ~6000 cal yr BP (Anderson et al., 2001). Similarly, analyses of a sediment core from Lake Wolverine, located in the Kobuk Valley of northwestern Alaska, suggest that the lake became deeper at ~5800 cal yr BP (Mann et al., 2002). The onset of cooler and wetter conditions after ~5000–4000 cal yr BP is also evidenced by glacial advances in the Brooks Range and elsewhere in Alaska (Ellis and Calkin, 1984; Calkin, 1988).
Rising water levels presumably would have affected the mollusk community directly by reducing the availability of shallow-water habitat in the center of the lake. In addition, the mid-Holocene increase in effective moisture may also have contributed to the decline of mollusks by triggering other ecological changes. For example, as the lake became deeper it may have achieved a depth at which it could support predatory fish. Lake trout (Salvelinus namaycush) have been shown to exert strong controls on mollusk communities in lakes in the Arctic Foothills (Hershey, 1990; Merrick et al., 1991, 1992; Hershey et al., 1999), and thus an increase in their population as the lake deepened would have exacerbated the decline in mollusk abundance. The mollusks in Red Green Lake may also have been affected detrimentally by changes in water chemistry resulting from climate-induced changes in aquatic or terrestrial ecosystem processes (e.g., Kling et al., 1992, 2000; Hobbie et al., 1999). Additional studies that employ both palaeoecological and palaeolimnological approaches are needed to understand past changes in the linkages between terrestrial and aquatic ecosystems in the Arctic.

ACKNOWLEDGMENTS

The author thanks Terrence J. Frest, Daniel Gavin, Linda Brubaker, Feng Sheng Hu, George Kling, Patricia Anderson, Thomas Brown, Gerald L. Mackie, and the staff of the Toolik Field Station for their contributions to this research. The manuscript was greatly improved by the comments of two anonymous reviewers. This research was funded by National Science Foundation grant OPP-9615947.

LITERATURE CITED


Mytella charruana (Bivalvia: Mytilidae): a new, invasive bivalve in Mosquito Lagoon, Florida

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INTRODUCTION

Biological invasions are recognized as one of the most serious problems confronting the integrity of native species and ecosystems around the world (Carlton and Geller, 1993). Invasive species often have no natural enemies to limit their reproduction and spread; hence, they frequently become established at the expense of the native species and entire ecosystems (Ellstrand and Schierenbeck, 2000). In aquatic ecosystems, extreme examples include establishment of the zebra mussel Dreissena polymorpha (Pallas, 1771) in the Great Lakes region of the United States in the 1980s and the introduction of the Asian green mussel Perna viridis (Linnaeus, 1758) to Tampa Bay, Florida in 1998 (Griffiths et al., 1991; Ingrao et al., 2001). Both of these mussel species: 1) have spread extensively from the point of introduction via dispersal larval stages, 2) have cost millions to hundreds of dollars to control, 3) have altered biodiversity, primarily by out-competing or overgrowing native species, and 4) were so abundant when discovered that eradication was not an option (Ludyanskiy et al., 1999; Fajans and Baker, 2003; Diggins et al., 2004).

Knowing that early detection and rapid response are critical to preventing establishment of non-native species that may cause ecological and economic havoc, we need to be proactive when new invasions are reported. This is especially true when the number of individuals of the invasive species is persistent, suggesting either multiple introductions or a resident breeding population. An example of this is presently occurring along the Atlantic coast of North America in Florida. The bivalve, Mytella charruana (d’Orbigny, 1835), a South American and Mexican Pacific Coast native, has recently been described in low numbers (94 individuals) in the oyster reef communities of the northern Indian River Lagoon system.

Mytella charruana (d’Orbigny, 1835) in Florida

The indigenous range of the mytilid Mytella charruana extends along the eastern coast of South America from Venezuela to Argentina (Keen, 1971; Carlton, 1992; Szefler et al., 1998; Bochs et al., 2004). The charru mussel also occurs on the eastern Pacific Ocean from Guaymas, Sonora, Mexico to El Salvador and the Galapagos Islands (Cardenas and Aranda, 2000).

Mytella charruana resembles the common edible blue mussel Mytilus edulis (Linnaeus, 1758) in shape. Maximum recorded shell length is 4.5 cm (Szefler et al., 1998). Its external shell color may vary from light green to black, and may be uniform or banded in a criss-cross pattern (Keen, 1971) (Figure 1). Internal shell color is deep purple (Keen, 1971). This tropical mussel is a lagoonal species that typically occurs on mudflats, in shallow lagoons and attached to mangrove roots, being able to withstand salinity variations in the 14–41%e range (Ruelas-Inzuma and Paez-Osuna, 2000; Bochs et al., 2004).

Mytella charruana first appeared in the United States in large numbers in the seawater intake pipe of a power plant in Jacksonville, FL in 1986 (Lee, 1987; Carlton, 1992). The probable source of invasion was ballast water from tankers transporting oil from Venezuela (Carlton, 1992). Fortunately, M. charruana never became established, as the founder population was extirpated during the winter of 1987; this has been attributed to cold temperatures (H. G. Lee, pers. comm.).

Since the 1986–1987 arrival in northern Florida, M. charruana had not been recorded in this location or any other in the United States until 2004. On August 20, 2004, M. Boudreaux discovered a population of M. charruana in the waters of Mosquito Lagoon, the northern-most region on the Indian River Lagoon system along the east coast of central Florida (170 km south of Jacksonville). In this environment, M. charruana was initially found attached to clusters of the eastern oyster Crassostrea virginica (Gmelin, 1791) as well as attached to disarticulated oyster shells in the intertidal and subtidal zones within Canaveral National Seashore (28°90.68' W, 80°82.06' N). These waters were then surveyed monthly for the occurrence of this mussel for the next 13 months.
Systematic surveys were conducted looking at a wide variety of substrates and places where mussels are known to thrive, including blades and bases of the cordgrass *Spartina alterniflora* (Loisel., 1807), submerged man-made structures and debris (e.g., dock pilings, PVC pipe, cinder blocks), natural debris (e.g., driftwood), red mangrove prop and cable roots, black mangrove pneumatophores, clusters of oysters, and disarticulated oyster shells. For each collected individual, the following information was recorded: GPS coordinates, water temperature (°C), water salinity (%), mussel length, width and depth (cm), weight (g) and substrate.

Thirty-nine live individuals of *M. charrana* were found between August 2004 and February 2005 and one dead individual was collected on March 20, 2005. Despite continued monthly surveying, no individuals were found again until August 28, 2005, when 14 live individuals were collected. On our last observation date, October 1, 2005, an additional 40 live individuals were collected. *Mytella charrana* was found attached to both man-made debris, especially cinder blocks and PVC, and the same small crevice locations on driftwood and oyster clusters/shells as the native mussel *Geukensia debrissia* (Dillwyn, 1817). In Mosquito Lagoon, water temperature on dates when *M. charrana* was collected ranged from 15–32 °C. The salinity at collection locations ranged from 24–36% on survey dates.

To date, a total of 94 individuals of *Mytella charrana* have been found and removed, indicating an invasive population that is still quite small. Although individuals up to 4.4 cm in length have been recorded in its native range, the sizes of *M. charrana* found during one year in Mosquito Lagoon were consistently small, ranging from 0.5–2.7 cm (Mean ± S.E.: 1.3 ± 0.1 cm). The mean length of individuals collected from August 2004–February 2005 was 1.8 ± 0.1 cm, whereas the mean length for the August–October 2005 collection was 1.1 ± 0.1 cm. When compared with one-way analysis of variance, the mean length of the August 2004–February 2005 individuals was significantly larger (ANOVA: F = 32.61; p < 0.0001) (Figure 2). Likewise, the weights of live individuals collected in August–October 2005 were significantly lower than weights of live individuals collected earlier (ANOVA: F = 34.69; p = 0.0003). This suggests multiple introductions or an established reproductive population, with us locating only newly recruited individuals. If ecological conditions are optimal for continued survival and establishment of *M. charrana*, this population has the potential to greatly increase in numbers and out-compete native mussels in the area. Additional research on this species is warranted to determine its extent of colonization, source of introduction, environmental conditions necessary for establishment, and impacts on biodiversity. Voucher specimens are catalogued at the Florida Museum of Natural History, Gainesville, Florida (FLMNH 372689, 372691) and The Bailey-Matthews Shell Museum, Sanibel, Florida (BMSM 34067).

ACKNOWLEDGMENTS

We thank A. Benson (USGS) and H. G. Lee for the identification and J. H. Lead for the photographs of *Mytella charrana*. Surveys of Mosquito Lagoon were undertaken by the spring 2005 Marine Ecology of Florida class at the University of Central Florida (UCF). P. Sacks, J. Sacks, A. Barber, and the Camp Fire USA Sunshine Council. Funding was provided by UCF and Florida Sea Grant. We thank Canaveral National Sea-
shore for permission to conduct research within Park boundaries. We thank P. Mikkelsen and an anonymous reviewer for critically reading and improving the manuscript.

LITERATURE CITED


Notice

THE 2006 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2006 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the museum for a period of one week. Abbott Fellows will be expected, by performing collection-based research, to assist with the curation of portions of the Museum’s collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1550
Sanibel, FL 33957
jleal@shellmuseum.org

Applications for the 2006 Visiting Curatorship should be sent no later than June 30, 2006. The award will be announced by late July. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

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Text must conform to the dimensions of 8 ½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

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<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Title</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. G. Harasewych</td>
<td>Rediscovery, range extension, and redescription of <em>Calliostoma torrei</em> Clench and Aguayo, 1940 (Gastropoda: Vetigastropoda: Calliostomatidae)</td>
</tr>
<tr>
<td>George R. Sedberry</td>
<td><em>Sasakiconcha elegansima</em> new genus and new species (Gastropoda: Vetigastropoda: Anatomidae?) with disjointly coiled base</td>
</tr>
<tr>
<td>Daniel L. Geiger</td>
<td>A review of <em>Typhisopsis</em> Jousseaume, 1880, and <em>Typhisiana</em> Jousseaume, 1881 (Gastropoda: Muricoidea) of the eastern Pacific</td>
</tr>
<tr>
<td>Roland Houart</td>
<td>New buccinoid gastropods from uppermost Cretaceous and Paleocene strata of California and Baja California, Mexico</td>
</tr>
<tr>
<td>Carole M. Hertz</td>
<td>Authorship of the <em>Ovulidae</em> (Gastropoda) of the <em>Zoology of the Voyage of the Samarang</em></td>
</tr>
<tr>
<td>Richard L. Squires</td>
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Rediscovery, range extension, and redescription of Calliostoma torrei Clench and Aguayo, 1940 (Gastropoda: Vetigastropoda: Calliostomatidae)

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ABSTRACT

Two living specimens of Calliostoma torrei were recently collected feeding on bamboo coral (Keratosia orcuttii Verrill, 1878) east of Jacksonville, Florida, at a depth of 843 m. This represents a considerable range extension of a species that was previously known only from the holotype, collected dead off Matanzas, Cuba, in 704 m. A redescription of the shell and first descriptions of the operculum, gross anatomy, and radular morphology are provided, partial sequences of the genes for 16S rDNA and cytochrome c oxidase I have been determined and added to the GenBank database. These new data suggest that Calliostoma rugosum Quinn, 1992, from unknown depths in the Straits of Florida is a synonym of C. torrei. The radula most closely resembles that of C. yucatecum Dall, 1881, suggesting placement in Calliostoma sensu stricto according to the criteria of Clench and Turner, 1960.

INTRODUCTION

A number of unusual and noteworthy gastropods were collected during the NOAA Ocean Exploration Cruise Estuary to Abyss, Exploring Along the Latitude 31–30 Transect, conducted 20 August to 1 September, 2004, off the coasts of South Carolina, Georgia, and northeastern Florida. Among these were two exceptionally large specimens of the pleurotomarid Bayerotrochus midas ‘F. M. Bayer, 1965’, which extends the range of this species northward from the Little Bahama Bank to off the coast of southern Georgia, and two small calliostomatid trochoids. The calliostomatids are members of a rare and poorly known group of species, characterized by a stepped spire, that are known to inhabit bathyal depths in the Straits of Florida, throughout the Bahamas and the Antilles, southward to Argentina, and eastward to the Azores and western Africa. Both specimens appear closest in morphology to the Calliostoma torrei Clench and Aguayo, 1940, a taxon known only from the dead-collected holotype dredged in 704 m off Matanzas, Cuba; our specimens are smaller and presumed to be immature. To a lesser extent, they resemble Calliostoma rugosum Quinn, 1992, a taxon that is also based on a single, dead-collected specimen from the Straits of Florida, but for which neither depth nor exact location are known.

We provisionally consider all four specimens to be conspecific and Calliostoma torrei to be the oldest available name for this taxon. Because this species was previously known only from dead and damaged specimens, we provide a detailed description of the shell, operculum, radula, and gross anatomy based on the newly collected specimens. Partial sequences of the mitochondrial genes for 16S rDNA and cytochrome c oxidase I (CO I) have been entered into GenBank, but no sequences for either of these genes from any species of Calliostoma were available for comparison at the time of this writing.

Within the fauna of the western Atlantic, the genus Calliostoma is unusually diverse, with 94 living species (Quinn, 1992; Rosenberg, 2005) inhabiting principally hard-bottom substrates from intertidal to mid-bathyal depths (0–2000 m) at latitudes ranging from 42° N to 55° S (Rosenberg, 2005). Other species inhabit comparable depths in the Azores and eastern Atlantic. This genus is thus ideally suited for studies of fine-scale biogeography and bathymetric zonation once sufficient data are accumulated to produce a robust phylogenetic framework. Institutional abbreviations are: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; SERTC/SCDNR, Southeastern Regional Taxonomic Center/South Carolina Department of Natural Resources, Charleston, South Carolina; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.
SYSTEMATICS (Follows Bouche et al., 2005)
Clade Vetigastropoda Salvini-Plawen, 1980
Superfamily Trochoidea Rafinesque, 1815
Family Calliostomatidae Thiele, 1924
Genus Calliostoma Swainson, 1840
Calliostoma torrei Clench and Aguayo, 1940 (Figures 1–20)

Calliostoma (Calliostoma) torrei Clench and Aguayo, 1940, 79–80, pl. 14, fig. 5; Clench and Turner, 1960, 59–61, plate 10; Abbott, 1972, 46, 47, Quinn, 1992, 79, figs. 50, 81.

Calliostoma rugosum Quinn, 1992: 102–103, figs. 78–79.

Description: Shell (specimen in Figures 9–12) 22.2 mm high, 23.0 mm in maximum diameter, rather thin, with very narrow umbilicus nearly sealed by parietal fold. Spire stepped, weakly concave, spire angle 76.5°. Color whitish, pale golden yellow between periphery and suture, iridescence of aragonitic nacre visible through thin calcitic outer layer. Protoconch (Figures 14–15) pincushion, smooth, glassy, translucent, increasing from 150 to 500 μm in diameter in about 1/3 whorl (270° rotation). Transition to teleoconch marked by flared terminal varix. Teleoconch of 7 1/5 whorls. Step between peripheral cord and suture concave in first teleoconch whorl, becoming angular, then progressively more convex with increasing whorl number. Base inflated, convex, evenly rounded. First teleoconch whorl with 21 well-defined axial ribs and two strong spiral cords (Figure 15, P2 + P3; following cord terminology of Marshall, 1995) that produce reticulate sculpture at their intersections. Axial ribs decrease in prominence by 4th teleoconch whorl, replaced by increasingly prominent beads at intersections with spiral cords. Apical cord (Figures 14, 15, PI) begins as spiral thread in first teleoconch whorl, 3/4 whorl after the onset of spiral cord P2, expands to form cord by second teleoconch whorl. Cord P3 remains at periphery. Fine spiral threads appear between adjacent spiral cords at onset of whorl 4, expanding to form beaded cords by the next whorl. The process repeats, increasing the number of broad, beaded cords between P1 and P3 on the body whorl to 6, in addition to 2 fine and 2 weakly beaded threads. Region between peripheral cord (P3) and suture smoothly concave in teleoconch whorls 1–3, with fine thread appearing at onset of whorl 4 and expanding to form beaded cord by the next whorl, the process repeating to produce 2 beaded cords and 2 fine threads on penultimate whorl, and 4 beaded cords and 2 threads on body whorl. A single, smooth cord appears between suture and P1 near end of teleoconch whorl 7. Base with 21 smooth cords between umbilicus and periphery. Cords broad near umbilicus, becoming narrower towards periphery. Aperture tangential, with plane offset from coiling axis by 32°, 11.1 mm wide, 9.6 mm high, outer lip symmetrically elliptical, inner lip with thickened columnella forming an angle of 87° with the base of previous whorl and 17° with the coiling axis of the shell. Columnella rounded, nacreous indument nearly seals very narrow umbilicus.

Operculum: Corneous, thin, transparent, yellowish amber in color, multispiral, with thin growing edge. Maximum diameter 8.8 mm.

Gross Anatomy: Exposed portions of animal yellowish tan. Foot long, narrow, posteriorly tapering; epipodium broad, with broad, scalloped, inflated and narrow, tapering, enrolled, exhalant neck lobes: 4 epipodial tentacles per side. Cephalic lappets small, simple, cephalic tentacles long, eye stalks short, with very large, black eyes. Snout large, cylindrical, papillate ventrally, with split ventral lip.

Radula (Figures 16–20): Radular ribbon 8.65 mm long, 1.6 mm wide, with 97 rows of teeth. Rachidian teeth (Figure 18, r) simple, triangular, with very finely serrated edges. Lateral teeth (Figure 18, l) 7 per side, with broad attachment area and narrow, simple, curved, finely serrated along entire outer edges, with or without fewer, more widely spaced cusps along distal portion of inner edge. Innermost marginal teeth (Figures 18, 19, im) broad, thick, with 5 short, conical cusps along the inner distal edge. Marginal teeth become progressively longer and narrower toward the outer edge of the radular ribbon, with an increasing number of fine cusps along the inner, distal portions of the scythe-shaped teeth. Compare inner marginal teeth (Figure 19, im) with outer marginal teeth (Figure 20, om).

Jaws large, broadly rounded, anterior ends broadly rounded with short fringe.

Material Examined: Holotype of Calliostoma torrei Clench and Aguayo, 1940, ATLANTIS Station 3985, off Matanza, Matanzas Province, Cuba (23°13' N, 81°22' W), in 385 fathoms [704 m], MCZ 135165: Holotype of Calliostoma rugosum Quinn, 1992, JAMES M. GILLIS Cruise 7307, Station 13, Straits of Florida, depth and exact location unknown, USNM 860262, JOHNSON-SEA-LINK II Dive 3470, Cutthroat Cliff, about 220 km E of Jacksonville, Florida, (30°17.147' N, 79°20.147' W), in 863 m (SCDNR Collection Number T10041600), larger specimen (Figures 9–12) USNM 1069300, smaller specimen (Figure 13) SERC/SCDNR collection S1005.

Habitat and Ecology: The bottom at the Cutthroat Cliff collection site was sloping at approximately 20°, and was composed mostly of hard, broken, pavement-like rock, some carbonate sand and coral rubble in mound formations (up to 10 m high) composed of loosely aggregated coral fragments and rubble. Scattered dark broken manganese-phosphorite pavement and rocks (Popenoe and Manheim, 2001) were frequently encountered. Bottom temperature was 7.7°C; currents were 0.1–0.2 knots from the south (180°).

The Calliostoma torrei specimens were living on, and apparently grazing on, a bamboo coral, Keratoisis ornata. The coral was attached to a small (20 × 30 cm) manganese-phosphorite rock or outcrop that protruded through light-colored carbonate sand. Stalked eunicoids, small globular and encrusting sponges, and small erect hard corals (Lophelia spp.) were common on the dark rocks. A few cutthroat eels (Symphobranchus spp.) swam nearby. The coral branches on which the snails were found (and some adjacent branches) were devoid of polyps, which were abundant and exposed on other branches of the colony.

DNA Sequences: Partial sequences of the mitochondrial genes for cytochrome c oxidase I (COI) (Genbank DQ 314293) and 16S rDNA (Genbank DQ 314294) have been determined using standard protocols for DNA extraction, amplification and sequencing.

A search of the Entrez nucleotide database revealed that only a single sequence for any species of Calliostoma was present in the database, that for a 302-bp fragment of the 28 S rDNA gene of Calliostoma zygophyllum Linnaeus, 1758.

Remarks: Calliostoma torrei was described on the basis of a single, very large (41 mm) but dead-collected specimen, that has deteriorated over time, primarily through delamination of the outer, calcareous shell layers from the inner nacreous layers (compare Clench and Turner, 1960; pl. 40; Quinn, 1992: figs. 80, 81; with Figures 1-4 herein). Clench and Turner (1960: 60) commented that this species was among the largest in the western Atlantic and was not closely related to any other species in the region. They suggested that it was perhaps closest to the large (to 55 mm), shallow water (30–65 m), South American species Calliostoma militare Thiering, 1907 [as C. amazonicum Finlay, 1930] (Rosenberg, 2005), and, to a lesser extent, to Calliostoma atlantis Clench and Aguayo, 1940, from comparable depths (603 m) off Mariel, Cuba.

Quinn (1992: 103) described Calliostoma rugosum from a single, dead-collected and damaged specimen dredged in the Straits of Florida from unknown depths, differentiating this from C. torrei based on its smaller size, broader shell, and differences in the sculpture of the cords.

The two juvenile, live-collected specimens are intermediate in morphology between the holotypes of C. torrei and C. rugosum. The spire angle of both is closer to that of C. rugosum, but the sculpture is closer to that of C. torrei. Distinctions between the four specimens appear to lie primarily in the relative coarseness of spiral sculpture, especially when compared at corresponding whorls. We provisionally consider these specimens to be conspecific, recognizing that additional material will be required to better delineate intraspecific variation over a range of sizes.

In their review of western Atlantic Calliostoma, Clench and Turner (1960) did not assign C. torrei to any subgenus, as neither the morphology of the jaws nor the radula were known. When compared to the few species for which radial morphology has been published, the radula of C. torrei appears most similar to that of C. greatcamun Dall, 1894 (see Clench and Turner, 1950: pl. 4, fig. 4), especially in having radidian teeth without a broad basal area, narrow lateral teeth, and similarities in the morphology of the innermost and inner marginal teeth. Radular and jaw morphology of C. torrei suggest an affinity with Calliostoma sensu stricto.

Quinn (1992: 103) suggested that both C. rugosum and C. torrei were closely related to the Pliocene C. caribbicaum Weisbord, 1962, from the Mare Formation of Venezuela. Based on shell characters, he (Quinn, 1992: 99) hypothesized that the species C. atlantis (603–628 m,
off Mariel, Cuba and Great Inagua), C. torri (including C. rugosum synonymized herein) (704–570 m, NE Florida to Cuba), C. denticulatum (Watson, 1879) (640 m, Recife, Brazil), C. atlantoides Quinn, 1992 (417–559 m, St. Lucia), C. rota Quinn, 1992 (20–30 m, Brazil), and C. coronatum Quinn, 1992 (568–505 m, Brazil) form a distinctive species group. In this group, he also provisionally included C. cubanus Clench and Aguayo, 1940 (896 m, Cardenas, Cuba) and the central and eastern Atlantic species C. grimaldii Dautzenberg and Fisher, 1896 (1250–2165 m, Azores, Morroco), C. leptolyphus Dautzenberg, 1927 (550–845 m, Azores), C. normani Dautzenberg, 1927 (599–1600 m, Azores) and C. caroli Dautzenberg, 1927 (1250 m, Azores). With the exception of C. rota, all members of this diverse and widespread group inhabit bathyal depths, most in the 500–1000 m range, with depths increasing eastward.

ACKNOWLEDGMENTS

Funding for submersible operations was provided by a grant (No. NA08ROAR4600055) G. R. Sedberry, Principal Investigator) from the National Oceanic and Atmospheric Administration Office of Ocean Exploration. Susan Devictor, of the SERTC/SCDNR laboratory, identified the coral on which the Calliostoma were collected. The SERTC staff assisted in processing the NOAA-0E samples and submersible pilot Tim Askew, Jr. (Harbor Branch Oceanographic Institution) assisted in collections. This is Contribution Number 582 of the South Carolina Marine Resources Center, and Smithsonian Marine Station at Fort Pierce Contribution Number 648.

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Sasakiconcha elegantissima new genus and new species (Gastropoda: Vetigastropoda: Anatomidae?) with disjointly coiled base

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ABSTRACT
Sasakiconcha elegantissima, a new genus and species from the Western Pacific is described. The specimens are most similar to members of Anatomidae (Anatoma, Thiecella) with a peripheral selenizone, but close the slit to a foramen, and lack a columella because of a disjointly coiled base resulting in an umbilical trough. Additionally, an aberrant specimen of Scissurella morretesi Montouchet, 1972, which shows repeated closure of the slit to form foramina, is discussed with respect to the evolutionary pathway from the ancestral open slit to its modification as a single or a series of foramina.

Additional Keywords: Protoconch, teratology, biodiversity, scanning electron micrographs, SEM

INTRODUCTION
The study of the scissurellid grade has revealed a significant number of new taxa over the last few years, from species to family-level (e.g., Marshall, 1993; 2002; Kase and Kano, 2002; Bandel, 1998; Geiger, 2003; 2006; Geiger and Jansen, 2004a, b). With these new taxa, more and more discrete shell types have been discovered. Shells with flat spires (Satondella Bandel, 1998; Maxellella Bandel, 1998), the calyptraeform Depressizona Geiger, 2003, and even the new slit-less forms such as Troglocoucha Kase and Kano, 2002, expanded on the more common trochiform shell morphologies.

Until recently, the above forms had been classified in Scissurellidae; however, recent molecular studies have shown that Scissurellidae is a grade (Geiger and Thacker, 2005). More specifically, Scissurellidae (Scissurella, Stinezona, Satondella, Incisura) and Anatomidae (Anatoma, Thiecella) do not form a clade, whereas other lineages (Sutillizinae, Temnocinclinae, Depressazoninae) have yet to be included but are likely not to be part of either of the sequenced lineages (see Geiger and Thacker, 2005 for discussion).

The careful study of existing museum collections has been the main driving force behind these discoveries. Here, I report on some specimens found in the collection of the Muséum National d'Histoire Naturelle, Paris that exhibit yet another new shell morphology. Additionally, a note on an abnormal specimen of Scissurella morretesi Montouchet, 1972, shows that the transition from single slit to multiple foramina can occur even in modern species.

MATERIALS AND METHODS
Specimens were mounted on double-sided carbon tabs (Ted Pella, Redding, California), sputter-coated with gold in a Cressington 108 auto sputter coater with rotary- planetary stage, and viewed in a Zeiss EVO40 XVP (Zeiss, Cambridge, UK) scanning electron microscope. Specimens of the new species were cleaned with a wet artist brush and a tungsten needle; the specimens appeared to be too fragile to withstand ultrasonic cleaning. The number of specimens is indicated by the number separated by a comma from the museum acronym (see below). Protoconch whorls are counted following Geiger (2003).

Institutional abbreviations used in the text are: AMS: Australian Museum Sydney, New South Wales, Australia; BMNH: The Natural History Museum, London, Great Britain; LACM: Natural History Museum of Los Angeles County, Los Angeles, California, USA; MNHN: Museum National d'Histoire Naturelle, Paris, France; NMNZ: Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; UMUT: University Museum, University of Tokyo, Japan; USNM: United States National Museum, Smithsonian Institution, Washington, DC, USA.

SYSTEMATICS
Vetigastropoda Salvini-Plawen, 1980
Sasakiconcha new genus
Type species: *Sakiconcha elegantissima* new species.

**Differential Diagnosis:** *Anatoma* and *Thieleella* share the position of the slit at the periphery, but the slit remains open, and the suture is always below the lower keel of the selenizone, even in the most depressed species, *A. paucispiralia* (Bandel, 1998).

**Description:** Shell depressed biconical, whorls rapidly increasing in size, no nacre. Protoconch sometimes partially covered by suture of subsequent whorl. Whorls not touching at base forming umbilical trough; no columella. Selenizone and foramen at periphery. Suture mostly at or above upper keel of selenizone of previous whorl. Umbilicus wide. Animal unknown.

**Etymology:** *Sasaki*—honing Takenori Sasaki of the University Museum of the University of Tokyo for his significant contributions to the systematics of bivalve gastropods. *-concha:* Latin for shell. Sasaki’s shell. Gender feminine.

**Remarks:** *Sakiconcha* is tentatively placed in Anatomiidae because of the peripheral position of the selenizone. That position was shown to discriminate between major scissurellid/anatomid lineages in an exploratory phylogenetic analysis of shell characters (Geiger, 2003). The most likely alternative hypothesis is that *Sakiconcha* represents yet another independent lineage of silt-bearing, small vetigastropods.

Many species of *Anatoma* show converging margins of the slit, but in no species do they fuse and enclose a foramen. *Sakiconcha* is not based on senior specimens of *Anatoma*, as the foramen is found over a wide range of shell sizes (4–8 mm). Not a single specimen of *Anatoma* or *Thieleella* with a closed foramen is known.

*Sakiconcha* must form its foramen by a different process compared to most *Sinea* or *Sakashitrochus*. *Sakiconcha* closes the foramen from fairly early growth onward, i.e., at about half-maximum size, in contrast to most scissurellids, which close the foramen at about 4/5 of maximum size. It implies that, with growth, the anterior margin of the foramen is resorbed, while shell material is added at the apertural margin, leaving a foramen of approximately constant proportion over a wide range of shell sizes (4–8 mm). In contrast, juveniles of *Sinea* and *Sakashitrochus* have an open slit, which only closes once the animal is fully grown. Only *Sinea* globosa Geiger, 2006, known from the two type specimens and USNM 500687 (Caribbean locality data most likely wrong), also closes the foramen in fully grown specimens (Geiger, 2006). Comparison to other foramen-bearing small vetigastropod genera of the scissurellid grade (*Sutiliza*, *Temnicrinitis*, *Temnozoga*, *Depressizonia*) is not possible due to the scarcity of material.

The overgrowth of the selenizone by the shoulder of the subsequent whorl is unique among Recent Vetigastropoda, but is known from some fossil genera (Brookes-Knight et al., 1990; e.g., *Aguiesella* Cossmann, 1909 [*Portlockiellidae*], *Unibotropis* Perner, 1903 [*Gosseletini*]), and *Catachisma* Branson, 1909 [*Gosseletini*]). The overall shell morphology is most similar to the cernogastropod genus *Cochleolites* Stimpson, 1835 [*Vitrinellidae*], though this latter misses the selenizone indicative of a vetigastropod placement for *Sakiconcha*. Sowerby (1820–1834) illustrated *Scissurella elatior* Sowerby, 1831, on an unnumbered plate with the selenizone overgrown by the subsequent whorl. This character is not discussed as the species was introduced as a *nomen et figura*, without indication of where it was found. Sowerby (1842, 1852) placed it as a Recent species occurring off the coast of Britain, from where only *Anatoma crispata* (Fleming, 1825) is known. It is thus most likely that Sowerby’s (1820–1834) figure was stylized and is erroneous with respect to the overgrowth of the selenizone. The whereabouts of the type material of Sowerby’s species is unknown.

*Sakiconcha elegantissima* new species
(Figures 1–2)

**Differential Diagnosis:** The cited generic characters will readily identify *S. elegantissima*. The most similar species is *Anatoma paucispiralis* (Bandel, 1995) described from Saton) Indonesia. Shared characters include the overall biconical depressed shell shape, the protoconch lacking an apertural varix, and the short teleoconch. The protoconch is half the size in *A. paucispiralis* (150 μm vs. 325 μm). teleoconch is longer in *A. paucispiralis* (0.125 whorls vs. 0.05), the suture is below the lower keel of the selenizone of the previous whorl (i.e., the selenizone is not obscured), the sculpture of the shoulder has distinct axial and spiral components, the base has reticulate sculpture, and the slit is open although the aperture of the illustrated holotype (Bandel, 1995: pl. 14, figs. 2–4) is slightly chipped.

**Description:** Shell biconical-depressed, *Sinnus*-shaped, to 8.5 mm (holotype); thin, fragile. Protoconch 255–325 μm (mean = 311 μm, n = 4, 325 μm in holotype), 0.75 whorls, flocculent sculpture (mostly eroded in holotype), no apertural varix, apertural margin convex; sometimes partially covered by suture of subsequent whorl. Teleoconch I <0.05 whorls. Teleoconch II up to 1.75 rapidly expanding whorls. Shoulder slightly convex, early teleoconch I with axial cordlets only, interstices irregular with tiny pits; after 0.5 whorls, axial cordlets with approximately one dozen nodule; nodules becoming spiral elongated with strength of axial cordlets decreasing; after 1.25 whorls, sculpture transformed into approximately 50 spirally arranged, irregularly spaced, nodular cordlets; interstices with finest axial growth marks. Base with fine, stepped, longitudinally undulating, spirals, reaching just into uppermost portion of umbilical cavity, approximately 30 in 4 mm specimen, approximately 40 in 8 mm specimen. Umbilicus wide, walls steep, smooth; umbilical wall not connecting with previous whorl, forming spiral trough between umbilical wall and previous whorl produced by inner surface of shoulder. Selenizone at periphery, usually hidden by suture of...
subsequent whorl: slit closed anteriorly to form foramen, foramen formed in specimens ≥4 mm. In fully mature specimens (holotype), last 0.125 whors descending. Aperture oblong, D-shaped, roof overhanging. Animal unknown.

**Type Material:** Holotype (MNHN type collection): paratypes: MNHN, 1 (Figure 2: left), 477–493 m, BORDAU1, DW1432, off Fiji, 17.333° S, 178.733° W; MNHN, 1 (Figure 2: middle), 300–302 m, BORDAU2, DW1523, Eua Tonga, 21.300° S, 175.000° W; MNHN, 2 (one illustrated in Figure 2: right), 391–421 m, BORDAU2, DW1537, haut-fond, 21.653° S, 175.317° W; UMUT RM29213, 1; MNINZ M.273290, 1, 700–707 m, BORDAU1, DW1485, Fiji, 19.050° S, 178.500° W.

**Type Locality:** 970–983 m, BORDAU2, DW1531, Eua Tonga, 21.200° S, 174.933° W.

**Etymology:** *Elegantissima*: elative of Latin adjective: extremely elegant referring to the overall aspect of the shell.

**Other Material Examined:** Fiji: MNHN, 1, 700–707 m, BORDAU1, DW1485, 19.050° S, 178.500° W; Tonga: MNHN, 1, 456–510 m, BORDAU2, DW1500, Tongatapu, 21.053° S, 175.367° W; MNHN, 2, 578 m, BORDAU2, DW1585, Vavau group, 18.550° S, 173.950° W; French Polynesia: MNHN, 1, 600–620 m, BENTHIAUS, DW1899, east of Kap, 27.613° S, 144.262° W.

**Distribution:** Western Pacific (17–27.5° S, 144–175° W), 300–981 m [all shells only].

**Remarks:** *Sasakiconcha* is not a morphological endpoint in a series of undescribed *Anatoma* species. The MNHN collection contains 23 undescribed *Anatoma* and...
Figure 2. Paratypes of *Susakiconcha elegantissima* new genus and new species. First row: apertural view; second row: lateral view showing closure of slit to foramen; third row: umbilical view; fourth row: apical view; fifth row: protoconchs. Left: MNHN, 1, 477–893 m, off Fiji, 17.33° S, 178.73° W; middle: MNHN, 1, 300–302 m, Enu, 21.30° S, 175.00° W; right: MNHN, 2, 391–421 m, Huit-fond, 21.68° S, 175.34° W. Only in one of the smaller specimens on the left the slit is still open. In the other two, which are approximately half the size of the holotype, the slit is already closed to a foramen. Scale bars shells = 1 mm; scale bars protoconchs = 100 μm. TL: extent of teleoconch 1.
Thielevella species from the Indo-Pacific await detailed study through electron microscopy. None of these even remotely approaches Sasakicoucha.

The umbilical trough is a character not known from any other scissurellid sensu lato or anatomid and is to my knowledge a novel configuration in gastropods; its function is unclear. Umbilical modifications have been shown to function as brood pouches in Larocheinae (Marshall, 1993).

Sasakicoucha elegantissima is a fairly large anatomid species, and one with a diameter of 8 mm does not even qualify as a micromollusk, which usually is defined as shells smaller than 5 mm. Despite its size, it is not the largest known anatomid. A specimen of Anatomina elegypta (Pelseneer, 1903) from Antarctica is 10.5 mm in diameter (Zelaya and Geiger, unpubl. data).

The protococh of Sasakicoucha elegantissima is the largest known of any scissurellid/anatomid species by a factor of approximately two. It implies that rather large eggs are formed and that the number of eggs is relatively small, as has been observed in other scissurellids and anatomids [Sinezona rimuloides (Carpenter, 1865); Anatomina elegypta; Geiger, unpubl. data]. This is quite unlike the more familiar gonad condition in the large broadcast spawning Vetigastropoda with millions of eggs (e.g., Bevelander, 1985). Large eggs themselves do, however, not entail brooding or parental care. Eggs may also be deposited onto any available hard substrate as shown for Scissurella jucunda Smith, 1890 by Strasoldo (1991).

Repeated Closure of the Selenizone

The selenizone with associated slit or foramen foramina is typically found in Vetigastropoda, including Scissurellid sensu lato (not in Larocheinae), Anatomidae, Pleurotomariidae, Fissurellidae, and Haliotidae, whereas in other families it is absent (Trochoidea, Lepetodrilidae, Peltospiridae, Neomphalidae). A sinus is formed in Seguenziidae, which had prompted Locard (1898) to include Seguenziia in Scissurellidae, whereas this latter genus is placed today in its own group beside Vetigastropoda.

That the open slit is the ancestral condition can be argued both based on data from the fossil record as well as from the ontogeny of Recent species. The open slit is found in the various pleurotomarioid families since the Paleozoic (Brookes-Knight et al., 1990; Harasewych, 2002), as well as in juveniles of Sinezona and Sakashitroclus, which eventually closes the slit to form a foramen at maturity (Geiger, 2003). Mature shells can be recognized by the distinct descending last quarter whorl of the adult shell. Haliotidae have modified the shell in a particular fashion in that they repeatedly open and close the slit to form a series of foramina (Dellhaes, 1990). Most likely, the closure of the foramen lends more stability to the apertural margin of the shell. Similar shells of Scissurella with an open slit break more easily than those of Sinezona with a closed foramen. As Haliotidae usually live in high energy regions of the intertidal and shallow subtidal (Shepherd, 1973), a strengthening of the apertural margin throughout their life makes the repeated formation of foramina advantageous. The underlying mantle has a single, anteriorly open, slit, covering all open foramina (Crofts, 1929), while in foramen bearing Fissurellidae all stages from open mantle-slit to fused mantle skin can be observed (McLean and Geiger, 1998).

Intermediate forms are not widely known. Dellhaes (1990) discussed the keyhole-shaped double foramen of the fossil pleurotomarioidlean in the genera Ditomaria and Phragmagnostoma. Ontogenetically, Haliotidae immediately form a series of holes after a short slit-less teleconch I (Bevelander, 1988: fig. 4.1; Sasaki, 1998: fig. 28; fig. 3), unlike in Sinezona, where the juvenile has an open slit, which is closed only once at maturity (Geiger, 2003).

A single specimen of an aberrant Scissurella morretesi is shown here (Figure 4). Two specimens of the species were available in conjunction with the original description of Montochet (1972). As it is virtually impossible to legally obtain loans from Brazil at this time, no further material was available. No further exemplars of the species were found out of a total of 29,566 specimens examined (major collections include: AMS, BMNH, LACM, MNHN, XMNZ, USNM; many smaller collections not listed). Despite other abnormalities observed such as selenite closure of foramen in Scissurella spp., the condition of the S. morretesi specimen discussed here is unique. The first SEM illustrations of the species are provided here.

As for all Scissurella species, usually the slit remains open throughout life. In the particular specimen, the slit was closed and re-opened three times successively. It does not appear to have been caused by damage to the shell; the shoulder and base of the shell in the vicinity of the closure show no growth irregularities. It rather seems
to have been caused by some sort of mutation/developmental abnormality. The specimen provides an illustration of a possible pathway from the ancestral open slit, to irregularly repeated closure of the slit, to patterned closure of the slit as seen in Haliotidae.

ACKNOWLEDGMENTS

This study was made possible by a Visiting Curatorship from MNHN, and NSF grant MRI 0402726 to Henry Chaney, Michael Caterino, and Daniel L. Geiger. I would like to thank all staff at MNHN for their hospitality and assistance during the stay. James McLean and Diego Zelaya offered constructive criticism that helped to improve the manuscript. Richard Petit provided details on the dating of some of Sowerby’s works.

LITERATURE CITED


A review of Typhisopsis Jousseaume, 1880, and Typhisala Jousseaume, 1881 (Gastropoda: Muricoidea) of the eastern Pacific

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ABSTRACT

Typhisopsis Jousseaume, 1880, and Typhisala Jousseaume, 1881, are redescribed and the included species reviewed. Typhisopsis coronatus (Broderip, 1833) is considered as the senior synonym of T. quadratus (Hinds, 1843), Murex siphouferusLesson, 1844, and Typhis martyrca Dall, 1862. In addition, Typhisopsis carolskoglundae new species is described from western Panama. Its range extends to Sonora, Mexico. The new species is compared with Typhisopsis coronatus, Typhisala grandis (A. Adams, 1855) and T. clarki (Keen and Campbell, 1964).

The four species have different shell morphology, especially in the number, height, and breadth of the spiral cords, the morphology of the axial ribs and the siphonal canal. The protocochs of the four species are illustrated for the first time. Lectotypes are designated for Murex siphouferus and for Typhisala grandis.

INTRODUCTION

A few months ago, the senior author received a lot of specimens of "Typhis" species from Costa Rica for identification. At first sight that lot was separated into two species: Typhisopsis coronatus and Typhisala grandis. However, after more careful examination and discussion, we began a complete re-evaluation of the whole group occurring in the eastern Pacific. Typhisopsis coronatus was described from a sub-adult specimen. Another species, previously identified as a dwarf form of Typhisala grandis by D’Attilio (1987) and D’Attilio and Hertz (1988) was re-examined. It is here described as a new species of Typhisopsis.

Keen (1944), Gertman (1969), Radwin and D’Attilio (1976), Vokes (1988), and other authors classified all the Typhis-like species in the Muricidae, subfamily Typhinae. Cossmann, 1903, D’Attilio and Hertz (1988) included the species related to Typhis in the family Typhidae [as in Sacco (1904) and Garrard (1963)] and split it into two subfamilies: Typhinae and Tripterotyphinae D’Attilio and Hertz, 1988. Their study was based on morphological differences of shell and radular structure. The validity of Tripterotyphinae is not questioned herein. Subsequent authors, however, chose to retain Tripterotyphinae as well as Typhinae, as a subfamily of Muricidae instead of Typhidae (Vokes, 1980a, 1980b, 1996; Houart, 1991, 1994, 2002; Absalio and Santos, 2003). DNA work currently underway elsewhere (Oliverio and Houart, in prep.) for Typhinaellus labiatus (Cristofori and Jan, 1832) (= Typhis sowerbyi H. and A. Adams, 1858) as well as future DNA work may help clarify the taxonomy in this group. Radular terminology follows Houart (1991) based on D’Attilio and Hertz (1988).

Abbreviations used in this study are: BM(NH): Natural History Museum, London, Great Britain; CAS: California Academy of Sciences, San Francisco, California, USA; IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium; LACM: Natural History Museum of Los Angeles County, California, USA; MNHN: Muséum national d'Histoire naturelle, Paris, France ; MZCR: Museo de Zoología, San José, Costa Rica; SBMNHI: Santa Barbara Museum of Natural History, California, USA; SDNHM: San Diego Natural History Museum, California, USA; SUPTC: Stanford University Paleontological Type Collection, Stanford, USA; USNM: National Museum of Natural History, Washington, D.C., USA; CJH: Carole and Jules Hertz Collection, San Diego, California, USA; CS: Carol Skoglund Collection, Phoenix, Arizona, USA; RH: Roland Houart Collection, Landen, Belgium; RZ: Ricky Zadafi Collection, Abaco, Bahamas; spec.: live-taken specimen; dd spec.: empty shells, dead collected.

SYSTEMATICS

Subfamily Typhinae Cossmann, 1903

Description: Shells with aperture entire, usually with projecting peristome and no sulcus; usually four or more
varices per whorl, either wing-like or with axial swellings; rounded, ventrally sealed anal tubes originating from adapical spiral cord, only current anal tube functional, older tubes sealed; siphonal canal ventrally sealed with left side overlapping right side.

Genus Typhisopsis Jousseaume, 1880

Type Species: Typhis coronatus Broderip, 1833, eastern Pacific, by original designation.

Description: Shell with four varices; apertural varix of adult with varical flange, frilled abaperturally. Varices heavy, rounded, rope-like. Shoulder spines broad-based, triangular, flat, tapering inwards to a sharp point. Partition connecting apertural shoulder spine and last teleoconch whorl. Anal tubes situated near preceding varix. Siphonal canal broad, ventrally sealed. Left side of canal broadly overlapping right side.

Typhisopsis coronatus (Broderip, 1833)

Typhis coronatus Broderip, 1833: 158; Sowerby, 1841, pl. 200, figs 3, 4.
Typhis quadratus Hinds, 1843: 8; Hinds, 1844: 10, pl. 3, figs 3, 4.
Vexa siphoniferus Lesson, 1844: 168.
Typhis martyr Dall, 1902: 590, Dall, 1898, pl. 15, fig. 11.
Typhisopsis coronatus.—D'Attilio, 1975: 57, text fig.; D'Attilio, 1976: 28, text figs; Radwin and D'Attilio, 1976: 212, pl. 32, figs. 10–12; Abbott and Dance, 1982: 157, text fig.;

D'Attilio, 1975: 34–35, figs 7–11; D'Attilio and Hertz, 1985, 21, fig. 109.

Typhis coronatus.—Kächer, 1978: card 1595.

Typhis (Typhisopsis) grandis.—Keen, 1971, 540, fig. 1052 [not Typhis grandis (A. Adams, 1855)].
Not Typhis (Typhisopsis) coronatus.—Keen, 1971, 540, fig. 1051 (left) not Broderip, 1833 [=Typhis grandis (A. Adams, 1855)].

Description: Shell up to 40 mm in length. Biconic, heavy; spire high, acute; protoconch off-white, of 2.75 rounded whorls, first protoconch whorl pustulose, remaining whorls smooth; terminal lip thin, raised, curved (Figures 44–46). First four teleoconch whorls smooth, glossy, with no microsculpture; intritacally covering penultimate and final whorl with microsculpture consisting of regular gourge-like pits (Figure 57). Shell with six weakly shouldered, nodose teleoconch whorls. Last whorl broad, suture moderately impressed and mostly obscured. Axial sculpture of four broad, rounded, rope-like varices, each bearing a broad, flat, triangular, strongly inward-bent, shoulder spine at intersection with P2. On last whorl apertural varix broadly expanded, edge reflected dorsally, frilled abaperturally with posterior edge extending into a sharp, dorsally incurved spine at shoulder; anal siphon (tube) adjacent to preceding varix and appressed to partition connecting the varix of previous whorl. Final anal siphon long and dorsally directed.

Spiral sculpture on three earliest varices of heavy raised spiral cords (P3–P6) becoming less prominent at the anterior end, intervarical spiral sculpture faint or absent. Siphonal canal long, broad (Table 1), ventrally

Figure 1. Morphology of the spiral cords in Typhisopsis coronatus (Broderip, 1833).
Table 1. Terminology used to describe the spiral cords (based on Merle 1999, 2001)

<table>
<thead>
<tr>
<th>Cord</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>Primary cord</td>
</tr>
<tr>
<td>s</td>
<td>Secondary cord</td>
</tr>
<tr>
<td>P1</td>
<td>Shoulder cord</td>
</tr>
<tr>
<td>P2-P6</td>
<td>Primary cords on the convex part of the teleoconch whorl</td>
</tr>
<tr>
<td>s1-s6</td>
<td>Secondary cords on the convex part of the teleoconch whorl</td>
</tr>
</tbody>
</table>

Example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.

ADP  = adapertural primary cord on the siphonal canal
MP   = median primary cord on the siphonal canal
APB  = adapertural primary cord on the siphonal canal
ads  = adapertertural secondary cord on the siphonal canal
ms   = median secondary cord on the siphonal canal
abs  = adapertural secondary cord on the siphonal canal

Type Material: Typhis quadratus: Costa Rica, Golfo de Nicoya, and Ecuador, Bahia de Guayaquil, dredged from a muddy bottom 7 to 18 ft (13–33 m) (Golfo de Nicoya is here designated as type locality), holotype BM(NH) 1844.6.7.35; Murex siphoniferus: Mexico, Acapulco, Guerrero, 1 lectotype MNHN (here selected); Typhis martygia: Golfo de California, off San Pedro Martir, 26 m, sand, holotype USNM 1300629.

Other Material Examined: Mexico, Bahia Magdalena, Baja California Sur, 1 spec. (SBMNH); San Felipe, Baja California, 1 spec. (SBMNH); Bahia de los Angeles, Baja California, dredged 27 m, 1 spec. (SDNHM 23/216 [figured in Badwin and D’Attilio, 1976]; off Isla San Marcos, Baja California Sur, divers, 12 m on Spondylus princeps, 1 spec. (CS); Isla Carmen, Baja California, 1 del spec. (SDNHM); Isla Danzante, Baja California Sur, dredged 35–40 m, 5 spec. (CS); dredged 30–45 m, 3 spec. (CJH); Bahia Concepcion, Baja California, 1 spec. (SBMNH); Cabo Tepoca, Sonora, dredged 20–30 m, sand bottom with rocks, 5 spec. (CS); Guaymas, Sonora, dredged, 24 m, 1 spec. (RH); 1 spec. dredged (SDNHM 43812); 55 m 1 del spec. (MNHN); Bahia Bacochoibampo, Sonora, dredged 42 m, 1 spec. (MNHN); dredged 18–27 m, 2 spec. (CJH); 150 spec. (SBMNH); Sonora 1 spec. (MNHN), 2 spec. (RH); off Bahia San Carlos, Sonora, 19–38 m, 1 spec. (IRSNB IC 26,158); dredged 18–22 m, 98 spec. (CJH); dredged 15–30 m, 14 spec. (CS); 4 spec., 31 m (SDNHM 90537); dredged 100 m, 3 spec. (SDNHM 571920); off Tetas de Cabras, dredged 56–100 m, 1 spec. (SDNHM 92766); Tenacatita, Jalisco, 2 spec. (SBMNH); Manzanillo, Colima, near harbor entrance, 15–22 m, 1 spec. (RH); dredged 10–30 m, 3 spec. (CS); dredged 31 m, 4 spec.(SDNHM); dredged 100 m, 3 spec. (SDNHM); dredged 60–100 m, 7 spec. (SDNHM); 16 spec. (SBMNH); Salina Cruz, Oaxaca, 5 spec. (SBMNH); Costa Rica, Plazas del Coco, Guanacaste dredged 24 m, 4 spec. (CS); dredged 24–36 m, 4 spec. (CJH); dredged 24–36 m, 2 spec. (SDNHM 90774); 1 del spec. (SDNHM 91506); 1 spec. (SBMNH); Panama, 21 spec. (SBMNH); Isla Santa Catalina, dredged 5–8 m, 5 spec. (RH); Boca de la Honda, 7°27'N, 89°51'W, in white sand, 2 spec. (RH); SE Isla Rancheria, Golfo de Chiriqui, dredged 15–30 m, 1 spec. (SDNHM 90775); Isla Cébaco, off Golfo de Montijo, Veraguas, in silty sand and rubble, 6–9 m, 1 spec. (MNHN); Bahia Montijo, Veraguas, 19 m, 1 spec. (RH); Arenas de Quebro, dredged 19–38 m, 1 spec. (RH); Isla Venado, 1 del spec. (SDNHM 64236); Ecuador, Islas Galápagos, Isla San Salvador, close to Bahia James, 30–35 m, coll. D.R. Shasky, 1 spec. (SBMNH 366002).

Distribution: San Felipe, Baja California and Cabo Tepoca, Sonora, Mexico, to Guayaquil, Ecuador and Islas Galápagos, 5–42 m.

Remarks: Subadult specimens of T. quadratus (Figures 11–12, 62), as in the type, have an incompletely formed apertural lip which gives the shell a narrower and more slender outline. The first four teleoconch whorls (to a length of approximately 15 mm) of T. quadratus are smooth and shiny without the microsculpture evident on mature shells. In juvenile specimens the siphonal canal is also narrower, having a more centrally situated suture line.

Of the two syntypes of Murex siphoniferus (MNHN), one is Typhisalas grandis, the other is conspecific with Typhlopsis coronatus. As first revisers, and in order to maintain the name T. grandis as it was illustrated by recent authors, we designate that latter specimen of Murex siphoniferus as lectotype (Figures 6–7). Two of the three syntypes of Typhloidea grandis (A. Adams, 1855) are specimens of Typhlopsis coronatus (see under that species for further explanation). The holotype of T. quadratus (BM(NH)) has the siphonal canal broken, but the overall shape of the shell is quite the same as the intact specimen illustrated by Hinds (1844, pl. 3, figs 3–4). No other specimen was located in the type material.
Typhisopsis carolskoglundiae new species (Figures 17–25, 47–49, 59, 63)

Typhisala grandis.—D’Attilio, 1987: 32, figs. 1–6; D’Attilio and Uetz, 1988: 72–73, figs. 108a–c [not Typhisala grandis (A. Adams, 1855)].

Description: Shell up to 30.9 mm in length, slender, heavy. Spire high, 40–48% of total shell length. Protoconch off-white, conical with 2.7 rounded protocochn whorls, first whorl pustulose, remaining whorls smooth, ending with delicate, thin, weakly erect and curved terminal lip (Figures 47–49); teleoconch with up to 5 or 6 broad, strongly shouldered whorls. Suture impressed, partly obscured; axial sculpture of first three teleoconch whorls with sharp varices; remaining teleoconch whorls consisting of four strong, broad, rounded varices with remains of sharp lamina visible on varices of last whorl; each varix with a broad, flat, long, strongly inwards pointed triangular, flat spine at adapical extremity touching previous whorl. Anal tube adjacent to leading edge of varix and appended to previous partition. Varices broader and swollen at shoulder periphery. Apertural varix with a moderately broad, recurved, sinusous flange, a slightly broad, long, somewhat curved spine at posterior edge, spine attached to previous whorl by an axially grooved partition densely sculptured spirally; lip edge rounded curving into siphonal canal approximately 1/4 from the end.

Apertural varix with strong spiral cords beginning at its outer lip and over-ridden by strong axial fimbriation; outer recurved edge of abapertural side squamous. Spiral sculpture of raised, heavy, primary cords on varices. Last whorl with 15 cords (P1, P2, s2, P3, s3, P4, s4, P5, s5, P6), followed by rounded cords on siphonal canal, probably ADP, ads, MP, ms and ABP, forming a broad expansion at adapical extremity of apertural varix. P1 with sealed, rounded anal tube near preceding varix. P2 with flat, triangular spine at intersection with varices. Intervarcal sculpture faint or absent under magnification (20×). Sealed rounded anal tube appended to partition preceding varix, forming an angle of approximately 50–90° with axis of shell. Spiral cords ending as short, strongly backward curved spines at edge of apertural varix.

Aperture subcircular, forming a continuous peristome, erect at outer lip and anterior portion of columellar lip and appressed posteriorly. Siphonal canal comparatively short, broad, ventrally sealed. Sutural line strongly shifted to the right, left side of canal broadly overlapping right side. Intact specimens ending with canal dorsally reflected and curved to the right at extremity.

Fresh, not overly cleaned specimens, with a simple, chalky off-white intricately showing occasional axial sliae. Protoconch off-white with white pustules on first whorl. Teleoconch color white to cream with brown on shoulder spines and anal tubes; 2–5 brown spots on edge of outer apertural lip and often visible on leading edge of previous varices. One brown spot midway intervarically on each varix except the apertural varix, as in Typhisala grandis. Operculum light brown with 12–14 concentric lamellae and terminal nucleus. Radula not examined.

Type Material: Holotype: SDNHM 90773, Costa Rica, Playas del Coco, Guanacaste, on mud bottom, 24–37 m; Paratypes: Costa Rica, Playas del Coco, Guanacaste, on mud bottom, 24–37 m, 1 paratype (SDNHM 93358); on mud bottom, 24–37 m, 1 paratype (CJH); dredged 12–25 m, 3 sp., (CS): 2 spec., 18–27 m in coarse sand, broken shell bottom (SBMNH 359431); 1 paratype (SBMNH 359436); 5 spec., 9–30 m (SBMNH 359435); 1 paratype (USNM 1081298); 1 paratype (LACM 3066); Isla Negritos, Golfo de Nicoya, 3 paratypes, 21–27 m, coarse sand, broken shell (SBMNH 359430); Panama, Arenas de Quebro, Veraguas, 19–37 m, 1 paratype (RH); Boca de la Honda, 7°27′ N, 80°51′ W, in white sand, 1 paratype (BM(NH) 20050371); 1 paratype (MZCR UCR 6153); 1 paratype (MNHN Moll 6991); 2 paratypes (RIU); off Isla Gobernadora, intertidal, 1 paratype (RH); off Isla Venado, Bahía Panamá in muddy sand at low tide, 1 paratype (IRSNB IC 26817/666); Bahía Chiriqui, 74 m, 1 paratype (IRSNB IG 25/466/677); Contadora, Perlas Archipelago, Bahía de Panamá, 4 paratypes, 15–30 m (SBMNH 359432); 1 paratype (SBMNH 359439); Ecuador, Isla Santiago, Islas Galápagos, 1 paratype (SBMNH 359433).

Other Material Examined: Mexico, Bahía San Carlos, Sonora, 31 m, 1 spec. (RH).

Type Locality: Costa Rica, Guanacaste, Playas del Coco, on mud bottom, 24–37 m.

Distribution: Sonora, Mexico to Isla Venado Bahía de Panamá, Panama, from the intertidal to 74 m and Islas Galápagos, Ecuador.

Etymology: This species is named in honor of Carol Skoglund of Phoenix, Arizona, author and specialist in Panamic mollusks, who first collected the type material of this species and donated the holotype and a paratype to the SDNHM. She has also donated additional paratypes of this species from her private collection to the USNM and to the LACM.

Remarks: Typhisopsis carolskoglundiae differs from T. coronatus in having a broader siphonal canal with an expanded varical flange, extending almost to the tip of the siphonal canal; flange sinuous midway to the anterior end, rounded curving into the siphonal canal, approximately 1/4 from the end and constricted at the base. It has a relatively smooth shell surface under a chalky, simple intratixal, compared to the squamous, pitted intratixal in T. coronatus. The axial ribs are usually broader at the shoulder, and there are more numerous and slightly narrower spiral cords on the last teleoconch whorl, 15 in contrast to 11–12 in T. coronatus. The varices appear broader in coronatus and the spiral cords are less pronounced in the new species.

The holotype of Typhisopsis carolskoglundiae was il-
illustrated in D'Attilio (1987: figs. 1 and 2 [left]) and D'Attilio and Hertz (1988: fig. 108, a–e), as a dwarf Typhisala grandis, but Typhisopsis carolskoglundae differs from Typhisala grandis in having a smaller, narrower shell at maturity and fewer and broader spiral cords on the last teleoconch whorl (15 in Typhisopsis carolskoglundae in contrast to 20–23 on Typhisala grandis). Typhisopsis carolskoglundae also has broader, shorter, flat varicose shoulder spines, typical of Typhisopsis and narrower less sharp axial ribs with the flange on the apertural varix more strongly constricted at the base of the teleoconch than in Typhisala grandis.

Typhisopsis carolskoglundae differs from Typhisala clarki in having broad, rounded varices, rather than the sharp varices in T. clarki, in having anal tubes adjacent to the leading edge of varices rather than midway between varices, and in having brown spots on the aperture edge and on previous varices, which are lacking in Typhisala clarki. The new species is similar to grandis and clarki in having an expanded, strongly fimbriate varical edge and a smooth shell under a simple chalky intratricica.

Genus Typhisala Jousseaume, 1881

Type species: Typhis grandis A. Adams, 1855, eastern Pacific, by original designation.

Description: Shell with four varices; apertural varix of adult with broad apertural varical edge extending to almost the tip of siphonal canal, fimbriate abaperturally; other varices sharp, narrow. Shoulder spines narrow; spines of three abapical teleoconch whorls narrow, twisted, curved inwards; partition connecting apertural spine and last teleoconch whorl. Anal tubes situated near preceding varix, pressed against preceding partition. Siphonal canal broad, ventrally sealed; left side of canal overlapping right side.

Typhisala clarki (Keen and Campbell, 1964) (Figures 26–29, 30–34, 50–52, 58, 64, 68)

Typhis (Typhisopsis) clarki Keen and Campbell, 1964: 48, pl. 9, figs. 15, 19, 23.

Description: Shell up to 27 mm in length, biconic, lamellate, delicate. Spire moderately high, 39–42% of total shell length; protoconch of 2.5 off-white, smooth, convex, conical whorls, first whorl pistilose, remaining whorls smooth (Figures 50–52); teleoconch with six angulate, strongly shouldered whorls. Suture impressed, partly obscured by succeeding whorl. Axial sculpture of teleoconch consisting of four high, sharp, narrow, lamellate varices, each with a slightly open, long, twisted, inward curved spine adapically, each varix composed of two compressed laminae, one on the receding edge extending further than the one on leading edge, the two forming the slightly open spine at shoulder. Apical sinuate (tube) forming an angle of approximately 85–90° with axis of shell, placed approximately midway between varices and apertured to previous partition, last tube only complete, long, open. Apertural varix flange-like, strongly fimbriate, dorsally reflected as shallow, open spinelets at outer edge. Apertural spine broad, triangular, weakly or strongly dorsally curved, connected to last teleoconch whorl by a broad, high, lamellate, partition. All other spiral cords ending as short, weakly or strongly backward curved, open spinelets at edge of apertural varix. Spinal sculpture faint, where present, 12–14 intervarical lines visible on some specimens under magnification (10x) corresponding to open spinelets at outer apertural edge. On fresh specimens, not over-cleaned, intratricica sculpture of simple axial striate present. P1 with sealed, tapering, anal tube. P2 ornamented with long, upwards curved spine at intersection with varix.

Aperture small, ovate, forming a continuous peristome, erect at outer lip and anterior portion of columellar hill. Siphonal canal long, broad, ventrally sealed, tapering to a slender, dorsally curved tube at distal end. Sutural line weakly shifted to right, left side of canal weakly overlapping right side. Color of protoconch off-white with white pustules on first whorl; teleoconch brown, green or yellowish-white (sometimes with all three colors on one shell), having darker brown anal tubes, shoulder area, shoulder spines, and tip of siphonal canal. Apertural flange often white even on brown shells. On fresh specimens, not over-cleaned, intratricica sculpture of simple axial striate present. Operculum conical, light brown with 12 or 13 concentric lamellae and terminal nucleus. Rachula (Figure 68) with rachidian tooth bearing a long central cusp, and on each side 2 shorter, narrower, lateral denticles of approximately same strength and length, and a broad lateral cusp, slightly shorter than central cusp. Lateral teeth sickle-shaped, broad.

Type Material: Holotype: Panama, Isla Venado, Bahía Panama, Panama CASIZ 064667 (formerly SUPTC 9724); 1 paratype CASIZ (formerly SUPTC 9725); 1 paratype BM(NH) 1964433.

Other Material Examined: Mexico: Pta. San Felipe, Baja California, intertidal, in mud and rocks, 28 spec. (CH); intertidal, in mud between rocks, 7 spec. (CS); intertidal, −1.8 m tide, 19 spec. (SDNHM 81088); 2 spec., intertidal, −1.5 m tide (SDNHM 53432), figured in Radwin and D’Attilio, 1976); intertidal, 9 spec. (SDNHM 82565); 31 spec., intertidal (SBMN10); Bahía la Chollita, Sonora, intertidal in sand over rocks, 7 spec. (CS); intertidal, −1.5 m tide, 2 spec. (SDNHM 90835);

3 spec. (SBMNH); Panama: off Isla Cébaco, dredged in 6-9 m, silty sand and rubble, 1 spec. (RH); Isla Venado, under stones at low tide, 1 spec. (RH); 21 spec. (SBMNH); in muddy sand at low tide, 1 spec. (IRSNB 26817); intertidal, 9 spec. (CS); Isla Gobernadora, intertidal, 1 spec. (SDNHM 93342); Bahía de Panamá intertidal (SDNHM 62807); Isla Pedro Gonzales, Islas Perlas, 2 spec. (SBMNH).
Distribution: San Felipe, Baja California and Bahía la Cholla, Sonora, Mexico to Panama, intertidally to 6 m.

Remarks: The elegant lamellae of the varices, the smooth or nearly smooth shell surface, and the lack of brown spots on the apertural lip and previous varices of T. clarki distinguish it from the other three species

Typhisala grandis (A. Adams, 1855)  

Murex siphoniferus Lesson, 1844: 168 (paratype MHNJ)  
see under Typhisala coronata).

Typhis grandis A. Adams, 1855: 42, pl. 27, fig. 4.
Typhis Typhisala grandis.—Keen. 1944: 54, fig. 18: Abbott.  

Typhisala grandis.—D'Attilio, 1975: 57, 1 text fig.; Radwin and  
D'Attilio, 1976: 211, pl. 29, fig. 1; Abbott and Dance, 1982:  
158. 1 text fig.

Typhis (Typhisalis) coronata.—Keen. 1971: fig. 1051 (left)  
(not T. coronata Broderip, 1833).

Not Typhis (Typhisalis) grandis.—Keen, 1971: 540, fig. 1052  
(= Typhisalis coronata).

Not Typhisala grandis.—D'Attilio, 1975: figs. 1–6; D'Attilio  
and Hertz. 1988; fig. 105, a–c (= Typhisalis carolsko-  
glundiae new species).

Description: Shell up to 37.9 mm in length, broad,  
heavy. Spire low or moderately high, angulate; proto-  
couch off-white of 2.5 rounded, smooth whorls, first  
whorl not pustulose (Figures 53–55); teleoconch of up  
to six strongly shouldered whorls, broadly rounded on last  
two whorls. Suture deeply impressed, obscured by suc-  
ceeding whorls. Axial sculpture from first teleoconch  
whorl to antepenultimate whorl consisting of four low,  
sharp, varices, becoming broadly rounded at periphery of  
penultimate and last whorl with a sharp flange extending  
out from the varix becoming fimbriate on its leading  
edge; each varix with a moderately slender, curving spine  
at its adapical extremity. Immediately adjacent to the  
spine is a deep indentation anteriorly, next to which the  
adul siphon (tube) rests against the former partition. Fi-  
nal anal siphon (functioning tube) long, at approximately  
90° to the shell axis. Apertural varix broadly expanded,  
constricted at anterior end; outer edge, reflected and  
densely fimbriate; connected to previous teleoconch  
whorl by a broad, high, densely lamellose partition. Ap-  
ertural spine short, sharply dorsally curved.

Spiral sculpture of sharp, raised primary cords, sec-  
ondary cords visible under magnification (10×). Last  
whorl, including siphonal canal with 22–23 cords. P1  
with sealed, rounded anal tube. P2 ornamented with  
short spine at intersection with varix. Other cords cannot  
be quantified. Spiral cords of approximately same mag-  
nitude, more obvious on varices, ending as short, strongly  
backwards curved, short spine at outer edge of apertural  
varix.

Aperture round-ovate, forming a continuous erect  
peristomes; outer lip with 3–5 brown spots often appear-  
ing as well on leading edge of varices, brown spot also  
appearing on each intervarical area: Siphonal canal long,

broad (Table 1) ventrally sealed. Sutural line strongly shifted to the right, left side of canal broadly overlapping right side. Microsculpture of thin, low, curved, lamellae covering the canal and weakly overlapping varices, except apertural varix. Intratacalx off-white, sometimes thick, with occasional axial striae.

Color milky-white to lavender, light tan, tan or almost entirely dark brown with brown colored spines, anal tubes, and shoulder area. Other brown spots between spiral cords, on outer lip of aperture, on leading edge of varices, not intervarically and occasionally on sutural line of siphonal canal. Operculum corneus, light brown, with 11–12 concentric lamellae and terminal nucleus.

Radula (Figure 69) with rachidian tooth bearing a long central cusp, and on each side 3–4 short, narrow, lateral denticles of varied strength and length, occasionally fused

67. Typhisopsis coronatus (Broderip, 1833), Islas Galápagos, Isla Isla. 68. Typhisalara clarki (Keen and Campbell, 1964), Mexico, Baja California, San Felipe. 69. Typhisala grandis (A. Adams, 1853), Mexico, Bahía de Banderas. Unknown magnifications.

or split, and a long, broad lateral cusp slightly shorter than central cusp. Lateral teeth sickle-shaped, broad.

Type Material: BM(NH) 197-470, 3 syntypes here selected as lectotype and paralectotypes (Figures 35–36), “California” (see Remarks).

Other Material Examined: Mexico: Punta Doble, San Carlos, Sonora, 20–22 m, in rubble, 1 spec. (RH); 2 dd spec. 20–21 m diving. (SDNHM 90531); 18–21 m, 4 spec. (CS); divers, 20–21 m in rubble, 2 dd spec. (SDNHM); off Bahía San Carlos, Sonora, dredged 31–75 m, 12 spec. (CS), 3 spec. (CJH); dredged 60 m, 2 spec. (CJH); dredged 3–5 m, 4 spec. (SDNHM 76475); 64 spec. (SBMNH); 3 m SE San Antonio, Guaymas, Sonora, dredged 100 m, 2 dd spec. (SDNHM 90764); Mazatán, Colima, 20 spec. (SBMNH); in 6 m. (SDNHM 23215 [as quadratus]); Costa Rica: Isla Ballena, Puntarenas, offshore, 12–25 m, 4 spec. (RH); 4 spec. (RZ); Isla Ballena, Canton de Osa, Puntarenas, offshore, between 12 and 25 m, 10 spec. (subadult, dd) (RH); 3 spec. (CJH); 2 spec. (RZ); Panama: 10 spec. (SBMNH); Islas Gobernadora 1 spec. (MNHN); extreme low tide, in muddy sand near rocks, 1 spec. (RH); low tide, in muddy sand, 1 spec. (RH). Isla Cébaco, dredged in 37 m, sand and gravel bottom, 1 spec. (RH); 62–93 m, 1 spec. (IRSNB 1G 26.817); 37–52 m, 1 spec. (IRSNB 1G 27.037); Isla Santa Catalina, dredged 5–8 m, 1 spec. (RH); Isla Venado, intertidal, 1 spec. (CS). Ecuador: Islas Galápagos, Isla San Salvador, close to Bahía James, 30–35 m, coll. D.R. Shanks, 1 spec. (SBMNH 36606).

Distribution: Punta Doble, Sonora, Mexico to Panama and the Islas Galápagos, Ecuador, intertidally to 62 m.

Remarks: Of the three syntypes of Typhisopsis grandis housed in BM(NH), two are Typhisopsis coronata, the other is Typhisala grandis. In order to maintain the status of T. grandis as it was illustrated by recent authors (except Keen, 1971), one syntype specimen is here designated as the lectotype (Figures 35–36). The type locality is doubtful because, to our knowledge, no specimen has ever been reported from California since then. Many times in old publications “California” is also used for “lower California” now known as Baja California which is part of Mexico. It is probably the case here. Subadult forms of T. grandis (Figures 40–43, 66) differ from the adult form, in having a narrower, lower partition, a rounded apertural varix without varied flange, a narrower, more acute, siphonal canal, with the ventral natural line being more central. In adults the left side of the canal extensively overlaps the right side (Figure 65).

Discussion: Both Typhisopsis and Typhisala seem to be closely related, and it seems questionable whether both are separate or not. However, several differences have been detected so far. In Typhisopsis the varical spine is flat, broadly triangular and strongly inward bent (Figures 56, 59), compared to the longer, weakly twisted spine in Typhisala (Figures 57, 60) and the apertural varix of Typhisala is fimbriate and broadly expanded whereas the apertural varix of Typhisopsis is narrower and more rounded with heavy raised spiral cords. The question is whether or not such differences are significant enough to warrant separate genera. Maybe DNA work would be useful in this particular case.

ACKNOWLEDGMENTS

We are most grateful to M. G. (Jerry) Harasewych and Paul Greenhall (USNM) for the loan of Typhis martynjia Dall, 1902; to Kathie Way and Phil Crabb (BMNH) for digital images; to Vincent Héros and Delphine Brabant (MNHN) for help in searching literature and specimens from the collection of MNHN and for digital images; to Paisley Cato and Laura Halverson (SDNHM) for loan of the two type specimens of Typhisopsis carolsglthiniae; to George Metz, Novato, California, for digital images of the holotype of Tyllyphis clarki at CAS; to Kelvin Barwick (City of San Diego EMS Lab) for digital images of the holotype and paratype of Typhisopsis carolsglthiniae; to Daniel Geger (SBMNH) for SEM photographs of the protoconch of the four species; to Patricia Salegham (SBMNH) for digital images of the complete speci-
Table 2. Characters of Eastern Pacific Species of Typhisopsis and Typhisala.

<table>
<thead>
<tr>
<th>Character</th>
<th>Typhisopsis coronata</th>
<th>Typhisopsis carolinskghanum</th>
<th>Typhisala grandis</th>
<th>Typhisala clarkii</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Protoconch</td>
<td>2.75 white, conical, rounded whorls, pulastose on first whorl</td>
<td>2.66 rounded whorls, pulastose on first whorl</td>
<td>2.5 cream-colored, rounded whorls, none pulastose</td>
<td>2.75 white, smooth, conical rounded whorls, pulastose on first whorl</td>
</tr>
<tr>
<td>Last teleoconch whorl*</td>
<td>Moderately broad</td>
<td>Broad</td>
<td>Broad</td>
<td>Broad</td>
</tr>
<tr>
<td>4. Shoulder spine</td>
<td>Flat, broad, not twisted at base, sharp, incurved at acute end</td>
<td>Flat, not twisted, long, broad at base, curved at acute end</td>
<td>Weakly twisted, long, broad at base, bent dorsally</td>
<td>Weakly twisted, broad base, long, open at distal end</td>
</tr>
<tr>
<td>2. Anal tube position</td>
<td>Tubes adjacent to leading edge of preceding varix and appressed to previous partition</td>
<td>Tubes adjacent to leading edge of varix and appressed to previous partition</td>
<td>Tubes adjacent to preceding varix, appressed to preceding partition</td>
<td>Tubes approximately midway between varices, appressed to preceding partition</td>
</tr>
<tr>
<td>3. Number of spiral cords (siphonal canal included)</td>
<td>10-11, broad</td>
<td>13-15, narrow, broadly spaced</td>
<td>21-22, narrow, broadly spaced on siphonal canal</td>
<td>12-14, only visible on sharp edge of axial ridges, otherwise smooth</td>
</tr>
<tr>
<td>4. Axial ribs</td>
<td>Broad, rope-like rounded varices, apertural varix with varical flange</td>
<td>First three teleoconch whorls with sharp varices; remaining whorls broad, rounded; apertural varix with broad varical flange, roundly curving into siphonal canal approximately 0.25 before distal end</td>
<td>Broad, rounded; apical portion with small, thin, erect lamellae; apertural varix with broad varical flange</td>
<td>Angulate, sharp, formed by two appressed lamellae; apertural varix expanded</td>
</tr>
<tr>
<td>5. Apertural varical flange</td>
<td>Edge reflected; weakly squamose, spiral cords obvious, more strongly squamose on outer portion</td>
<td>Broad, recurved; fimbriate on its outer portion, roundly curving into siphonal canal</td>
<td>Broadly expanded, recurved; strongly fimbriate on its outer portion, strongly constricted at anterior end</td>
<td>Broad, reflected as shallow open spinelets; strongly fimbriate on its outer portion</td>
</tr>
<tr>
<td>Siphonal canal*</td>
<td>Moderately broad, long, tapering</td>
<td>Moderately broad</td>
<td>Broad</td>
<td>Tapering, long</td>
</tr>
<tr>
<td>1. Mean breadth/length</td>
<td>6.08/7.76 mm</td>
<td>8.05/7.85 mm</td>
<td>9.41/9.57 mm</td>
<td>4.91/7.62 mm</td>
</tr>
<tr>
<td>2. Position of the suture line</td>
<td>Broadly overlapping the right side</td>
<td>Broadly overlapping right side</td>
<td>Broadly overlapping the right side</td>
<td>Strongly overlapping the right side</td>
</tr>
<tr>
<td>Intratrace</td>
<td>Distinctive, chalky, off-white, deeply irregularly pitted</td>
<td>Chalky, off-white, simple with occasional axial striae</td>
<td>Chalky, often thick, off-white, simple, with occasional axial striae</td>
<td>Chalky, thin, off-white to cream, simple with occasional axial striae</td>
</tr>
</tbody>
</table>

* Characters of adult shells only

mens with protocochns; to Jacky Van Goethem, Claudine Claes and Dana Hoortman (IRSNB) for help in searching literature and access to the collection of IRSNB; to Ricky Zandal, Marsh Harbour, Abaco, Bahamas, for the loan and gift of specimens, and to Carol Skoglund for donating type material of the new species to the USNM and LACM as well as lending comparative material of the four species for study.

LITERATURE CITED


New buccinoid gastropods from uppermost Cretaceous and Paleocene strata of California and Baja California, Mexico

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ABSTRACT

Two new genera and three new species of extinct buccinoid gastropods are described and named from the Pacific slope of North America. The buccinid? Ornopsis? dysis new species is from uppermost Maastrichtian (uppermost Cretaceous) strata in the Dip Creek area, San Luis Obispo County, west-central California. The fasciolariid? Saxituberosa? new genus is comprised of the lineage Saxituberosa? four? new species, from lower Paleocene (Danian) strata in Los Angeles County, southern California, and Saxituberosa? titan? (Waring, 1917), from middle Paleocene (Selandian) strata in Ventura and Los Angeles counties, southern California, and northern Baja California, Mexico. The fasciolariid? Perrillihatula? califia? new genus and new species is known from middle Paleocene (Selandian) strata in Ventura County, southern California, and northern Baja California, Mexico. Ornopsis? dysis and Perrillihatula? califia? are similar in morphology and geologic age to Gulf Coast Ornopsis? glenni? Wade, 1916, and Fasciolariia? plumieri? Gardner, 1933, respectively; whereas probable congener for Saxituberosa are unknown, and it appears to be endemic to the northeastern Pacific.

INTRODUCTION

Four species, three of which are new, are described in this report. They are of similar aspect in having fusiform shells with tabulate whorls ornamented by knobs and spiral ribs. They are recognized as being of three different genera, two of which are new.

Saul (1986a), in her exploratory work on shallow-marine mollusks from the Lake Nazcaimento area, San Luis Obispo County, west-central California, illustrated a specimen of Ornopsis? n. sp. from the uppermost Cretaceous part of the El Pino Formation along the east side of Dip Creek (Figure 1). Saul (1986a), furthermore, reported that Ornopsis? n. sp. is apparently the "Trachytriton? titan" Waring, 1917, that was included in the Dip Creek macrofaunal list provided by Talaferrro (1944). This present work was initiated in order to provide a better understanding of the relationship between Ornopsis? n. sp. and "T." titan. Saul's Ornopsis? n. sp. is herein assigned to Ornopsis? dysis new species, and its genus assignment cannot be made with certainty until more specimens are found. Ornopsis sensu stricto Wade, 1916, heretofore has been reported with certainty only from Upper Cretaceous (upper Campanian to upper Maastrichtian) strata of the southeastern United States (Sohl, 1964). "Trachytriton? titan" is herein found to occur in middle Paleocene strata in southern California. Its characteristics separate it from the cymatiid Trachytriton Meek, 1864, and "T." titan is assigned to Saxituberosa new genus, which is also represented by Saxituberosa? four? new species, of early Paleocene age.

The fourth species described in this report, Perrillihatula? califia? new genus and new species, is the largest of the four. It occurs in middle Paleocene strata in northern Baja California, Mexico.

The classification system used here follows that of Bouchet et al. (2005). All of the new taxa are neogastropods and are placed in superfam Bucinoidae Rafinesque, 1815. The familial classification for each of the new taxa described below is tentative, especially because no information is known about their protoconchs nor about the anterior portions of their shells. Another factor to take into account is the observation made by Bandel (1993: 8), who stated that modern groups of gastropods "can usually easily be connected with their relatives that lived during Tertiary times, but when crossing over into the Mesozoic comparisons become increasingly difficult due to convergence observed in regard to the teleoconch as well as the protoconch." We agree with his observation, and, furthermore, we believe that it is possible that the taxa described below might eventually be placed in new suprageneric categories. This study, nevertheless, adds substantially to our knowledge of Pacific slope of North America latest Cretaceous to Paleocene neogastropods, a rather poorly known group. Institutional abbreviations used in the text are: CAS, California Academy of Sciences; San Francisco; IGM, Mexico.
paren tally endemic to the study area. Details of the morphologic comparisons are given under "Systematic Paleontology."

The latest Cretaceous Ornopsis? dysis is similar to Ornopsis (Ornopsis) glemni Wade, 1916, the type species of this genus. Ornopsis is known with certainty (Sohl, 1964) only from upper Campanian and Maastrichtian beds in Tennessee and Arkansas. Reports of Ornopsis from elsewhere in the world are highly doubtful (Sohl, 1964). As mentioned by Wade (1926), there might be an occurrence of Ornopsis from Maastrichtian strata in the Netherlands. This occurrence is based on a gastropod reported by Kamhown (1897: 86-89, pl. 13, fig. 13) and identified by him as Fusus (Hemifusus) meridiformis Kamhown, 1897. It has the fine-spiral sculpture and strong collared structure like that of Ornopsis glemni, as well as the characteristic single fold above the siphonal canal. Reports of Ornopsis from the Congo basin and Angola, west-central Africa (Rennie, 1929; Darteville and Brebion, 1956) are highly doubtful because the specimens are internal molds (Sohl, 1964), and one of the specimens (Darteville and Brebion, 1956; pl. 6, figs. 5a, 5b) has an umbilicus, which is a feature not associated with genus Ornopsis.

Based on the known distribution of Ornopsis, it is very plausible that surface currents flowing westward from the southeastern United States toward the Pacific slope of North America allowed for the dispersal of this genus into California. These currents, which existed during the Late Cretaceous (Gordon, 1973; Johnson, 1999) and continued into the Paleocene and Eocene (Saul, 1986a; Squires, 1987), were part of a circumglobal-tropical current that contributed to a widespread dispersal of marine biota (Haq, 1981).

The Paleocene Perlillata califia is most similar to Fasciolariidae planusca Gardner, 1933, and to Fasciolariidae new species Gardner, 1933, both from lower Paleocene (Danian) strata of the Midway Group in Texas. It is plausible that this genus was dispersed westward from the

<table>
<thead>
<tr>
<th>Age (Ma)</th>
<th>System/Series</th>
<th>Stage</th>
<th>New Taxa ranges</th>
<th>Turrillella Zones</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Palaeocene</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>60</td>
<td>Lower</td>
<td>Middle</td>
<td>dysis</td>
<td>T. peninsulars</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Danian</td>
<td></td>
<td></td>
</tr>
<tr>
<td>65</td>
<td>Lower</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Mass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper</td>
<td>Cret</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. Chronostratigraphic positions of the new taxa. Ages of stage boundaries from Gradstein et al. (2004). Turrillella zones from Saul (1985).
Figures 3-13. New fasciolariid gastropods. Specimens coated with ammonium chloride. 3-7. *Ovainopsis? dysis* new genus and species. 3-4, Paratype LACMIP 13352, LACMIP loc. 26527, height 31.1 mm, diameter 20.9 mm. 5. Apertural view. 6. Abapertural view. 7. Holotype LACMIP 7564, LACMIP loc. 26525, height 37.6 mm, diameter 32 mm. 5-7. Apertural view turned slightly to right. 7. Abapertural view. 8-11. *Saxituberosa fons* new genus and species. 8-9, Holotype LACMIP 13354, LACMIP loc. 21591, height 55.6 mm, diameter 40.4 mm. 8. Apertural view. 9. Abapertural view. 10, Paratype LACMIP 13355, LACMIP loc. 21590A, apertural/eight-lateral view (specimen crushed), height 48.4 mm, diameter 35 mm. 11. Paratype LACMIP 13356, LACMIP loc. 1988, apertural view, height 52.5 mm, diameter 42 mm. 12-13. *Saxituberosa titan* (Waring, 1917) new combination. Holotype LACMIP 10053, LACMIP loc. 22688, height 60.4 mm, diameter 50.2 mm. 12. Apertural view. 13. Right-lateral view.
Gulf Coast into California, via the same circumglobal-tropical current mentioned above.

SYSTEMATIC PALEONTOLOGY

Order Neogastropoda Thiele, 1929
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815

Discussion: Buccinids are of medium size, having a fusiform shell in which the spire makes up 40 to 50% of the total shell height. The smooth protoconch is paucispiral (approximately two whorls) and is low. There is usually no collar on the ramp. The shoulder usually has tubercles and collabral ribs. A posterior "notch" and an umbilicus can be present. The columella is callused and almost always smooth. The outer lip is smooth or with small teeth; the interior of the outer lip is smooth or biform. The siphonal canal is short to moderately long, and the siphonal fasciole is usually strong, twisted to the left, and upturned. The operculum is chitinous. The growth line is generally prosoclinal on the ramp but ostioclino elsewhere.

Genus Ornopsis? sensu stricto Wade, 1916

Discussion: Wade (1926) placed Ornopsis in family Fusidae Swainson, 1840. According to Ponder and Warén (1988), this family name, based on homonymy, is unavailable and is equivalent to family Fasciolariidae Gray, 1855. Wenz (1941) placed Ornopsis in the family Buccinidae Rafinesque, 1815, but Sohl (1964) placed it in the family Fasciolariidae. Snyder (2003: 24) included Ornopsis in his list of "genera removed from family Fasciolariidae." He made no taxonomic decisions in his work, relying instead on previously published work; nevertheless, he did not report who removed Ornopsis from the fasciolariids nor the basis for this removal.

Bandel (1993: 40) reported that the relatively simple embryonic whorls and smooth larval whorls of the protoconch of Ornopsis Wade, 1916, probably indicate that this genus is a buccinid. In addition, the low spire and rounded last whorl of Ornopsis? dysis new species also resemble that of a buccinid. This new species, however, also has a single fold on the columella immediately posterior to the siphonal canal. The only buccinid that we know of that has this type of fold is Afer Conrad, 1858, a genus traditionally placed in the tudiclids, but placed by Frasnson and Hadorn (1999) in the family Buccinidae. The presence of a single fold on the columella immediately posterior to the siphonal canal, however, is not unique to any one family, as it can be found in certain members of other families including the following: sargamids (e.g., Sargamia Stephenson, 1923), but in comparison to O.? dysis these gastropods have umbilicate shells with ornate sculpture: strepsidurids (e.g., Strepsidura Swainson, 1840), but these gastropods have small shells with a narrow spire and usually a smooth last whorl; tudiclids (e.g., Tudicla Roding, 1798, and Rapopsis Saul, 1988), but these gastropods have shells with a very depressed spire, and, in the case of Rapopsis, the shell is also umbilicate.

Although three subgenera of Ornopsis were recognized by Sohl (1964), based on shell shape and growth-line trend, the new species described below is more like Ornopsis sensu stricto because the other two subgenera, Rippeyella Harbison, 1945, and Pornopsis Sohl, 1964, have shells that are slimmer, more elongate, higher spired.
and possess a sinuous growth-line trend with a strong sinus. Ornopsis? dysis new species, is most like the buc-
cinid? Ornopsis (O.) glenni because the new species has the following features: bucciniform shape, prominent
sculpture, posterior collar, a single strong fold above the
siphonal canal, a posterior siphonal notch, and a twisted
siphonal canal.

**Type Species:** Ornopsis (Ornopsis) glenni Wade, 1916, by original designation; Late Cretaceous
(late Campanian and Maastrichtian), Tennessee and Arkansas.

**Ornopsis? dysis** new species

(Figures 3–7, 20)

**Ornopsis?** sp. Saul, 1986a: 30, figs. 57–58.

**Diagnosis:** Large Ornopsis? with weak collar, wide
pleural angle, and strong collumellar fold.

**Description:** Shell medium (up to 36 mm estimated
height and 21 mm diameter, same specimen). Juvenile
and early adult shell moderately inflated (height to di-
meter ratio approximately 1.5, estimated); adult shell
more inflated (height to diameter ratio approximately
1.2). Buccinoid. Spire low, approximately 38% of shell
height. Pleural angle approximately 90°. Protoconch
and upper spire unknown. Teleoconch approximately three
whorls. Whorls inflated medially but constricted poste-
riorly on ramp. Ramp broad, slightly concave, usually
smooth, and bearing weak subcollumellar collar. Ramp
without spiral ribs or, on adult specimens, with two very
weak ribs. Suture moderately impressed, wavy. Sculpture
subdued and consisting of many collabral ribs intersect-
ing spiral ribs on inflated medial part of whorls; inter-
sections demarked by weak nodes. Nodes most promi-
nent on shoulder and occasionally becoming transversely
elongate toward outer lip. Collabral ribs moderately
widely spaced and most prominent on shoulder and on
inflated portion of last whorl; approximately 11 nodes on
shoulder of last whorl with nodes becoming stronger to-
ward outer lip. Collabral ribs usually extending very
weakly across ramp and oblique on base and neck of last
whorl. Spiral sculpture consisting of numerous narrow
and moderately widely spaced ribs, more prominent than
collabral ribs. Approximately 1–13 spiral ribs on last
whorl from shoulder to neck; spiral ribs becoming
slightly weaker on neck. Aperture narrow on juvenile and
early adult shells but moderately wide on adult shell.
Posterior notch present. Columella slightly concave and
smooth except for single fold just above (posterior to)
siphonal canal where aperture becomes constricted to
form narrow siphonal canal, twisted to left. Growth lines
sinuous, prosocline on ramp, slightly opisthocline on per-
iphery, and sigmoidal on base and neck area.

**Holotype:** LACMIP 7564, tip of spire and siphonal
canal missing, 37.6 mm height, 32 mm diameter.

**Paratypes:** LACMIP 13352 and (unfigured) 13353.

**Type Locality:** LACMIP loc. 26525.

**Geologic Age:** Late Cretaceous (late Maastrichtian).

**Distribution:** El Piojo Formation, Dip Creek, Lake
Nacimiento area, northern San Luis Obispo County,
west-central California.

**Etymology:** Greek dysis, meaning a dipping or setting:
in reference to Dip Creek.

**Discussion:** The new species is based on three speci-
mens. Their sculpture is subdued, probably because of
preservation. They range in estimated height from 21
mm to 36 mm. None is complete.

*Ornopsis? dysis* is similar to *Ornopsis (O.) glenni*
Wade (1926: 463, pl. 24, fig. 1; Sohl, 1964: 215–216, pl.
29, figs. 8–10, 15, 16), from Upper Cretaceous (Cam-
panian to Maastrichtian) strata in Tennessee and Arkansas
(Sohl, 1964), but the new species differs by being smaller
and having a narrower pleural angle (at least on the adult
shell), narrower ramp, stronger posterior collar, more
close spaced and more spiral ribs, and stronger collab-
ral ribs.

*Ornopsis? dysis* resembles *Hydrotribulus nodosus*
Wade (1916: 465, pl. 24, figs. 4, 5; Wade, 1926: 147, pl.
51; figs. 6, 7; Sohl, 1964: 245–246, pl. 36, figs. 19, 20)
from Upper Cretaceous (Campanian to lower Maastrich-
tian) strata in Tennessee (Sohl, 1964), but the new spec-
ies differs by having rounded rather than tabulate should-
ers, a fold on the columella rather than a ridge, absence
of nearly cancellate sculpture, and absence of a strong
parietal tooth.

The new species somewhat resembles *Buccinopsis
crusa* (Wade, 1917: 291, pl. 19, figs. 6, 7; Wade, 1926:
145, pl. 50, figs. 9–12; Sohl, 1964: 189, pl. 22, figs. 1, 2)
from Upper Cretaceous (upper Campanian to lower Maas-
trichtian) strata of Tennessee and Texas, but the new
species differs by having a much stronger fold on the
columella and an absence of a highly inclined, broad
siphonal fasciole bordered above by a narrow deep slit.
Bandel (1993: 40) reported that *Buccinopsis* is probably
a buccinid.

**Family Fasciolariidae** Gray, 1853

**Discussion:** Fasciolariids are of medium to large size,
having a fusiform shell in which the spire makes up 40 to
50% of the total shell height. The smooth protoconch is
usually moderately high (approximately three whorls),
but in rare cases, it is low or bulbous. The teleoconch can
have spiral ribs or can be smooth. A collar is usually not
present. The shoulder bears tubercles; collabral ribs
most prominent on the shoulder, whereas spiral ribs dom-
inant elsewhere. The columella has none or one to three
folds, extending posteriorly upward into aperture. The
outer lip edge is smooth or with small teeth. The outer
lip interior is smooth or lilate. The siphonal canal is long
and narrow, and the siphonal fasciole is usually weak,
slightly twisted to the left, and slightly upturned. The
growth line is generally prosocline to almost orthocline.

**Subfamily Fasciolariinae** Gray, 1853

**Discussion:** On fasciolariines, the shoulder bears tu-
bercules, the columella has one to three folds, and the
ramp is concave. The fusiform shape, high spire, concave ramp, two teeth on the columella, tabulate whorls shoul-
dered with tubercles, and well developed collabral and spiral ribs make it likely that Saxituberosa is a fasciolari-
ne.

Genus Saxituberosa new genus

Type Species: Saxituberosa titau (Waring, 1917); middle Paleocene, southern California.

Description: Shell moderately large, (up to approximately 50 mm height). Fusiform-tubulate. Spire moderately high, approximately 44 to 48% of shell height. Pleural angle approximately 70°. Protoconch and uppermost spire unknown. Teleoconch up to at least 5.5 whorls. Whorls inflated peripherally but constricted posteriorly on ramp. Ramp broad, smoothish, slightly concave, and bearing very weak subcircular collar. Sculpture consisting of collabral ribs intersecting spiral ribs on inflated medial part of whorls, intersections demarked by nodes (11–13 on last whorl), usually strong but dying out anterior and posterior to shoulder. Spiral ribs prominent on anterior part of last whorl. Aperture elliptical. Columella slightly concave and bearing two oblique folds just posterior to siphonal canal; folds near ventral side of columella. Siphonal canal slightly twisted to left. Growth lines prosocline on ramp, slightly opisthochine to orthochine on periphery, sinuous on anterior part of most inflated part of body whorl, and nearly orthochine on neck.

Geologic Age: Early Paleocene (Danian) to middle Paleocene (Selandian).

Etymology: Combination of Latin swarm, meaning rock or stone, and Latin tuberosus, meaning full of lumps; in reference to the stone tubercules that help characterize this genus.

Discussion: Saxituberosa resembles genus Lupira Stephenson, 1941, which Sohl (1964) placed in the family Nancidae Pilsbry, 1922. As far as it is known, this genus is restricted to Upper Cretaceous (upper Campanian to Maestrictian) strata in the southeastern United States (Sohl, 1964). Saxituberosa differs from Lupira by having a higher spire, fewer folds (two) on columella (rather than rarely two and usually three to six), more anteriorly located folds, more widely spaced folds, fusiform shell shape (rather than pyriform), narrower pleural angle, less prominent spiral sculpture (especially near shoulder), fewer spiral ribs on inflated medial part of last whorl, fewer nodes (11–13) on shoulder (rather than 13–16), tuberculate nodes on shoulder and absence of uniformity in size of nodes on inflated medial part of last whorl, and inner lip not heavily callused.

Saxituberosa somewhat resembles the shape and sculpture of various species of genus Taionia Finlay and Marwick, 1937, but Taionia lacks folds on its columella and has a growth line that trends opposite to the direction of Saxituberosa. The familial affinities of Taionia are not well understood. Stibwell et al. (2004) reviewed the history of the contentious placement of this genus, and they concluded, with some reservation, that if it a fusinim fasciolariid, Taionia is apparently confined to the Cretaceous and Tertiary of South America, Antarctica, New Zealand, and Greenland (Griffin and Hünicken, 1994; Stibwell et al. 2004). Bouchet et al. (2005) classified Taionia as a neogastropod in its own family, family Taio-
midae Finlay and Marwick, 1937, superfamily unassigned.

The location of the two folds near the ventral side of the columella and near the anterior end of the aperture of Saxituberosa is very similar to that of Fasistoplex Marwick, 1934, known from the Eocene of New Zealand. The new genus differs considerably from Fasistoplex by having a much higher spire, a fusiform rather than a vasiform-like shell, and a narrower aperture.

Saxituberosa four new species (Figures 8–11, 21)

Diagnosis: A Saxituberosa with moderately low spire and strongly noded sculpture. Pleural angle 90°. Suture can be obscured by shell material on ramp. Columella with two folds immediately posterior to siphonal canal.

Description: Shell medium large (up to 55 mm estimated height and 47.7 mm diameter, same specimen); height to diameter ratio approximately 1.2. Fusiform-tubulate. Spire moderately low, approximately 44% of shell height. Pleural angle approximately 80° (all specimens crushed). Protoconch and upper spire unknown. Teleoconch with at least five whorls. Whorls inflated medially but constricted posteriorly on ramp area. Ramp broad, concave, smooth; possibly bearing very weak subcircular collar. Ramp can be filled by inductura. Suture usually indistinct. Sculpture consisting of many collabral ribs intersecting spiral ribs on inflated medial part of whorls; intersections demarked by strong nodes or tubercules. Collabral ribs moderately closely spaced and most prominent on shoulder and on inflated portion of last whorl; approximately 12–13 nodes or tubercles on shoulder of last whorl. Collabral ribs not present on ramp and obsolete on base and neck of last whorl. Spiral sculpture consisting of numerous strong and moderately closely spaced ribs. Ramp without spiral ribs. Spiral ribs most prominent on last whorl in area from shoulder to neck. Spiral ribs unmoded on base of last whorl and on neck. Aperture moderately wide. Columella with two folds immediately posterior to siphonal canal where aperture becomes constricted to form siphonal canal. Growth lines sinuous, prosocline on ramp, opisthochine on periphery, prosocline near neck area, and almost orthochine on neck.

Holotype: LACMIP 13354, siphonal canal missing, 55.6 mm height, 40.4 mm diameter.

Paratypes: LACMIP 13355 and 13356.

Type Locality: LACMIP loc. 1588.

Geologic Age: Early Paleocene (Danian) (Turritella peninsularis zone of Salt, 1983).
**Distribution:** Lower San Francisquito Formation, Warm Springs Mountain, northern Los Angeles County, southern California.

**Etymology:** Latin *fons*, meaning spring; in reference to Warm Springs Mountain.

**Discussion:** A total of 14 specimens of this new species were studied. The specimens range in size from 23.1 mm height and 21.8 mm diameter (same specimen) to 70.2 mm height. None of the specimens is complete, and the largest one is broken in half, longitudinally. The most complete specimen is 55 mm height and 47.7 mm diameter, with a height to diameter ratio of 1.2. Preservation of this species is poorer than the other two new species, and the aperture and siphonal canal regions are crushed and usually missing.

*Saxituberosus fons* is most similar to *S. titan* from which it differs by having a wider pleural angle, lower spire, much less tabulate whorls, stronger tubercles, and occasionally broader ramp bordered by indistinct sutures.

*Saxituberosa titan* (Waring, 1917) new combination (Figures 12–16, 22)

*Trachytriton titan* Waring, 1917: 57, pl. 14, fig. 18.

*Pennion titan* (sic) (Waring).—Zinsmeister, 1983a: table 1, pl. 3, figs. 22, 23.

*Pennion titan* (Waring).—Zinsmeister, 1974: 141–142, pl. 15, figs. 1, 2; 1983b: 1294, figs. 3 H, 3 I.


**Diagnosis:** A *Saxituberosa* with moderately high spire and strong sculpture. Pleural angle approximately 70°. Columella with two folds immediately posterior to siphonal canal.

**Description:** Shell large (up to 67.4 mm height and 42.5 mm diameter, same specimen), height to diameter ratio approximately 1.7. Sub fusiform with turreted spire. Spire approximately 45% of shell height. Pleural angle approximately 65°. Protoconch and upper spire unknown. Teleoconch with at least 5.5 whorls. Whorls inflated medially but constricted posteriorly on ramp area. Ramp broad, concave, smooth, and bearing very weak substural collar. Suture moderately impressed, somewhat wavy. Sculpture consisting of spiral ribs intersecting with collateral ribs, intersections demarked by strong nodes or tubercles. Sculpture dying out above and below inflated medial parts of whorls. Upper spire whorls with single row of tubercles on tabulate shoulder; single row gradually passing into double row of equally strong tubercles on later whorls. Penultimate whorl shoulder with approximately 15 nodes. Last whorl with four spiral rows of tubercles on most inflated part of whorl; posterior pair of rows closely to widely spaced and bearing strongest tubercles. Last whorl shoulder with approximately 12–13 nodes. Anterior pair of rows on most inflated part of last whorl with less projecting tubercles, becoming somewhat elongated in parietal region. Anteriormost part of last whorl with one to two rows of subdued nodes. Neck with approximately six spiral ribs, unmoded. Aperture moderately wide and elliptical. Columella straight to slightly concave (on adults), with wide calloused area, and bearing two strongly raised folds immediately posterior to slightly twisted?, narrow siphonal canal. Growth lines sinuous, prosocline on ramp, opisthocline over periphery, sigmoideal on base, and nearly orthocline on neck.

**Holotype:** CAS 61926.01 (= LSJU 142), very worn and incomplete specimen (uppermost spire missing) with columella buried in matrix. 81 mm height, 60.5 mm diameter.

**Hypotypes:** LACMIP 10982 (= UCLA 59254) and LACMIP 10983 (= UCLA 59255).

**Type Locality:** CAS loc. 61901.

**Geologic Age:** Middle Paleocene (Selkirkian) [= *Turriritaella pennadulis* Zone of Saul, 1983).

**Distribution:** San Francisquito Formation, Pinyon Ridge near Big Rock Creek, Valynera area, northern Los Angeles County, southern California; and lower Santa Susana Formation ("Martinez marine member" of Nelson, 1925), Meier Canyon, Simi Hills, eastern Ventura County, southern California.

**Discussion:** A total of 12 specimens of *S. titan* were studied, five from the Pinyon Ridge area and seven from the Simi Hills, including the two hypotypes UCLA 59253 and UCLA 59254, both illustrated by Zinsmeister (1974, 1983a, 1983b). Preservation of these specimens is generally good to excellent, except that each specimen is missing the protoconch and most of the siphonal canal. The dimensions of the specimens range from 31.6 mm height and 18 mm diameter (same specimen) to 67.4 mm height and 42.5 mm diameter (same specimen). The smallest specimen is nearly complete and has a height to diameter ratio of 1.75, whereas the largest specimen is missing most of its siphonal canal. Another, mostly complete, specimen has 60.5 mm height and 36.1 mm diameter, and its height to diameter ratio is 1.7. We conclude, therefore, that the height to diameter ratio of *S. titan* is approximately 1.7.

Waring (1917) placed this species in genus *Trachytriton* Meek, 1864. The type species of this monotypic genus is *Buccinum vicalium* Hall and Meek, 1854, and this type species was reported by Wenz (1941) as being in the oceanic genus *Argobuccinum* Bruguière, 1792. *Trachytriton* does not have the tabulate whorls, substural collar, strongly noded sculpture, nor the folds on the colomellar that characterize the shells studied herein.

Waring (1917) reported that *titan* is very similar to *Trachytriton tejonensis* Gabb (1869: 154, pl. 26, fig. 341) from the Eocene Tejon Group in Live Oak Canyon. The holotype of *T. tejonensis* is mostly an internal mold, and it has a varix, which is a morphologic feature not found on *titan*. Stewart (1926) [1927] placed *T. tejonensis* into synonymy with the oceanid *Olequahia horii* (Gabb, 1864).

Zinsmeister (1974, 1983a, 1983b) assigned *S. titan* to
the bucinnid genus *Penion* Fischer, 1884, which ranges
from the early Paleocene (Danian) to Holocene (Wenz,
1941). Although *Saxituberosus* and *Penion* can have simi-
lar shell shape, the presence of one or two collumellar
folds on *Saxituberosus* readily distinguishes it from *Pe-
nion*. Zinsmeister (1974, 1983a, 1983b) did not report
the presence of any folds on the two specimens of *S. tita-
n* that he illustrated, but when the specimen shown here in
Figures 12–14 was carefully cleaned by the junior author,
two collumellar folds were observed (Figure 13). The
other specimen, which is shown here in Figure 15, is
missing the part of the collumella that bears the folds.

The specimen (IGM 4431) that Paredes-Mejia (1989; pl.
8, figs. 3, 4) identified as *Penion cf. P. tigrina* (Waring),
which is from the Sepultura Formation in Baja Califor-
nia, Mexico, is not *Saxituberosa tigrina* even though it has
sculpture similar to that found on *S. tigrina*. This Sepultura
Formation specimen is a turrit because its ramp has a
well-developed, deep symmetrical sinus that is so char-
acteristic of turrits.

*Saxituberosa tigrina* is most similar to *S. fusus* new spe-
cies, and *S. tigrina* differs by having a narrower pleural
angle, higher spine, much more tabulate whorls, and a
more distinct suture.

*Saxituberosa tigrina* strongly resembles the shell shape
of the fossil *Sureda* *magni* Hanna and Isalsky (1925:
45, pl. 7, fig. 12), known from beds transitional with the
Heath Formation near Quebrada Mancora, in the ex-
treme northwestern coastal region of Peru. The locali-
description for this species is very imprecise, but it is
likely that the species occurs in the transitional beds be-
tween the Heath and Mancora formations, both of which
are early Miocene in age, according to Dunbar et al.
(1990). *Saxituberosa tigrina* differs from *Sureda* *magni*
by having spiral ribs and two collumellar folds. It is likely
that *“S.”* *magni* belongs to genus *Taionw* Finlay and
Marwick, 1937, which was discussed earlier.

*Saxituberosa tigrina* resembles the cassid *Galeodea*
(Taionw) klingeri Kiel and Bandel (2003; figs. 6.6–6.8)
from the Upper Cretaceous (middle Santonian-lower Cam-
panian) Unzambar Formation in South Africa. The new
species differs by having folds on the collumella,
stronger collabral sculpture, straighter collumella, less
twisted posterior portion of the siphonal canal, and an
absence of a small pseudo-umbilicus. In addition, *S. tigrina*
appears not to have a posterior canal.

?Subfamily Fusininae Wrigley, 1927

**Discussion:** On fusinines, the shoulder is rounded, the
collumella lacks folds, and shells can be large with high
spires and long siphonal canals. The subfamilial place-
ment of *Perrillata* new genus is uncertain, mainly be-
cause the collumella and aperture are not complete. In
addition, the growth lines on the ramp area are not pre-
served. *Perrillata* might be a fusine based on its fusin-
iform shape, large size, high spine, and absence of any
collumellar folds, but its strongly shouldered whorls with
tubercles, as well as strong spiral ribs overlying collabral
ribs, however, are features that are not usually found on
fusinines.

**Perrillata** new genus

**Type Species:** *Perrillata califia* new species; middle
Paleocene (Selandian), southern California and Baja
California, Mexico.

**Description:** Shell large, up to 101 mm height. Fus-
iform with very spire high. Tabulate whorls. Ramp moder-
ately broad and concave. Nodes strong on shoulder.
Sprial ribs very prominent and closely spaced on periph-
ery and base. Neck smoothish. Columella long, straight,
and callosed.

**Geologic Age:** Middle Paleocene (Selandian).

**Etyymology:** Named for Maria del Carmen Perrilliat
(IGM), in recognition of her important contributions on
Cretaceous and Cenozoic mollusks of Mexico.

**Discussion:** The new genus somewhat resembles *Her-
corynnus* Conrad, 1858, known with certainty only from
Upper Cretaceous (upper Campanian to Maastrichtian)
strata in Tennessee, Mississippi, Alabama, and Georgia
(Wade, 1926; Sohl, 1964), but the new genus differs by
having a higher spine, a narrower pleural angle, growth
lines prosocyt rather than opisthocoel on medial part of
last whorl, and sculpture obsolete on neck. In addition,
the new genus apparently does not have an umbilical
chink opposite the posterior end of the siphonal canal,
but the presence of an umbilical chink on *Herco-
nynus* is a variable feature. The new genus might have a con-
striction at posterior end of neck, like that present on
*Herco-
nynus*.

Sohl (1964) and Snyder (2003) placed *Herco-
nynus* in the fusine *fusiniformis*, but Bandel (1993; 40)
considered the genus probably to be a buccinid, based on its
protoconch, which is similar to that of the bucinnid *Or-
nepis*. Cossmann (1901: 73) considered *Herco-
nynus* to be a subgenus of *Streptosiphon* Gill, 1867, and
Wenz (1943: 1306) considered *Streptosiphon* to be a syno-
ym of *Afer* Conrad, 1858, hence making *Herco-
nynus* a subgenus of *Afer*, which, as mentioned earlier,
was placed in family Bucinidae by Franssen and Haddons
(1999). Sohl (1964: 220), however, cited that the ap-
erture features, the higher spine, and the lack of any col-
umellar folds negates that *Herco-
nynus* belongs to ei-
ther *Streptosiphon* or *Afer*.

The new genus resembles *Saxituberosa* by having tabulate
whorls with strong sculpture but differs from the type spe-
cies of *Saxituberosa* by having a much higher
spire, much more sinuous growth lines on the ramp, no
posterior collar, stronger spiral ribs, straighter collumella,
and no folds on the collumella.

**Perrillata califia** new species

(Figures 16–19, 23)

?*Penion* sp. Paredes-Mejia (1989: 257–259, pl. 8, figs. 1, 2).

**Description:** Shell large (up to 101 mm height and
51.5 mm diameter, same specimen), shell height to di-
The geologic age of the specimens from the Sepultura Formation is not known with certainty because the specimens are float material. The geologic age of the specimens from the Simi Hills, however, is well constrained as being middle Paleocene (Selandian) based on the associated mollusks. Using the Simi Hills specimen as control, we infer that the Sepultura Formation specimens are the same geologic age.

The new species is similar in shape, size, and sculpture to Fasciolaria? plummeri Gardner (1933: 246–247, pl. 22, figs. 1–3) from the Paleocene Kincaid Formation of the Midway Group of Texas. Dockery (1956, fig. 1) correlated the Midway Group to the lower Paleocene (Danian) and correlated the Kincaid Formation to the lowermost part of the Danian. Gardner (1933) reported that F.? plummeri is unusually large (93 mm height) for a Paleocene gastropod and that this species is one of the few elements in the Midway fauna that is reminiscent of the Cretaceous. The new species differs from F.? plummeri by having a wider pleural angle, occasional spiral ribs on the ramp; slightly wider, more closely spaced, and more spiral ribs on the anterior swollen part of the last whorl; no spiral ribs on the neck; and no hint of a siphonal fasciole.

The new species is somewhat similar to Hercorhyncus (Haplolvoluta) trilittatus Sohl (1964: 223–224, pl. 30, figs. 17–20, 23–24), which is known from upper Campanian to upper Maastrichtian strata in Tennessee, Alabama, and Georgia. The new species differs by having a narrower pleural angle, higher spire, more whorls, ramp spirally ribbed rather than smooth, and spiral ribs on swollen part of the last whorl more numerous and more closely spaced.

The new species resembles Saxithuberosa titan but differs from S. titan by having a much higher spire, no folds on the columella, much stronger spiral ribs, and, as far as it can be ascertained, a straighter columella.

ACKNOWLEDGMENTS

Maria del Carmen Perrilliat kindly provided high-quality replicas of IGM specimens that were collected and figured by Paredes-Mejia (1989), Lindsey T. Groves and Steffen Kiel critiqued the manuscript.

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Stephenson, L. W. 1941. The larger invertebrate fossils of the Navarro Group of Texas (exclusive of corals and crustaceans and exclusive of the fauna of the Escondido Formation). The University of Texas Publication 4101: 1-640.


APPENDIX

LOCALITIES CITED

Localities are LACM1P, unless otherwise noted. All quadrangle maps listed below are U.S. Geological Survey maps.

CAS 6190. [\= LSU J 4]. Exact location unknown, see Waring (1917: fig. 3) for general location; Calabasas Quadrangle (7.5 minute, 1952, photorevised 1967), north side of Calabasas Simi Hills, Ventura County, southern California. Coll.: C. A. Waring, summer 1970.

21579. Limney and sandy shale in canyon bottom, south side of East Fork Fish Canyon, 1158 m east and 1630 m south of northwest corner of Warm Springs Mountain Quadrangle (7.5 minute, 1958), Los Angeles County, southern California. Lower Paleocene (Danian). San Francisco Formation (lower part). Coll.: R. W. Webb and E. H. Quayle, June 5, 1941.

21560. Concretionary shale in canyon wall about 9 m above stream bed, south side of East Fork of Fish Canyon, 1160 m east and 1463 m south of northwest corner of Warm Springs Mountain Quadrangle (7.5 minute, 1958), Los Angeles County, southern California. Lower Paleocene (Danian). San Francisco Formation (lower part). Coll.: R. W. Webb and E. H. Quayle, June 5, 1941.

21558. Concretionary shale along alluvial ridge crest, south side of Warm Springs Canyon, 1463 m north and 792 m west of Warm Springs Mountain, Warm Springs Mountain Quadrangle (7.5 minute, 1958), Los Angeles County, southern California. Lower Paleocene (Danian). San Francisco Formation (lower part). Coll.: R. W. Webb and E. H. Quayle, June 16, 1941.

22330. Beds cropping out on nose of spur on northwest side of Meier Canyon, approximately 183 m north of second "n" in Meier Canyon, Calabasas Quadrangle (7.5 minute, 1952, photorevised 1967), south side of Simi Valley, Simi.

22688. Near summit of Simi Hills, 61 m southeast of hill 2150, on ridge trending almost due south of hill 2151, 1753 m east and 3079 m south of northwest corner of Calabasas Quadrangle (7.5 minute, 1952, photorevised 1957), Ventura County, southern California. Santa Susana Formation (lower part). Middle Paleocene (Selandian). Coll.: J. H. Fantozzi, circa June, 1951.


PU 1334. Float material from eastern part of Cajiloa Creek on northwestern slope of Mesa San Carlos, Baja California, Mexico. Middle Paleocene (Selandian). Sepultura Formation. Coll.: L. M. Paredes-Mejia, circa 1987.
Authorship of the Ovulidae (Gastropoda) of the Zoology of the Voyage of the SAMARANG

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ABSTRACT

The Mollusca portion of the Zoology of the Samarang was authored by Arthur Adams and Lovell Reeve. The new species of Ovulidae therein, universally attributed to Adams and Reeve in the modern literature, were described by G. B. Sowerby II, who should be cited as author.

Additional Keywords: Adams and Reeve, G. B. Sowerby II

The Zoology of the Voyage of H.M.S. SAMARANG was edited by Arthur Adams. It contains monographs by various authors, the Mollusca being coauthored by Arthur Adams and Lovell Reeve. The Mollusca monograph was published in 1848 and 1850 as detailed in the References Cited herein. Species placed in the genus Ovulum, the subject of this paper, are in the part published in 1848.

Adams and Reeve’s first grouping under the Gastropoda [sic] is the Convoluta. Although not given a rank by them, the Convoluta is a Family in Reeve’s Tabula Methodica (Reeve, 1841, 1842) consisting of the genera Erato, Cyprea, Ovula, Terebellum and Conus. In the discussion under the heading Convoluta the authors state that “out of from eighty to a hundred species of Cones collected during the voyage of the Samarang, only four proved to be new, the greater number of those of recent discovery being anticipated by Mr. Cuming during his researches among the Philippine Islands and described in the ‘Conchologia Iconica.’” They continue with the following two sentences (Adams and Reeve, 1848: 17):

“The genus Ovulum, not having been examined since the publication of Mr. Sowerby’s ‘Species Conchylorum,’ afforded a greater amount of novelty. Mr. Sowerby, jun., being engaged in preparing a monograph of this genus for the forthcoming number of his ‘Thesaurus,’ it was thought desirable to place the specimens collected in his hands for comparison, and we are indebted to him for the descriptions and figures of eleven new species.”

The fact that the descriptions and figures were both by Sowerby has escaped the attention of all later workers except Sowerby and the Adams brothers. All of the new species are listed and correctly attributed to Sowerby by H. and A. Adams (1854, 1: 270-272) under either Amphiperae or Voluta, the spelling of Ovula bullata being corrupted to Amphipera bullulata.

Under Article 50.1.1 of the Code (International Commission on Zoological Nomenclature, 1999), these names should be attributed to G. B. Sowerby II. In the Thesaurus these new Ovulum species are correctly attributed by Sowerby to himself with reference to the Samarang figures.

In the introduction, where Owen is given credit for having produced a section of the Mollusca, Sowerby is not mentioned. There are other oddities about this work and a detailed paper is in preparation.

It is surprising that these names have not been properly attributed. However, this has happened in a few other works where subsequent workers have paid heed only to parts of particular interest without reading introductory material. Even the venerable Sherborn attributed them to Adams and Reeve. Modern monographs of the Ovulidae that would be expected to be thorough enough to catch errors such as this one have yet to be written. Schilder’s (1952) The living species of Amphiperae, which includes all of the species involved in this discussion, cites references to only a few works in abbreviated form and even then some are inaccurately dated.

The seemingly most complete modern work is Cate’s (1973) A systematic revision of the Recent Cypraceid family Ovulidae. All of the species from the Samarang are included in Cate’s work and all are attributed to Adams and Reeve. Although Sowerby’s Thesaurus, where the names are correctly attributed, is in Cate’s list of Literature Cited (misdated as 1848), no entries from that work are listed in the chresonyms of any of the Samarang species. It must be mentioned that a Sowerby entry does appear under “Phanacovolva acuminata” (A. Adams and Reeve, 1848).” That reference is:

1859 Ovula acuminata: Sowerby 2nd, Index Brit.
Shells: 21, pl. 20, fig. 3.

The meaning of “21” is not clear as Sowerby’s work is not paginated but Plate 20, figure 3, is identified by Sowerby as “Ovula acuminata Brug.” This European species
was originally described as *Bulla acuminata* Bruguière, 1792, and is now usually placed in the genus *Bilitoros* in the family Retusidae. This clearly has nothing to do with the *Samarang* species.

In the “Monograph of the genus *Ovulum*” of his *Conchologia Iconica*, Reeves also attributed the names to Adams and Reeve. Most recently, Alison Trew’s (1992) *Henry and Arthur Adams’s new molluscan names* attributes the *Samarang* ovulids to Adams and Reeve. In short, as stated above, all authors except G. B. Sowerby II and the Adams have misattributed these names. The eleven new names are listed below in alphabetical order by species name. Current generic placement of these taxa is beyond the scope of this paper.

*Ovulum acuminatum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum bella* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum bullatum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum coarctatum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum conchiunum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum devatatum* G. B. Sowerby II in Adams and Reeve, 1848
[Procamptula; invalid, renamed *Prosimnia renovata* Iredale, 1930.]
*Ovulum fornicatum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum gracile* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum planicostatum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum recurvum* G. B. Sowerby II in Adams and Reeve, 1848
*Ovulum subrecessum* G. B. Sowerby II in Adams and Reeve, 1848

Thirteen species of Ovulidae are treated in the *Samarang*, the eleven listed above being new. Of these eleven, ten are still regarded as valid (Dr. Gary Rosenberg, personal communication, December 2005), which is rather remarkable.

This writer would like to express his appreciation to Dr. Gary Rosenberg for reading and commenting on a draft of this paper and providing information about ovulids.

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Reeve, L. 1865. Monograph of the genus *Ovulum*. Conchologia Iconica. 15: [unpaginated test]. 14 pls. [Plate 2 dated March 1862 in error; a paper on this entire work is in preparation.]


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CONTENTS

Bernard Landau
Carlos Marques da Silva
The genus Scaphella (Gastropoda: Volutidae) in the Neogene of Europe and its paleobiogeographical implications ............................................................... 81

M. G. Harasewych
Josiah Strauss
A new record of introduced Cerion (Gastropoda: Pulmonata: Cerionidae) in southeastern Florida ............................................................... 94

Thomas J. DeVries
Lindsey T. Groves
A new early Miocene Muracypraea Woodring, 1937 (Gastropoda: Cypraeidae) from the Pisco Basin of southern Peru ........................................ 101

K. J. Butkas
M. L. Ostrofsky
The status of unionid and dreissenid mussels (Bivalvia) in northwestern Pennsylvania inland lakes ........................................ 106

Eugene V. Coan
Richard E. Petit
Replacement names and type material: examples from Hertlein and Strong (1940-1951) and Keen (1958) ........................................ 112

Book Review ................................................................. 116
The genus *Scaphella* (Gastropoda: Volutidae) in the Neogene of Europe and its paleobiogeographical implications

**ABSTRACT**

The genus *Scaphella* supposedly has a long geological history on both sides of the Atlantic, extending back to the Paleocene. However, there are differences in both shell morphology and ecological preferences between the New and Old World representatives. This paper traces the history of *Scaphella* in the Atlantic. It is suggested that the group originated in the Cretaceous/Paleocene Tethys Sea, a genus such as *Caricella* dispersing during this time to the New World, and hence giving rise in the Neogene to *Scaphella*. In the Old World the record of *Scaphella* is uninterrupted from the Paleocene to the middle Neogene, after which the genus disappeared from the Eastern Atlantic. The genus *Scaphella* is heterogeneous, the European species differing in certain constant shell characteristics from the New World species. *Scaphella caricae* new species is described from the lower-middle Pliocene Mediterranean of the Estepona Basin (Spain) and a possible second new species is discussed, but not named due to the poor material available, from the lower Pliocene Atlantic of the Guadalquivir Basin (Spain).

**INTRODUCTION**

The subfamily Scaphellinae H. and A. Adams, 1858, comprises three extant genera: *Ampulla* Roding, 1798, *Scaphella* Swainson, 1832, and *Voluittius* Conrad, 1863 (Darragh, 1958). In the Recent fauna they occur in the western Atlantic Ocean, including the southeastern United States, Gulf of Mexico and Caribbean (*Scaphella, Voluittius*), and the eastern Atlantic, from southern Portugal and Spain to the West African coasts of southern Morocco and the Canaries (*Ampulla*). In the early fossil record another genus, *Caricella* Conrad, 1835, predominates, being present from the Cretaceous in the Tethyan record (Bandel, 2003) and in the New World Paleocene to Oligocene (*Doddery*, 1977). Bandel (2003), however, placed *Caricella* in a separate subfamily, *Caricellinae* Dall, 1907. In this paper we deal with the Old and New World taxa traditionally placed in the genus *Scaphella*.

The gastropods of the genus *Scaphella* today live in warm water, with a Recent subtropical to tropical distribution restricted to the western Atlantic, from the coasts of North Carolina (USA), southward through the Gulf of Mexico to Yucatan (Weaver and de Pont, 1970), the Caribbean, up to Colombia (Clech, 1946; Poppe and Goto, 1992). The genus has an widespread geological record in the Americas, with a few records in the Paleocene, an extensive Neogene history, but is not recorded from the Eocene or Oligocene.

In the Old World the Scaphellinae have an equally long geological record extending back to the Paleocene of the North Sea Basin (Ravn, 1933). The group flourished in the Miocene, extending its distribution into the Atlantic and reaching the southern Atlantic coast of Iberia in the late Miocene (Pereira da Costa, 1966). In the Pliocene the Scaphellinae were abundant in the North Sea Basin (Marquet, 1997). Their range extended into the Atlantic, as far as central western Iberia (Mondego Basin) (Silva, 2001) and into the Mediterranean, where they were restricted to the Alboran Sea (Estepona Basin), except for a single unconfirmed report from Algeria (Lamotobre and Dautzenberg, 1997).

The last European records for *Scaphella* are from the upper Pliocene of the North Sea Basin. Today the Scaphellinae are represented in the European faunas by the monotypic genus *Ampulla* Roding, 1791. *Ampulla priamns* (Gmelin, 1791) occurs from the southern coast of Portugal (Nobre, 1938–40), or possibly from the southwestern coast of Portugal, were it is rare (G. Calado, pers. comm., 2006), south to the Canaries and southern Morocco (Poppe and Goto, 1992).

Pliocene Atlantic and Mediterranean records of *Scaphella* are scarce. Chavan and Coatman (1943) and Brebion (1964) recorded *S. lamberti* from the Pliocene of the Loire Basin. Silva (2001) listed *S. lamberti* from the Atlantic Pliocene of the Mondego Basin and Zbyszewski (1943, 1959) from the Lower Tagus-Sado Basin of central-western Portugal. There is only one unconfirmed report by Lamotobre and Dautzenberg (1997) of *S. lamberti* in the Mediterranean from the Pliocene of Algeria.

Recent work on the rich lower Pliocene deposits of the
Atlantic Guadalquivir Basin and Mediterranean Estepona Basin (southern Spain) revealed the presence of Scaphella in both these basins.

FOSSIL-BEARING LOCALITIES

The material discussed herein originates from three distinct Iberian localities, situated, from northwest to southeast, at:

1. Vale de Freixo, Pombal region, central-western Portugal, Atlantic, Mondego Basin. The Pliocene Carne de Sandstone Formation generally consists of fine micaceous sand without macro somatofossils (body fossils). Locally, the lowermost section of this formation contains a thin fossiliferous sequence consisting of a basal conglomerate and sand rich in fossil shallow marine mollusc shells. At Vale de Freixo, the basal fossiliferous beds of the Carne de Sandstone have a maximum thickness of approximately 1 m. These are dated as lower to middle Pliocene, uppermost Zanclean to lowermost Piacenzian (Silva et al., 2000; Silva, 2001; Silva et al., 2006).

2. Lucena, Huelva region, southern Spain, Atlantic, Guadalquivir Basin. The sandy, near-shore deposits of Lucena are part of the Arenas de Huelva Formation and dated as lower Pliocene, Zanclean (Civis et al., 1987).

3. Velerin, Estepona region, southern Spain, Mediterranean, Estepona Basin. These deposits consist of a variety of different lithologies, from fine clayey sands (Velerin carretera outcrop), deposited at relatively greater depths, to coarse conglomerates (Velerin conglomerates outcrop). These conglomerates, which must have been deposited relatively rapidly or in storm conditions (Sanz de Gallardo and Lopez Garrido, 1991), contain the richest fauna, a curious mixture of large and small abraded and perfectly preserved shells. These deposits are dated as middle Pliocene, lower Piacenzian (Guerra-Merchán et al., 2002).

For detailed location maps and a geological and stratigraphical overview of the fossiliferous deposits covered in this paper see La Perna et al. (2003) and Dell’Angelo and Silva (2003), for the Mondego Basin, Civis et al. (1987) for the Guadalquivir Basin, and Sanz de Gallardo and Lopez Garrido (1991) and Guerra-Merchán et al. (2002), for the Estepona Basin.

The Pliocene fauna from all three of these basins, according to Silva (2001), La Perna et al. (2003), and Landau et al. (2003), corresponds to the Mediterranean Pliocene Molluscan Unit 1 (MMPU1) of Monegatti and Raffi (2001).

The material herein discussed is housed in the following collections: IHScNB: Institut royal des Sciences naturelles de Belgique; BLP coll.: B. Landau collection; CMS coll.: Carlos Marques da Silva collection, Departamento de Geologia da Faculdade de Ciências de Lisboa; RM coll.: collection B. Marquet (will be incorporated into the collection Institut royal des Sciences naturelles de Belgique in the near future); CG coll.: = Chris Garvie collection, USA; M-N coll.: Manuel Molin/Daniele Velo collection, Bonares, Spain; AC coll.: Alain Cluzaud collection, France.

SYSTEMATIC PALEONTOLOGY

The genus Scaphella

The type species of the genus Scaphella is Voluta junonia Shaw, 1808, by subsequent designation of Gray, 1847 (Clench, 1946). Scaphella junonia is a western Atlantic species, characterized by axially ribbed post-nuclear whorls, prominent columnar plications and a well-developed siphonal fasciole.

Clench (1946) recognized Scaphella sensu stricto characterized by shells that were a little more massive, nuclear whorls extended and the calcarella usually worn away; and Scaphella (Aurinia) H. and A. Adams, 1853, in which the shell is strong, but not massive, and the nuclear whorls have a strongly developed calcarella. In a more recent work (Weaver and Du Pont, 1970), this division into subgenera was confirmed by differences in the radial structure. According to Clench (1946), the typical subgenus has wishbone shaped rachidian teeth, with the central denticle rather long and narrow, and the lateral shanks extending behind rather than to the sides, but no lateral denticles. In the subgenus Aurinia the rachidian teeth have a very strong central denticle, with shanks above extending at almost right angles, and at the base two very small lateral teeth, fused to the central denticle (Clench, 1946).

Later, Weaver and Du Pont (1970) recognized three subgenera. The subgenus Scaphella sensu stricto was characterized by a papiliform protoconch, usually with a spur-like calcarella present, the teleoconch "... is sculptured with spiral[ic] lirae and incised lines ... ", the colurnella has three or more anterior plats, and a siphonal notch and fasciole are present (Weaver and Du Pont, 1970: 140). The subgenus Aurinia differs in having a larger protoconch, with a projecting calcarella, in lacking a siphonal notch and fasciole, and in having no colurnellar plats or only weak ones. They recognized a third subgenus, Clenchina Pilsbry and Olsson, 1953, which differs from the nominal subgenus by smaller size, less solid shell, usually with an attenuated spire. These shell differences are small, and both Pilsbry and Olsson (1953) and Weaver and Du Pont (1970) separated the subgenera mainly by radial morphology. The nominal subgenus is characterized by uniserial Y-shaped radial teeth, without side cusps, Clenchina has small Y-shaped teeth with minute side cusps, and Aurinia has tricuspid rachidian teeth, with the central cusp broadest and the lateral cusps strong and sickle-shaped (Weaver and Du Pont, 1970).

Poppe and Goto (1992) placed 'shell similarity' above radial structure. They stressed that these subgenera were based mainly on radial characters, with conchologically similar species having quite different radial structure (Bayer, 1971), and recognized only a single genus Scaphella, without subgenera.
In the Recent fauna the representatives of the genus Scaphella are restricted to the western Atlantic. The number of species recognized varies considerably, from four (Weaver and du Pont, 1970) to 11 (Poppe and Goto, 1992) or 12 (Clench, 1946). All the Recent species, except S. gouldiana (Dall, 1857), have a color pattern of squarish red or black spots in spiral rows on a paler background, which has spiral bands in some species, and most species have axial sculpture on the early teleoconch whorls.

Scaphella in the fossil record

New World

Scaphella is well represented in the Neogene Caribbean fossil record. It is found in the upper Miocene Gurabo Formation of the Dominican Republic (Vokes, 1998) and represented by possibly numerous species in the Floridian Plio-Pleistocene (Petuch, 1994). It has not been recorded from the Tropical American Pacific. The earliest representative of the Neogene group of Scaphella in the American fossil record is the upper Miocene Dominican Republic species S. striata (Gabb, 1873), which is most similar to S. gouldiana in having strong axial nodes at the shoulder. Vokes (1998) noted that the shells of S. striata do not show the characteristic color pattern and were probably monochrome. All the specimens from the Florida Plio-Pleistocene illustrated by Petuch (1994) have axial sculpture on the early teleoconch whorls and a spotted color pattern.

The history of the genus in the New World before the Neogene is far more complex. Dall (1907) suggested that the Neogene group of Scaphella evolved in the western Atlantic from the genus Caricella Conrad, 1853, which is widespread in the Eocene and Oligocene western Atlantic assemblages (Gardner, 1937).

Caricella shares a similar shell shape and color pattern of squarish red dots (Dockery, 1977; MacNeil and Dockery, 1984). It therefore seems that this color pattern is a conservative character of the Caricella-Scaphella line of volutes (MacNeil and Dockery, 1984). Gardner (1937) described Caricella (Attraktius) pygnopecta Gardner, 1937 from the Shool River Formation of northern Florida and extended the upper range of Caricella into the lower Miocene. In our opinion this new taxon may have been based on a juvenile specimen of Scaphella. The holotype is 27.0 mm in height. The juvenile specimen of Scaphella sp. from the Floridian Pliocene herein figured (Figures 2–3) shows the same reticulate sculpture, which later disappears in the adult stage. Unfortunately we have not examined or been able to trace any larger Scaphella specimen from the Miocene of Florida, where they seem to be very rare.

Two species present in the Paleocene of the eastern United States (Porters Creek Formation, Matthews Landing Marl Member, Alabama) are much more similar in their tall, elongated shape to the Scaphella representatives in the Old World. We refer to the former two species as the Paleocene New World Scaphella group. The shell of Scaphella showalteri (Aldrich, 1886) (Figures 5–6) is very similar to the shells of the European species, but does have faint axial sculpture on the early teleoconch whorls, whereas the specimens of Caricella huenei Dall, 1890, (Figures 7–9) are very elongate, similar to the shell of North Sea Basin Miocene Scaphella specimens and most unlike any of the American Eocene-Oligocene Caricella species.

Old World

Traditionally, all the European Scaphella species had been assigned to the genus Scaphella sensu stricto Swainson, 1832. Darragh (1988) placed the European species in the subgenus Aurinia H. and A. Adams, 1853. However, as already noted by Darragh (1988) and Marquet (1997), this allocation is problematic. There are certain shell features the Old World Scaphella species share that are absent in the New World Neogene species. This will be fully discussed further on.

The earliest records of the genus Scaphella in Europe are Scaphella crenestria (Von Koens, 1885) and Scaphella faccoides (Bavne, 1902) from the Paleocene of Denmark (Bavne, 1933). The shells of these Paleocene species have the typical fusiform shape, but only three columellar folds (Bavne, 1933) rather than the four or five ones present in the shells of Neogene and Recent species. Scaphella reticulata Sowerby, 1836, from the Lower Eocene London Clay shows the typical Scaphella shape and also has three columellar folds (Edwards, 1855, pl. 23, fig. 4). Scaphella honi Gilbert, 1935 from the upper Eocene, Bartonian (Wemmelsea) of Belgium is somewhat unusual, with a carina on the last whorl bearing large sub-oblolute tubercles (Gilbert, 1935, pl. 4, fig. 2), but the protoconch and early teleoconch whorls are similar to those of other European specimens, and like the other early Scaphella, it has only three columellar folds. Scaphella is then represented in the North Sea Basin continuously from the Lower Oligocene, Lattorfan, of Germany, by S. siemensenii (Boll, 1851), which has an elongate shell with a tall spire, no axial sculpture at all, and no siphonal fasciole (Beez, 1950), to theKnisselsand S. (Marquet, 1997), Picenzian, middle Pliocene (Van Vliet-Lanoo et al., 2002). In the late Oligocene Scaphella reached the Atlantic, where it was represented by an undescribed species (Figures 11–13) from the upper Oligocene, Chattian of St-Paul-lès-Dax, Aquitaine Basin, France (AC coll.).

In the Miocene Scaphella is represented in the North Sea Basin by Scaphella bolli (Koch, 1861) (Figures 14–17), and in the Atlantic by S. miocenica (Fischer and Tournonier, 1879) in the middle Miocene, Serravallian, of the Loire Basin and S. carinellata (Grateloup, 1840) in the lower Miocene, Burdigalian of the Aquitaine Basin (Peyrot, 1928). The southernmost Miocene record is that of Voluta lauberti Sowerby, 1816 in the upper Miocene, Tortonian, of southern Portugal, Algarve Basin (Pereira da Costa, 1866).
In the Pliocene, *Scaphella lamberti* (Sowerby, 1816) (Figures 19–22) flourished in the North Sea Basin and was abundant in the Oordtens Sands of Belgium (Marquet, 1997). In the Atlantic it is recorded from the Loire Basin, northwestern France (Chavan and Coatman, 1943). *Scaphella* is also recorded from central-western Portugal, Mondego Basin (Silva, 2001) and lower Tagus-Sado Basin (Zbyszewski, 1943, 1959), southern Atlantic coast of Spain, Guadalquivir Basin (BLP coll.) and the Alborna Sea, Estepona Basin (BLP coll.), Lamothé and Dantzenberg (1997) recorded *S. lamberti* from the Pliocene of Algeria, although we have not found any further record to confirm this.

**The origin of Scaphella**

The subgeneric assignment of the European fossil *Scaphella* species is problematic. Darragh (1988) placed the European Cenozoic *Scaphella* species in the subgenus *Aurinia*, which according to him is characterized by the absence or reduction of the columellae plicae and the absence of a siphonal fasciole.

Marquet (1997) already noted that Pliocene North Sea Basin specimens of *Scaphella lamberti* do not fit neatly within these characters, having strongly developed columellar plications. The same can be said for the rest of the European *Scaphella* species, which all have strongly developed columellar plications.

One species, *Scaphella* (*Aurinia*) *johannae* Darragh, 1988, occurs in the Australian Aldahan, upper Eocene. It is similar in shape to the European species and has no sculpture on the early teleoconch whorls. As noted by Darragh (1988, p. 217), that species is more akin to the European stock of *Scaphella* than to the New World *Scaphella* species, and could be regarded as an example of a Tethyan element in the Australian Eocene fauna.

Thus, the shell characters of the Old World fossil species of *Scaphella* do not fit into any of the three existing subgenera of the genus. The early teleoconch whorls have no axial sculpture; the aperture combines strong columellar folds with the absence of a fasciole, and no color pattern whatsoever has been observed in any specimen under either normal or UV light.

Bondarev (1997) discussed the biogeography and history of the subfamily Scaphellinae, stating that they originated in the Tethys, and placed their roots in the Mesozoic. Bandel (2003) supported the Mesozoic Tethyan origin of the Voluitidae with the description of a Cretaceous voluitid assemblage from Egypt, from the southern shelf area of the Tethys Ocean, on the African continent. He also described the first and oldest member of the genus *Caricella* from this upper Cretaceous Tethyan assemblage; *Caricella (Milirinchio) klitzschii* Bandel, 2003.

The origin of *Scaphella* is therefore even less clear. Any hypothesis on dispersal of the Scaphellinae must encompass: the first appearance of *Caricella* in the Tethyan Realm; the presence of *Caricella* and *Scaphella* in the New World Paleocene, *Caricella* only in the New World Eocene to Oligocene, *Scaphella* only in the New World Miocene to Recent; the continuous presence of *Scaphella* in the Old World from the Paleocene to Pliocene, but not of *Caricella*.

It is plausible to assume, as suggested by Dall (1907), that the Neogene New World *Scaphella* group evolved from a *Caricella*-like ancestor, which migrated westward from the Cretaceous Tethys into the proto-Atlantic Sea along the predominantly westward flow of ocean currents, long before the closure of the Central American Seaway, when a more-or-less continuous tropical sea existed at low latitudes (Vermeij and Rosenberg, 1993).

Based on the new data of Bandel (2003), it is however more likely that both *Caricella* and *Scaphella* originated in the Tethys Sea, and that both independently dispersed to the New World, which could explain their presence there in the Paleocene, and the similarity between the Paleocene New and Old World *Scaphella* species. Subsequently, as there is no record of any *Scaphella* in the New World in the Eocene and Oligocene, the Neogene New World *Scaphella* evolved from the New World *Caricella*, explaining the differences between this stock of *Scaphella* species and the European stock, which remained more closely similar to the original Tethyan *Scaphella*.

However, none of the Recent Voluitidae produce planktonic larvae that could favor this westward transatlantic dispersal (Bouchet and Poppe, 1988; Darragh and Pouder, 1998). Some Cenozoic *Athleta* species produced planktonic larvae (Hansen, 1978); possibly some *Lyria* species (Bouchet and Poppe, 1988); some *Calliotrema* species (Bouchet and Poppe, 1995) and *Protocostor*, which appeared in New Zealand late in Pliocene time (Maxwell, 2003). However, we must note that the Ath.
letidae were considered as an independent family from the Volutidae by Riedel (2000) (but as a subfamily of the Volutidae by Bouchet and Rocroi [2005]).

In fact Bondarev (1997) stated that volutids are characterized by their high level of provincialism. Bouchet and Poppe (1988, p. 30) pointed out that "Volutids are the most holobenthic of all gastropods ...", and Darragh (1988) noted that the volute fauna of the areas where species occur today was largely established by mid-Tertiary time, little having been added since. The fact that, as far as we know, *Scaphella* in the New World never dispersed into the Pacific during the Neogene, and in the Old World it did not disperse into the Mediterranean (except the Albanian Sea) or Paratethys, is a testament to its poor dispersal ability. This has not, however, prevented the dispersal of some volutids over long distances, such as representatives of *Alctithoe* and *Lyria*, that probably "hopped" along underwater bridges or chains: these may have a short-lived demersal free-swimming larval stage (Bouchet and Poppe, 1988).

Bandel (2003) suggested that the protocodotype of the Cretaceous Egyptian Volutidae (including a *Caricella*-like species) suggested a non-planktotrophic development and that they spread only by crawling young and not by free-swimming larvae.

If Bondarev (1997) and Bandel (2003) are correct in their hypothesis that the Scaphellinae originated in the Cretaceous of Tethys Sea, and Dall (1907) is correct in his hypothesis that *Scaphella* originated from *Caricella*, it is likely that the New World Paleocene *Scaphella shoalwaleri* evolved from a Cretaceous/Paleocene Old World ancestor, which emigrated to the New World from the Tethys and in turn gave rise to the New World *Scaphella* stock. The European species traditionally assigned to *Scaphella*, showing consistently distinct conchological characteristics, therefore would constitute a separate stock from those in the New World fauna, and might even warrant a distinct genus-level taxon.

Family Volutidae Rafinesque, 1815
Subfamily Scaphellinae Gray, 1857
Genus *Scaphella* Swainson, 1832

**Type species:** *Voluta junionia* Shaw, 1808, by subsequent designation, Gray, 1847 (Clench, 1946). Recent, western Atlantic Ocean.

**Discussion:** Whilst including the European species traditionally assigned to *Scaphella* within this genus, we stress that they differ from *Scaphella* sensu stricto and the subgenus *Clenschina* in not having axial sculpture on the early teleoconch whorls, and in having no siphonal fascicle and no color pattern, and from the subgenus *Aurinia* by again not having axial sculpture or color pattern and having well developed columellar folds. Although the number of columellar folds is similar in *Scaphella* and its subgenera to that in the European Cenozoic species, and in both the folds become more oblique apically, there is a subtle difference in their shape. The folds in New World *Scaphella* specimens are highly asymmetrical; the anterior face is much less steep than the posterior face, giving the shells a ratcheted appearance (Figure 4). This is not true in the European shells, in which the folds are elevated and symmetrically rounded. This ratchet-like character of the columellar folds of the New World *Scaphella* shells is not present in *Caricella*, in which the folds are symmetrical and much finer than in *Scaphella*.

Although the absence of color pattern in fossil shells is not always a reliable guide to the color of the living animals, almost all fossil *Scaphella* species from the New World (except *S. striata*) are characterized by shells with persistent color pattern (see Olsson and Petit, 1964; Campbell, 1993; Petuch, 1994). Many other shells from the Estepona and Mondego deposits have the color pattern preserved and one would have expected some of the strong spotted pattern of *Scaphella* to be seen if present, but none has been observed in the specimens from Estepona, Mondego, or in any other European fossil *Scaphella* species.

Unlike Recent American *Scaphella* species, which are tropical to subtropical, European fossil *Scaphella* species were predominantly warm-temperate to subtropical. Two of the three more southern deposits where European *Scaphella* have been found (Mondego and Estepona Basins), which were subtropical and tropical respectively (see Silva and Landau, in press), reflect areas where there was some degree of upwelling of cooler nutrient-rich waters (Landau, et. al., 2004; Silva et al., 2006). This ability of gastropods of temperate waters to survive in a tropical zone subjected to the periodical upwelling of colder nutrient rich waters has already been observed for species of the genus *Ammalina* (Landau and Silva, 2006). Even though European *Scaphella* were widespread and diverse during the early Pliocene, the genus did not survive subsequent Plio-Pleistocene cooling, and the youngest record is of *S. lamberti* from the upper Pliocene Kruusians Sands of Belgium, where it is rare (Marquet, 1997). Interestingly, European *Scaphella* did not follow the prevalent trend of southward migration seen in many other gastropod taxa as a...
result of the late Neogene cooling events (Monegatti and Raffi, 2001; Silva and Landau, in press), and does not survive off West Africa.

Scaphella carlac new species
(Figures 23–29, 49–51)

Description: Shell large, fusiform, of medium thickness, slender and elongate. Protoconch with 1.5 smooth flattened whorls. Nucleus of medium size, with a small, blunt-pointed calcarella, junction with teleoconch not sharply delimited. Teleoconch with five whorls. The first teleoconch whorl is short and flat, about three times wider than tall. Second teleoconch whorl increases in height rapidly, so that suture, nearly horizontal on first whorl, becomes more oblique. By third teleoconch whorl, width is 1.5 times height. Abapically the whorls become taller and more convex, with narrow, slightly concave sutureal ramp. Last whorl about 77% of total height, elongate, slender and not particularly inflated, slightly shouldered in some specimens. Sculpture of very faint to obsolete spiral threads, most evident on early whorls and below suture. Aperture 66% of total height, tall, relatively narrow. Outer lip not thickened, convex in profile. Columella weakly concave, bearing 4–5 oblique, symmetrical, elevated columellar folds of variable thickness, increasingly oblique abapically; middle folds most strongly developed, abapical fold absent in smaller specimens; folds strongest and somewhat flattened in gerontic specimens. Columellar and parietal callosity very thin and worn in most specimens. Siphonal canal long and slightly recurved abapically. Siphonal fasciole absent.

Type Material: Holotype; IRScNB 1ST 6994, height: 147.0 mm; paratype: IRScNB 1ST 6995, height: 147.0 mm.

Type Locality: Velerín conglomerates, Velerín, Estepona, province of Málaga, Spain.

Stratum Typicum: Velerín Conglomerates, lower Piacenzian, lower Pliocene.

Other Material Examined: Thirteen specimens, from the type locality, BLP coll.

Distribution: Lower Pliocene; western Mediterranean, Estepona.

Etymology: Named after Carla Santos, botanist, currently working at Coimbra University; companion and moral support to one of the authors (CMS).

Comparative Remarks: Scaphella carlac new species differs from the North Sea Basin Pliocene species S. lamberti in having a more elongate shell, with a higher spire, the spire whors are relatively taller and the last whorl less inflated, the outer lip is convex in profile and not sinusous as in S. lamberti, and the aperture is relatively smaller and much narrower. The protoconch of S. carlac consists of 1.5 flattened whors, with a small blunt calcarella at the apex. The protoconch of S. lamberti comprises about two whors, is smaller (7.3 versus 9.3 mm diameter), rounded, and more bulbous. Marquet (1997) discussed the variability in height/width ratio of S. lamberti in his Belgian assemblage. His ratio was 2.1 to 2.7 (average: 2.4). This is identical to the variability we have found (Figure 55) for the specimens of S. lamberti examined (BLP coll.). 2.1 to 2.6 (average: 2.3). These contrast markedly with the range observed in S. carlac, 2.7 to 3.1 (average: 2.9).

High-spired and elongate Scaphella bolli from the middle Miocene North Sea Basin is more similar in shape to S. carlac than S. lamberti. Indeed, the range of height/width observed by Marquet (1997), 2.8 to 3.1 (average: 2.96) is about the same as that for S. carlac. However, S. bolli has fewer columellar folds (3–4 versus 4–5), the spiral sculpture is more strongly developed and the protoconch is even smaller (5.3 mm diameter), with the first whorl even more bulbous and the calcarella more pointed in S. bolli than in S. carlac.

The middle Miocene Atlantic species Scaphella mio- caenica (Figure 18) from the Loire Basin has a broader, squatter, more solid shell, with more shouldered whors. The protoconch is rather similar in shape to that of S. carlac, with 1.5 flattened whors and a small blunt calcarella at the apex, but much smaller (7.0 versus 9.3 mm diameter).

Scaphella tarbelliana (Grateloup, 1840) from the Atlantic lower and middle Miocene Aquitaine Basin (Figures 30–31) has characters intermediate between those of S. carlac and S. lamberti. The protoconch of S. tarbelliana is about 6.2 mm diameter. It is smaller, narrower and less inflated than S. lamberti, but still broader, with a proportionally lower spire than S. carlac. The outer lip is convex in profile and not sinusous as in S. lamberti, and

Figures 32–51. Scaphella species. 32–33. Scaphella sp., juvenile (CMS coll.). Vale de Freixo, Pombal Region, central-western Portugal. Uppermost Zanclean to lowermost Piacenzian, lower-middle Pliocene, height 54.6 mm. 34. Scaphella sp., juvenile (CMS coll.). Vale de Freixo, Pombal Region, central-western Portugal. Uppermost Zanclean to lowermost Piacenzian, lower-middle Pliocene, height 31.4 mm. 35–37. Scaphella mio- caenica (Fischer and Tournoeur, 1859), juvenile (BLP coll.). Ferrière-Larçon, Loire Basin, France, Serravallian, middle Miocene, height 9.5 mm. 38–40. Scaphella sp., juvenile (MV coll.). Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene, height 34.1 mm. 41–43. Scaphella sp., juvenile (MV coll.). Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene, height 34.0 mm. 44–45. Scaphella lamberti (Sowerby, 1816), juvenile (BLP coll.), Vrasenedok, Kallo, Oost-Vlaanderen, Belgium, Oolderen Sands, middle Pliocene, height 35.8 mm. 46–47. Scaphella lamberti (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Belgium, Oolderen Sands, middle Pliocene, height 35.0 mm. 48, Scaphella lamberti (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Belgium, Oolderen Sands, middle Pliocene, height 32.0 mm. 49–51. Scaphella carlac new species, juvenile (BLP coll.). Velerín Conglomerates, Velerín, Estepona. Spain, lower Piacenzian, middle Pliocene, height 47.5 mm.
the aperture intermediate in width between the two. Nevertheless, the overall outline of *S. tarbelliana* is still considerably more inflated than that of *S. carlae*. *Scaphella miocaenica* differs from *S. tarbelliana* in being thicker-shelled, squat, and in having a lower spire and a more inflated, more shouldered last whorl.

Clibert (1952) noted that even at the juvenile stage *S. miocaenica* and *S. lamberti* were quite different, however, the character of the juvenile shell was not considered by subsequent authors. Certainly the juvenile shell of *S. miocaenica* is quite different from that of *S. lamberti* and *S. carlae*, being much broader, and the protoconch whorls more depressed. The shape of the juvenile shell of *S. carlae* is similar to *S. lamberti*, but in the latter the apex is more rounded, the calcarella more elevated and the diameter of the first teleoconch whorl is smaller.

*Scaphella* sp.  
(Figures 35-43, 52-57)

**Description**: Shell large, fusiform, relatively thick-shelled. Protoconch with about 1.5 smooth, flattened whorls, with small, blunt-pointed calcarella. Junction with teleoconch not sharply delimited. Teleoconch with 3-3.5 whorls. First teleoconch whorl short, flat, width about three times height. Second teleoconch whorl weakly angular in profile, increasing in height rapidly, so that suture becomes more oblique than on first whorl. Last whorl about 80% of total height, inflated, shouldered weakly a short distance below suture. Sculpure of very faint to obsolete spiral threads, most evident on early whorls and below suture. Aperture 74% of total height. Outer lip broken in examined specimen. Columella almost straight, bearing four narrow, elevated, oblique columellar folds, increasingly oblique abapically; adapical three folds of roughly equal strength, adapical fold much weaker. Columellar and parietal callus not preserved. Siphonal canal long and straight. Siphonal fasciole absent.

**Dimensions and Material**: Maximum height: 112.0 mm (although incomplete specimens suggest up to approximately 130 mm). Four specimens, BLP coll.; six specimens, M-V coll. All from Bonares, Guadalquivir Basin, Huelva, Spain. Zanclean, lower Pliocene.

**Discussion**: Despite intensive collecting by one of the authors (BL) and dedicated local collectors Manuel Molin and Daniela Velo for more than 30 years, only six incomplete adults and two juveniles have been found in the Guadalquivir Basin deposits. However, it is clearly not conspecific with *Scaphella carlae*. The lower Pliocene Atlantic specimens from the Guadalquivir Basin are thicker-shelled (maximum shell thickness 4.9 mm), squatter, with fewer whorls, the last whorl distinctly shouldered as opposed to convex or weakly shouldered, and there are only four columellar folds, which are narrower than in the coeval Mediterranean *S. carlae*. The maximum diameter of the protoconch (9.7 mm) is similar to that of *S. carlae*.

Of all the European species of *Scaphella*, the Guadalquivir Basin shells are most similar to the Atlantic middle Miocene Serravallian *S. miocaenica* from the Loire Basin of France. This latter species is also relatively squat, thick-shelled, with the last whorl shouldered, and with four folds on the columella. The protoconch diameter of *Scaphella* sp. is, however, greater than in *S. miocaenica* (9.7 versus 7.0 mm). The juvenile stage of *S. miocaenica* is quite characteristic, the last whorl very broad (Figures 35-37), unlike that of *S. lamberti* or *S. carlae*.  

**Figures 52-57. Scaphella* sp. (BLP coll.). Bonares, Guadalquivir Basin, Spain. Zanclean, lower Pliocene. 52-54. Height 98.7 mm. 55-56. Height 112.2 mm. 57. Height 90.4 mm.
**carlac.** Fortunately, two perfectly preserved juvenile specimens are available to us collected by Manuel Molin and Daniela Velo. The shape of the juvenile shell is most similar to that of *S. miocaenica,* possibly even more inflated, but larger at the same number of whorls, and the diameter of the protoconch and first teleoconch whorls is greater.

The specimens from the lower Pliocene Mondego Basin of Portugal (Silva, 2001) are both juvenile (Figures 32–34). Their protoconch characteristics and the shape of the juvenile shell are more similar to those of *Scaphella* sp. than *S. carlac,* and they have provisionally been added to the distribution.

**CONCLUSIONS**

In the Recent volutid faunas, non-planktrophic larval development most likely induces the establishment of locally distinct populations, which ultimately results in poorly defined species-group taxa, as with the *Cymbiola* *pulchra* group from Queensland, Australia (Darragh and Ponder, 1998).

The same applies to Recent *Scaphella* species in the New World, which explains the enormous discrepancy in the number of species recognized by different authors (four, Weaver and du Pont, 1970; 12, Clench, 1946). A similar situation occurs with European *Scaphella,* the species being restricted both geographically and stratigraphically. This is illustrated by the presence of two different species in the Atlantic Miocene Loire and Aquitaine Basins and the description of two coeval, but distinct species present on either side of the Straits of Gibraltar in the Pliocene. Most of the European species are relatively easily characterized, although the middle Miocene to lower Pliocene (lower to upper Redolian) *Scaphella* species from the Atlantic Loire Basin, northern France are less clearly distinguished. Bréjon (1964) recorded the presence of both *S. miocaenica* and *S. lamberti* in these deposits and observed a transition from one to the other from the middle Miocene to the Pliocene.

This study of European *Scaphella* revealed that the genus as traditionally regarded is heterogeneous, with clear and consistent differences in shell morphology between Old and New World species. Old World *Scaphella* occur continuously in the European Cenozoic from the Pliocene to the middle Miocene and form a distinct group from the Neogene to Recent New World species.

Assuming that Bondarev (1997) and Bandel (2003) are correct, and that the Scaphelliinae have a Cretaceous Tethyan origin, and that Dall (1907) is also correct, and that *Scaphella* originated from *Cavicella,* it is hypothesized that the New World Palaocene *Scaphella* originated from a Cretaceous/Paleocene Old World ancestor, which emigrated to the New World from the Tethys, and that the Neogene New World *Scaphella* species are a distinct stock, which evolved from *Cavicella.* This would explain the similarities between Old and New World Palaocene *Scaphella* and the differences with the New World Neogene stock. The European Palaocene to Miocene species traditionally assigned to *Scaphella* therefore would constitute a separate stock from those in the New World, and might even correspond to a distinct genus-level taxon.

**ACKNOWLEDGMENTS**

We would like to thank Dr. Alan Ben of the Institute of Geological and Nuclear Sciences (New Zealand) and Geerat Vermeij of the Department of Geology, University of California at Davis (USA) for their critical review of the manuscript. Chris Garvie of the Texas Memorial Museum, Texas (USA) for advice and photographs of the Palaocene North American Scaphelliinae. Phyllis Diegel of Florida (USA) for supplying specimens of juvenile American fossil *Scaphella,* Manuel Molin and Daniela Velo of Bonares (Spain), Robert Marquet (Belgium) and Alain Cluzaud (France) allowed us access to their collections and photographed specimens for this work. Inge-

![Figure 38. Morphometric comparisons between *Scaphella lamberti* and *S. carlac* new species. Measurements in mm.](image-url)
mann Schnettler of Langå (Denmark) for photographs of Danish Paleocene specimens. Contribution of the Portuguese FCT Project POCTI 32724/99—Comparative (palaeo)environmental analysis of oceanic and coastal domains, over the last 20 Ma, based on calcareous nanoplankton (CANAL). co-financed by European Union’s FEDER.

LITERATURE CITED


A new record of introduced Cerion (Gastropoda: Pulmonata: Cerionidae) in southeastern Florida

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ABSTRACT
A large, well-established colony of the land snail genus Cerion is reported from Delray Beach, Florida, far north from the range of the only native species in Florida, Cerion incanum (Binney, 1851) and its subspecies, and from the well-documented populations introduced by Paul Bartsch during the early 20th Century. Although hurricanes have frequently been proposed as agents of long distance dispersal of Cerion species, the Delray Beach Colony is more probably the result of intentional introductions during the mid-20th Century. The morphology of the shells in this colony is uniform except for the degree of pigmentation, yet it does not match precisely any of the fourteen named taxa from the Little Bahama Bank or the Bimini Islands, the nearest and most probable sources of the introduced propagules. Rather, the phenotype appears to combine elements of several taxa from both island groups, suggesting that the Delray Beach Colony may be a result of hybridization among animals from multiple and disparate introductions.

Additional Keywords: Introduced species, land snails, hybridization, Bahamas.

INTRODUCTION
The land snail genus Cerion has long been known for its extreme morphological diversity, especially in the faunas of Cuba, the Bahamas, and Cayman Islands (see Woodruff, 1978, and references therein). Although the oldest Cenozoic records of the genus are from the Oligocene of western Florida (Table 1A; Figure 1, ▶), Cerion is limited to a single species, Cerion incanum (with four subspecies or forms, see Table 1B; Figure 1, ◆) in the Recent fauna of Florida (Pilsby, 1946: 163, fig. 77). The species inhabits nearshore vegetation from Key Biscayne southward throughout the Florida Keys to Key West. Several authors (e.g., Binney, 1851: 153; Pilsby, 1902: 213; 1907: 193; 1946: 162; Dall, 1905a: 30) have suggested that C. incanum is not directly descended from a Florida Oligocene species but rather from Cerion that re-colonized the Florida Keys from Cuba following the interglacial high stands that had completely submerged southern Florida during the Pleistocene (Hearty et al., 1998). Pilsby (1902: 213) regarded Cerion incanum to be most closely related to the Cuban C. maritinum (Pfeiffer, 1839).

The Cerion fauna of Florida had been significantly increased through a series of well-documented experimental transplantations of non-native species begun by Bartsch in 1912 (see Bartsch, 1912; 1920; 1949, and references therein). Bartsch’s initial introductions were confined to two species that he subsequently named Cerion casablancae Bartsch, 1920, and Cerion viaregii Bartsch, 1920, both from Andros Island, Bahamas. Each of these was introduced to several of the Florida Keys, including the Dry Tortugas that were thought to be devoid of Cerion incanum (Table 1C). Bartsch later expanded his experiments to include introductions of an additional dozen species from Cuba, Puerto Rico, Curaçao, and several Bahaman islands, to sites in the Dry Tortugas, especially Fort Jefferson on Garden Key, and Loggerhead Key. He monitored and reported on these introduced colonies for decades. Most of the introduced colonies have since died out, but several (e.g., Cerion casablancae on Indian Key) flourish to this day, and some (e.g., C. viaregii on Newfound Harbor Key and C. casablancae on Bahia Honda Key) have hybridized with the native C. incanum (see Bartsch, 1920; Woodruff and Gould, 1957).

We have recently encountered a sizeable colony of Cerion in Delray Beach, Florida (Figure 1, ◆), far north of the known distribution of native Cerion incanum (Figure 1, ▶) and the sites of Bartsch’s introductions (Figure 1, ◆). The Delray Beach Colony inhabits vegetation on seaside sand dunes between the Atlantic Ocean and Route A1A, from Atlantic Avenue (26°27.696’ N, 80°03.483’ W) northward to near the northern limit of the Gulfstream Golf Course (26°29.284’ N, 80°03.218’ W), where the dunes and vegetation are replaced by private homes that extend to the beach. These Cerion are most abundant just south of George Bush Boulevard (26°28.350’ N, 80°03.373’ W), and near the northern end
Table 1. The family Cerionidae in Florida.

| A. Fossil Taxa (all Oligocene, from Bahut Point, Tampa Bay) |
| Cerion (Eostrophia) annulata Dall, 1890. |
| Cerion (Eostrophia) annulata var. floridanum Dall, 1890. |
| Microcerion floridanum Dall, 1915. |

| B. Living, Native Taxa (with their type localities) |
| Cerion incanum incanum (Binney, 1851). Key West. |
| Cerion incanum mactatum (Binney, 1859). Key Biscayne. |
| Cerion incanum saccharinum ‘Blancs’ Pillsbry and Vanatta, 1899. Sugarloaf Key. |
| Cerion incanum vacca (Pillsbry, 1902). Key Yacea. |

| C. Non-native species of Cerion introduced intentionally to the Florida Keys and the Dry Tortugas by Bartsch, 1912–1924. |
| Cerion viaregus Bartsch, 1920. From Andros, Bahamas, introduced to: Second Ragged Key North of Sands Key; Tea Table Key; Duck Key; Newfound Harbor Key; Key West; Boca Grand Key; Garden Key; Loggerhead Key; Man Key; Boy Key. |
| Cerion casablanca (Bartsch, 1920. From Andros, Bahamas, introduced to: First Ragged Key North of Sands Key; Sands Key; Indian Key; Bahia Honda Key; Loggerhead Key. |
| Cerion (Paracerion) tridentatum Pillsbry and Vanatta, 1895. From Cuba introduced to: Key West; Garden Key, north side of the parapet at Fort Jefferson; Loggerhead Key. |
| Cerion manila (Sowerby, 1834). From the point at Miami, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson. |
| Cerion elystalis (“Fernssac” Beek, 1857). From near Cabanas Fort, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson. |
| Cerion sculptum (Foey, 1838). From near the lighthouse at Mariel, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson. |
| Cerion “n. sp.” Young. From the point at Mariel, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson. |
| Cerion sp. [small, mottled]. From Andros, Bahamas, introduced to: Bird Key. |
| Cerion sp. Mottled. From New Providence, Bahamas, introduced to: Loggerhead Key. |
| Cerion crassilabiata (“Shuttleworth” Sowerby, 1857). From Puerto Rico, introduced to: Loggerhead Key. |
| Cerion new (Linne, 1758). From Curacao, introduced to: Loggerhead Key. |
| Cerion “magerii” (not clear if this is a typographical error for C. magerii Maynard and Clapp, 1920, or a manuscript name). From Middle Bight, Andros, introduced to: Loggerhead Key. |
| Unspecified Cerion. From Puerto Rico and “El Salvador,” introduced to: Loggerhead Key. |
| Cerion incanum (Binney, 1851). Source unspecified [Florida Keys], introduced to: Loggerhead Key, Man Key, Boy Key. |

of Gulfstream Golf Course (26°29’24” N, 80°03’22” W), where densities exceeded 15 individuals per square meter. The snails in this colony are fairly uniform in their shell morphology (Figures 3, 5–8), but vary in degree of pigmentation from pure white (Figure 7) to weakly (Figure 6, 8) or strongly (figures 2, 4) mottled with oblique bands of brown.

Many Cerion researchers (e.g., Pillsbry, 1907; Mayr and Rosén, 1956; Clench, 1957, Gould and Woodruff, 1978) accepted the hypothesis that hurricanes play a significant role in the long distance dispersal of Cerion species and are a major factor in determining biogeographic patterns within the genus. A review of historical hurricane tracks [http://hurricane.csc.noaa.gov/hurricanes/viewer.html] revealed that the Little Bahama Bank and the Bimini Islands (both within 120 km of Delray Beach) are the closest potential sources for this colony under this dispersal scenario. However, intentional human introduction during the mid-20th century is, in our view, a more credible explanation for the origin of this colony. Dr. Edward Pettuch (personal communication) recounted to us his conversations with the late P. L. and T. L. McGinty, in which they acknowledged introducing at least six different Bahamian populations of Cerion, “mostly from West End (Grand Bahama Island) and the Bimini Islands,” to the vicinity of their home in Boynton Beach. These second-hand accounts of Cerion introductions are given credence by an earlier report of an anomalous population of another land snail, Ligus fasciatus (Müller, 1774), from nearby Boynton Beach (Craig, 1973) that was subsequently documented as being the descendents of an intentional introduction by the McGinty brothers (Krieger and Austin, 1975). Whether transported by a hurricane or intentionally introduced, the most probable sources for the Delray Beach colony are the Cerion faunas of the Little Bahama Bank or of the Bimini Islands.

Nine species or subspecies of Cerion have been described from the Little Bahama Bank (Clench, 1957) (Table 2, Figures 9–18). Gould and Woodruff (1978) reduced these taxa to two semispecies, C. abacoensis Pillsbry and Vanatta, 1895, and C. bimbaei Pillsbry and Vanatta, 1896, based on morphometric and allozyme studies, but noted that the various shell morphotypes could be localized to specific regions on the Little Bahama Bank.

Clench (1955: 50) conjectured that Cerion milleri (Pfeiffer, 1867), described from Duck Key, Exuma
Group, might actually be from Duck Key in Cherokee Sound, off Abaco, noting that he could not find any “Duck Key” in the Exuma Group on modern maps. Gould and Woodruff (1978: 381) commented that if Clench were correct, C. mulleri would become the senior synonym of C. bendalli, but noted that they could not verify Pfeiffer’s locality, and that similar mottled Cerion occur throughout the Bahamas, including the Exumas. Perusal of Nautical Chart 26-D (Department of the Navy Hydrographic Office, 1965) reveals Duck Cay to be located west of the southern end of Great Exuma Island (23°27.22' N, 76°02.60' W), supporting Pfeiffer’s original type locality and excluding this taxon from the fauna of the Little Bahama Bank.

The Cerion fauna of the Bimini Islands consists of five named taxa (Table 3, Figures 19-23). Clench (1942) had synonymized three of these taxa (Cerion pillsburyi Pilsbry and Vanatta, 1897, C. canonicum Dall, 1905, and C. northropi Dall, 1905), but later (Clench, 1956) he named another taxon. Mayr and Rosen (1956) concluded that it was not possible to classify the existing colonies simply in terms of three nominal species, and noted that some colonies formed highly variable hybrid populations.

The transplantation experiments of Bartsch (1920) documented that colonies resulting from single introductions retain the morphology of their parental stock for multiple generations following transplantation. However, most Cerion “species” hybridize freely when commingled. In the short term, such hybrid populations produce morphological and molecular features not evident in either parent population (Bartsch, 1920; Woodruff, 1958). Over a period of decades, the hybrid phenotype and genotype may be gradually assimilated into that of the numerically dominant taxon (Woodruff and Gould, 1987), yet even after millennia, traces of past hybridization may persist as area effects (Goodfriend and Gould, 1996).

Shells from the Delray Beach colony do not resemble precisely any of the fourteen named taxa from either the Bimini Islands or the Little Bahama Bank as might be expected if this colony were the result of a single introduction. Rather, Delray Beach colony Cerion exhibit at-

Table 2. *Cerion* taxa described from the Little Bahama Bank, listed chronologically, together with their type localities, primary type specimens, and subsequent notes on distribution.

*Cerion abacosensis* Pilsbry and Vanatta, 1895. Abaco, Bahamas. Lectotype, ANSP 25337a (Baker, 1963: 206), now ANSP 25337. 4 paralectotypes ANSP 411926. Gould and Woodruff (1978: 379, fig. 1) report that this phenotype is restricted to the Crossing, Great Abaco.

*Cerion magnaardi* Pilsbry and Vanatta, 1895. Abaco, Bahamas. Lectotype, ANSP 25338a (Baker, 1963: 206), now ANSP 25338. 4 paralectotypes ANSP 411925. Gould and Woodruff (1978: 379) reported finding this phenotype only near Hole-in-the-Wall Light, on Great Abaco.


*Cerion oweni oweni* Dall, 1905. South side of Little Abaco, Bahamas. Lectotype, USNM 179436 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 12) is here designated as the lectotype], 17 paralectotypes. USNM 1086731. Dall (1905b: 443) reported the typical form to occur on Little Abaco, Great Abaco, and Grand Bahama Island. The type locality is that of the lectotype.

*Cerion oweni reticulatum* Dall, 1905. Sugar Loaves Rocks, NW of Elbow Cay, Great Abaco, Bahamas. Lectotype, USNM 179443 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 8) is here designated as the lectotype]. 13 paralectotypes, USNM 1086732.

*Cerion oweni incisum* Dall, 1905. Stranger Cay Beach, NW of Little Abaco. Lectotype, USNM 179440 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 10) is here designated as the lectotype], 4 paralectotypes, USNM 1086733.

*Cerion oweni terneolatum* Dall, 1905. Mathews Point, south side of Great Abaco, Bahamas. Lectotype USNM 179442 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 3) is here designated as the lectotype]. 3 paralectotypes, USNM 1086734.

*Cerion chrysaloides* Plate, 1907. Eight Mile Rock, Grand Bahama Island, MCZ 116008.

*Cerion liebmannorum* Clench, 1938. NW portion of Mores Island, 2 miles NW of Southwest Point, Great Abaco Island, Bahamas, paratype, MCZ 116018.

opportunities of several of the potential source populations. The broad shells with fewer, taller whorls, a longer, more acute conical portion of the spire, and thin parietal callus are most similar to *C. pillsburgii* and *C. eximium lerneri* from the Bimini Islands. However, the strong ribbing, patterns of pigmentation, as well as the shape, size, and orientation of the aperture and columella more closely resemble taxa from the Little Bahama Bank, particularly...
Table 3. Cerion taxa described from the Bimini Islands, listed chronologically, together with their type localities, primary type specimens, and subsequent notes on distribution.

| Cerion pilsbryi Pilsbry and Vanatta, 1897, Gun Cay. | Bahamas. Lectotype: ANSP 72136a (Baker, 1966: 207), now ANSP 72136. 3 paratypes ANSP 411921. |
| Cerion conica Dall, 1903, Gun Cay. Bahamas. Lectotype, USNM 127-160 (originally illustrated specimen (Dall. 1905b: pl. 58, fig. 131) is here designated as the lectotype). 4 paratypes. USNM 1086735. |
| Cerion norfolkii Dall, 1905, Bahamas. probably one of the westemmost islets near Gun Cay. Lectotype, USNM 124135 (originally illustrated specimen (Dall. 1905b: pl. 58, fig. 11) is here designated as the lectotype). 2 paratypes USNM 1086736. |
| Cerion biminiensis Henderson and Clapp, 1913. Southern end of North Bimini Cay, Bahamas. Lectotype. USNM 252849 (originally illustrated specimen (Henderson and Clapp: 1913, pl. 4 fig. 10) is here designated as the lectotype). 155 paratypes. USNM 1086737. |

C. abacoensis and C. oueni oueni. Shell morphology suggests that the Delray Beach colony may be the result of hybridization of snails from two or more populations introduced from the northern Bahamas some time near the middle of the 19th century. Future genetic analyses may aid in the identification of the source Bahamian population or populations for the Delray Beach colony.

ACKNOWLEDGMENTS

We are most grateful to Dr. Edward J. Petuch of Florida Atlantic University for sharing his recollections and reminiscences of conversations with the McGinty brothers, and for taking part in initial surveys for introduced populations of Cerion between Manalapan and southern Delray Beach, Florida. We also thank Paul Callomon, Department of Malacology, Academy of Natural Sciences of Philadelphia, and Adam Baldinger, Department of Malacology, Museum of Comparative Zoology, for the loan of type specimens in their care. This research was supported by NSF Grant # EAR 0106936.

This is Smithsonian Marine Station at Fort Pierce Contribution Number 653.

LITERATURE CITED


A new early Miocene Muracypraea Woodring, 1957 (Gastropoda: Cyraeidae) from the Pisco Basin of southern Peru

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ABSTRACT

The cypracid gastropod, Muracypraea ornemoi new species, is described from lower to middle Miocene beds of the uppermost Oligocene to middle Miocene Chilcatav Formation, Pisco Basin, southern Peru. It is the first cypracid reported from southern Peru and represents the southernmost occurrence of this genus. Muracypraea is normally a warm-water gastropod and its occurrence in the study area indicates dispersal by means of coastal countercurrents into waters possibly cooled by coastal upwelling. The new species shares a neritic habitat with endemic molluscan taxa and with taxa ranging northward from the Navidad Basin of central Chile.

INTRODUCTION

Muracypraea ornemoi new species is described from the Chilcatav Formation of the Pisco Basin, southern Peru. Associated mollusks and microfossils from correlative nearby strata indicate an age of approximately 20 Ma (early Miocene) for its occurrence. The new species represents a well preserved holotype and a poorly preserved specimen. This new species represents the southernmost occurrence of Muracypraea Woodring, 1957, and indicates a dispersal into waters of austral-coastal upwelling environments. The new species also shares a neritic habitat with endemic molluscan taxa and taxa ranging northward from the Navidad Basin of central Chile (DeVries and Frassinetti, 2003). Its occurrence at 15°S also accentuates the modern-day diminishment of the range of Muracypraea since the early and middle Miocene, because M. coffeae (Linnaeus, 1758), the last living representative of the genus, is restricted to the southwestern Caribbean coasts of Venezuela and Colombia (Lorenz and Hubert, 2000).

STRATIGRAPHY AND AGE

The Pisco Basin is a forearc basin that extends along the narrow coastal plain of southern Peru from Paracas to Nazca, Ica Department (Figure 1). Figure 2 indicates the type locality of the new species. Cenozoic marine beds are exposed throughout the coastal desert, including those of the upper Oligocene to middle Miocene Chilcatav Formation and the overlying lower middle Miocene through middle upper Pliocene Pisco Formation (DeVries, 1998).

CHILCATAV FORMATION

The name Chilcatav Formation was assigned to upper Oligocene to lower Miocene strata near Pampa Chilcatav, approximately 60 km west of Ica, by Dunbar et al. (1980). The Chilcatav Formation consists of basal sandstones associated with a transgression and seafloor cooling at approximately 25 Ma (DeVries, 2001). Tuffaceous sediments and diatomaceous siltstone indicative of shelf depths and a coastal-upwelling regime (Dunbar et al., 1990), and intercalated coarse-grained sandstone that may represent short-lived early Miocene eustatic sea-level events (DeVries, 1998). MacHaré and Fourtanier (1987) estimated the stratigraphic thickness of the Chilcatav Formation at approximately 250 m.

PISCO FORMATION

Unconformably overlying the Chilcatav Formation is the Pisco Formation of Adams (1909), named for steeply dipping, white and yellowish rocks exposed at the end of the Huarmán bridge over the Rio Pisco north of Pisco, Peru. Dunbar et al. (1990) reported that the age of the Formation is late middle Miocene through Pliocene (4–12 Ma), based on K/Ar dates combined with siliceous microfossil zonation, whereas DeVries and Schrader (1997), DeVries (1998), and DeVries and Frassinetti (2003) assigned an early middle Miocene to middle late Miocene age to this unit. It consists of tuffaceous sandstones and shales, with occasional conglomerates, with a thin (less than 0.5 m) lower Miocene age diatomaceous siltstone and the overlying middle Miocene age diatomaceous siltstone and tuffaceous sediments, and is thus distinct from the Chilcatav Formation.
Pliocene age to the bioclastic conglomerates, tuffaceous siltstones, and diatomaceous siltstones based on diatom biostratigraphy and their revised molluscan biostratigraphy. The formation varies in thickness throughout the Pisco Basin from about 200 to 1000 m thick (Dunbar et al., 1990).

Abbreviations: Abbreviations used for institutional catalog and/or locality numbers are as follows: DV, collecting localities of Thomas J. DeVries; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Measurement parameters are defined as follows: length = greatest distance between anterior and posterior termini, width = greatest distance between lateral margins, and height = greatest distance between base and dorsum. The systematic classification herein follows that of Schilder and Schilder (1971) with modifications by Kay (1996).

**SYSTEMATIC PALEONTOLOGY**

Superfamily Cypracinae Rafinesque, 1815
Family Cypracidae Rafinesque, 1815
Subfamily Bernayinae Schilder, 1927
Genus *Murraycypraea* Woodring, 1957

**Type Species:** *Cypraea mus* Linnaeus, 1758, by original designation. Recent, Venezuela and Colombia.

**Diagnosis:** Medium to large size, pyriform or triangular shaped; posterior portion of dorsal surface smooth, warty, or bituberculate, or rarely a central "spike-like" dorsal tubercle present; labial lip wide, slightly constricted near anterior end, teeth moderately strong; columella wide, teeth strong to weak or absent; aperture wide, curving in posterior direction toward columella; fossula indistinct, wide, shallow, smooth; anterior terminal ridges strong and may extend forward in a flattened or flange-like manner; terminal canals prominent.

**Geologic Range:** Early Miocene (Aquitainian) to Recent.

**Figure 1.** Index map showing location of the Pisco Basin in southern Peru and chronostratigraphy of the Pisco Basin (DeVries and Schrader, 1997).

**Figure 2.** Index map showing the type locality of *Murraycypraea ornata* new species at Ullujalla West (LACMIP loc. 17783), and locality DV 553-1 (LACMIP loc. 17615). Dashed lines indicate roads.
Geographic Range: Miocene: Dominican Republic, Haiti, Trinidad, Cuba, Jamaica, Venezuela, Colombia, Panama, Brazil, Ecuador, Peru, Costa Rica, Michoacán, Mexico, and Baja California Sur, Mexico; Miocene/Pliocene: Imperial County, California, USA; Pliocene: Venezuela, Panama, Ecuador; Pleistocene: Venezuela; Recent: Venezuela and Colombia.

Remarks: In a monograph of the Miocene Gatun Formation of Panama, Woodring (1959) acknowledged the variability of Muracypraea henekeni (Sowerby, 1850) and the excess of names applied to this species. He stated that “some of the names in the synonymy may prove to be useful for local populations when adequate samples are available.” Groves (1997) reviewed the cypraeiform gastropods of northwestern Ecuador and discussed the stratigraphic and geographic distribution of the M. henekeni group in Panama, Ecuador, and Colombia. Groves (1997, 1998) proposed that a distinctly rhomboidal, bituberculate lineage be recognized in the western Caribbean and tropical eastern Pacific that included specimens previously assigned to M. henekeni (Marks, 1951; Olsson, 1964), as well as the Pliocene Ecuadorian species M. cayapa (Pilsbry and Olsson, 1941).

**Muracypraea ormenoi** new species

(Figures 3–5)

Diagnosis: A medium-sized Muracypraea of weakly rhomboidal shape; outer lip extended posteriorly well beyond inner lip; dorsum bituberculate with posteromedia1 depression.

Description: Shell medium in size; slightly rhomboidal shape; dorsum moderately arched, maximum height (apex) slightly posterior to midpoint; base slightly flattened; surface generally smooth; lateral margin of right
side weakly corrugated ventrally; dorsum with broad, low tubercles; tubercle on labral side situated axially between apex and periphery; tubercle on columellar side smaller and situated slightly more posteriorly and closer to axial median; medial tubercle at apex absent or broken; medial posterior depression present between tubercles; aperture moderately wide, curved strongly posteriorly toward columella; outer lip extending posteriorly beyond inner lip; outer lip with 17 short simple teeth; columella with about 13 short weak simple teeth, fading posteriorly; denticles interstices smooth; terminal ridge not visible; fossula narrow, mostly covered; siphonal canal long, bordered by spatulate extensions of columella and outer lip; terminal canals moderately extended, very weakly rimmed.

**Comparison:** The new species is most similar to Woodring’s (1959) hypotype of Cypraca (Muracypraca) huenecui [= Muracypraca mus sthlnica (Schulker, 1927)], USNM 562603 (pl. 31, figs. 6–7) from the upper Miocene Catum Formation of Panama. *Muracypraca ormenoi* has fewer columellar teeth, a less inflated columella, deeper terminal canals, and is not as highly arched as *M. mus sthlnica*. Color pattern aside, when compared to several specimens of the Recent *M. mus bicornis* (Sowerby, 1870) [LACM 90–471 (LACM Malacology collection); see also Lorenz and Hubert, 2000, pl. 1, figs. 11, 16, 19], we note a striking similarity in overall morphology between *M. mus bicornis* and the new species. However, the new species has a more inflated columella, fewer columellar teeth, and deeper terminal canals than *M. mus bicornis*. *Muracypraca angustirima* (Spiecker, 1922), the other Peruvian muracypracidae species, from the early to middle Miocene Zorritos Formation of Tumbos Department, northern Peru, lacks the dorsal tubercles, has a straighter aperture, has more columellar teeth, and has a more inflated columella than the new species.

**Discussion:** *Muracypraca ormenoi* is the first cypracid reported from the Pisco Basin. Although post-burial processes have damaged the mid-dorsal and the posterior dorsal surfaces and the anterior columellar terminal ridge of the holotype of the new species, preservation is adequate for unequivocal generic assignment. The non-type specimen is a poorly preserved specimen consisting of three fragments, including labral and columellar lips and several internal whorls within matrix. Some mollusks associated with *M. ormenoi* in Peru range southward to the Miocene Navidad Basin of central Chile (Table 1; DeVries and Frassinetti, 2003). Other species associated with *M. ormenoi* range northward to the Talara Basin of northern Peru, situated at the same low latitudes where warm sea surface temperatures help define the modern Panamic Faunal Province. Despite the warm-water environment indicated by the southern Peruvian Miocene faunas, sedimentological indicators including diatomaceous siltstone, synsedimentary horizons of remobilized dolomite, and phosphatic concretions (DuBose et al., 2000) point to the existence of high primary productivity along the southern Peruvian margin during the early and middle Miocene. Then, as now, the impetus for high primary production and would have been coastal upwelling. Upwelled waters were probably cooler than surface waters, but temperatures may still have been more elevated at present, since the world’s oceans were warmer during the early Miocene, as well (Savin et al., 1985; Lourens et al., 2004).

**Material:** *Muracypraca ormenoi* new species is represented by the moderately well-preserved holotype from the upper Oligocene to lower Miocene Chilca Bay Formation and an incomplete specimen from the overlying lower middle Miocene to upper Pliocene Pisco Formation. The non-type specimen (LACMIP no. 13070) was collected by the senior author in June, 1987, near Cerro Submarino, east of Yesera de Amara, Ica Department.

**Table 1.** Mollusks from the Chilcatay and lowermost Pisco formations of southern Peru associated with *Muracypraca ormenoi* new species and their occurrence in depositional basins to the north and south.

<table>
<thead>
<tr>
<th>Species</th>
<th>Talara Basin Northern Peru</th>
<th>Navidad Basin Central Chile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthina katzi (Fleming, 1972)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Eucrassatella ponderosa (Philippi, 1857)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Ficus distans (Sowerby, 1846)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Glycymeris colelaginae (Hupé, 1854)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Glycymeris ibariformis (Frassinetti and Covacevich, 1984)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Miliola vidali (Philippi, 1857)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Oltacostaria chancophila (Duclos, 1835)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Testellum crepa (Sowerby, 1846)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Architectonica karsteni (Rutsch, 1934)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Chionopsis sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Conus spp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Dosinia sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Gonyscyon sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Phagdonites sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Terebran sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Turrilitella woodsii (Lisson, 1925)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Turrilitella infravirginata (Gryzowski, 1899)</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
Peru (14°34'26"S, 75°40'30"W) [DV 553–1, = LACMIP loc. 17615]

**Type Material:** Holotype LACMIP no. S197, 64.9 mm in length, 48.3 mm in width, 31.9 mm in height. Collected in October 2004 by Manuel Ormeño, Ocucaje, Peru.

**Type Locality:** LACMIP loc. 17783, between Yecora de Amara and the Rio Ica, less than one km north of Cerros Las Tres Pyramids [herein designated Ullatalla West] (about 14°34'50" S, 75°38'40" W; Lonnitis 1:100,000 quadrangle), Ica Department, southern Peru, upper Oligocene to lower Miocene Chilcatay Formation (Figure 2).

**Etymology:** Named after Manuel Ormeño who collected the holotype and was one of the principal field workers employed by Mario Urbina.

**ACKNOWLEDGMENTS**

We wish to thank Rodolfo Salas of the Universidad Nacional Mayor de San Marcos, Museo de Historia Natural, Laboratorio de Vertébrados, Lima, Peru, and Dr. Niels Valdés, director of the museum, for their support of invertebrate paleontology in Peru. We also thank James H. McLean and Ángel Valdés (LACM Malacology), Louella Saul (LACMIP), and Richard L. Squires (California State University, Northridge, Geological Sciences) for reviewing early drafts of the manuscript and offering helpful suggestions. The evaluations of Charles L. Powell, II (U.S. Geological Survey, Menlo Park, CA) and Robert J. Stanton (LACMIP) greatly enhanced this paper. Donald W. McMumie (LACM Research Library) assisted the second author in locating several obscure references. Additional thanks to Ángel Valdés for his generous assistance with the manipulation of digital images.

**LITERATURE CITED**


The status of unionid and dreissenid mussels in northwestern Pennsylvania inland lakes

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ABSTRACT

A survey of the native unionid fauna of the eight natural lakes in the glaciated region of northwestern Pennsylvania suggests that the documented species richness of regional lotic habitats cannot be extended to lentic habitats. Richness ranged from 0 to 5 species per lake, and population densities (<0.03 individuals/m\(^3\)) are low. The most frequent and abundant species were Pyganodon grandis and Utterbackia milthecellis, each occurring in five lakes, and making up 50% and 15% respectively of all unionoids collected. Two of the lakes have been successfully colonized by Dreissena polymorpha, with evidence of an unsuccessful introduction in a third. In Sandy Lake, 78% of the unionoids were fouled by Dreissena, with an average density of 271 Dreissena/unionid. Although none of the seven species of native unionoids found in this survey are regionally endangered, the prognosis for lake populations is poor.

Additional Keywords: Unionsids, zebra mussels, Pennsylvania lakes, Corbicula, Dreissena.

INTRODUCTION

With a historical richness of 292 species of Unionidae and five species of Margaritiferae, North America’s freshwater mussel richness (superfamily Unionoidea) is five times greater than that of any of the other continents (Bogan, 1993; Williams et al., 1993; Lydeard et al., 2004). However, as part of a worldwide pattern of decline in many non-marine mollusks, this fauna is declining rapidly and much faster than the continent’s mammal or bird fauna (Williams et al., 1993; Lydeard et al., 2004). The National Heritage Network lists 202 species that are presumed extinct, imperiled or vulnerable (Lydeard, 2004), and the Endangered Species Act recognizes that 13 species in the U.S. have gone extinct and that another 70 are threatened or endangered (U.S. Fish and Wildlife Service, 2005).

Potential reasons for these declines include siltation; release of toxic effluents from industrial, municipal, and nonpoint sources; channel modification; damming; heavy metal and pesticide bioaccumulation; anoxia due to anthropogenic eutrophication; a history of commercial exploitation; and the introduction of invasive species, particularly the zebra and quagga mussels (Dreissena polymorpha (Pallas, 1771) and Dreissena bugensis (Andrusov, 1897)) (Nalepa et al., 1991; Bogan, 1993; Coumou et al., 1993; Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994; Ricardi et al., 1996; Schloesser et al., 1998; Poole and Downing, 2004).

It is unclear how this loss of unionid richness and biomass will affect ecosystem function; burrowing bivalves have the potential to play important roles in many benthic and pelagic processes but these roles have gone largely understudied (Vaughn and Hakenkamp, 2001). However, rapid declines have focused recent attention on many facets of mussel biology. Researchers are working to better understand unionid life histories, distribution patterns, and taxonomy so that conservation efforts may be more effective. Part of this work involves taking inventory of current mussel diversity and distribution in various locales and focusing attention on conservation “hotspots”—places that are likely to harbor relatively high diversity.

The Pennsylvania portion of the Ohio River watershed is one of these “hotspots.” Before the recent wave of extinctions there was a relatively rich fauna of 53 species in this drainage (Bogan, 1992). Twelve species have been extirpated from the area, but 41 remain, including two federally endangered species Epiphrasna torulosa rangii (Lea, 1838) and Pleurobema clava (Lamarck, 1819) (Pennsylvania Biological Survey, 2003). Because of this relatively high richness, unionoid populations in the lotic waters of Pennsylvania’s Ohio River drainage have received considerable attention from such groups as the French Creek Project (Meadville, Pennsylvania), The Nature Conservancy, and the Western Pennsylvania Conservancy (Pittsburgh, Pennsylvania).

In contrast, the lentic waterbodies within Pennsylvania’s Ohio River drainage have received much less atten-
tion. It is possible that these lakes harbor some of the region's mussel diversity since several of them flow into French Creek, a particularly unionid-rich tributary of the Allegheny and Ohio Rivers. French Creek harbors 27 species of unionids, including Epioblasma torulosa ranigiana and Pleurobema clava.

These lakes are also at risk for dreissenid colonization because of active recreational boat traffic in the area, and close proximity to Lake Erie and to each other. If successfully colonized by dreissenids, these lakes could serve as reservoirs from which dreissenids could then travel to other waterbodies either by going downstream via passive means or by going overland via human transport. Thus, successful dreissenid colonization could negatively affect regional unionid diversity as it did in many other drainages (Gillis and Mackie, 1994; Schloesser and Xalapa, 1994; Ricciardi et al., 1996; Schloesser et al., 1998).

In light of the potential threat of dreissenid colonization of these lakes and the current and historical levels of regional unionid diversity, we sought to accomplish the following goals: 1) Provide a benchmark assessment of unionid richness and density in the natural lakes of northwestern Pennsylvania and 2) Determine the extent of successful dreissenid and any other invasive maldusk colonization.

STUDY AREA

Natural lakes in northwestern Pennsylvania are limited to a relatively small glaciated region (approx. 9200 km²) that includes all of Erie, Crawford, and Mercer counties, and small portions of adjacent counties. Within this region there exist 8 kettle lakes at elevations between 300 and 400 m above sea level (Figure 1). The lakes range in size from 6 to 37.8 ha, and are all between 20 and 50 km from the south shoreline of Lake Erie. However, all discharge to the south into the Ohio-Mississippi river drainage. Calcareous glacial deposits dominate the surface geology, and dominant land cover is mixed forest and agriculture. As a consequence, the lakes have moderately hard water, are mesotrophic to eutrophic, and undergo periodic deep-water anoxia during the summer months. All are headwater lakes, and most are drained by permanent streams that allow for easy dispersal of aquatic organisms. The single exception is Edinboro Lake that was enlarged by the construction of a 3 m hydraulic dam in the 19th century. Discharges from Canadota and Conneaut lakes are also regulated to prevent ice damage to docks, but the outlets are unimpeded between October and May. Physical and chemical characteristics of the lakes are shown in Tables 1 and 2.

MATERIALS AND METHODS

A census of between 15 and 20 quadrats (7.6 x 1.5 m) took place in each of the eight lakes between August and October 2002. Three to four locations were chosen in each lake to capture nearshore physical habitat variation. For example, if a lake had sandy, rocky, and weedy areas, all three were sampled. At each location, five quadrats were established—one from each of the following depth intervals: 0-0.6 m, 0.7-1.2 m, 1.3-1.8 m, 1.9-2.4 m, and 2.5-3.0 m. In most cases, the nearshore substrate conditions gave way to finer substrata as depth increased.

Quadrats were delineated with nylon rope string between PVC pipe "stakes" that were pushed vertically into the sediments or placed flat on impenetrable substrata such as rock. Using the nylon ropes as visual and tactile guides, a diver manually probed the substrate to a depth of about 5 cm for bivalves. Each quadrat was searched twice.

In quadrats with exceptionally high densities of dreissenids a 1.5 x 0.6 m sub-quadrat was delineated. For dreissenids, we tallied the number of live individuals. For unionids, we tallied both live and recently dead individuals of all species. Recently dead unionids were those whose valves could be paired and identified to species. Total unionid and dreissenid densities were recorded as individuals/m². Where unionids were fouled with dreissenids, the number of dreissenids per unionid was also recorded.

Bivalves were identified to species level using Bogan (1992), Strayer and Jirka (1997), Parmalee and Bogan (1998), and Cummings and Mayer (1992). Nomenclature follows Turgeon et al. (1998).

In addition to quadrats described above, littoral sub-
Table 1. Physical characteristics of northwestern Pennsylvania lakes. (Current bathymetric maps for Lake LeBoeuf and Sandy Lake are unavailable.)

<table>
<thead>
<tr>
<th>Lake</th>
<th>Location</th>
<th>Area (ha)</th>
<th>Drainage basin area (km²)</th>
<th>Max depth (m)</th>
<th>Mean depth (m)</th>
<th>Outflow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canadohta</td>
<td>41°48.91'N, 79°50.29'W</td>
<td>68</td>
<td>20.3</td>
<td>13.6</td>
<td>5.5</td>
<td>Oil Creek</td>
</tr>
<tr>
<td>Conneaut</td>
<td>41°37.5'N, 80°18.3'W</td>
<td>378</td>
<td>72.3</td>
<td>19.8</td>
<td>5.6</td>
<td>Conneaut Outlet to French Creek</td>
</tr>
<tr>
<td>Crystal</td>
<td>41°33.21'N, 80°22.14'W</td>
<td>6.1</td>
<td>0.28</td>
<td>7.1</td>
<td>3.3</td>
<td>Crooked Creek to Shenango River</td>
</tr>
<tr>
<td>Edinboro</td>
<td>41°52.78'N, 80°06.22'W</td>
<td>167</td>
<td>65.7</td>
<td>9.1</td>
<td>3.4</td>
<td>Conneaut Creek to French Creek</td>
</tr>
<tr>
<td>LeBoeuf</td>
<td>41°55.61'N, 79°58.96'W</td>
<td>32.2</td>
<td>158.6</td>
<td>9.1</td>
<td>—</td>
<td>LeBoeuf Creek to French Creek</td>
</tr>
<tr>
<td>Pleasant</td>
<td>42°00.22'N, 79°53.85'W</td>
<td>23.7</td>
<td>3.6</td>
<td>13.7</td>
<td>6.8</td>
<td>Lake Pleasant Outlet to French Creek</td>
</tr>
<tr>
<td>Sandy</td>
<td>41°20.71'N, 80°06.43'W</td>
<td>85.5</td>
<td>7.2</td>
<td>11.4</td>
<td>—</td>
<td>Unnamed stream to Sandy Creek</td>
</tr>
<tr>
<td>Sugar</td>
<td>41°33.94'N, 79°56.75'W</td>
<td>31</td>
<td>56.4</td>
<td>5.5</td>
<td>3.2</td>
<td>Lake Creek to French Creek</td>
</tr>
</tbody>
</table>

habitats less than 1.8 m in depth were further sampled for benthic macroinvertebrates. This was done to improve the likelihood of finding invasive mollusks at low densities or with small body sizes. We sampled in sandy, rocky, and weedy littoral sub-habitats, although not all of these sub-habitats were present in each lake. Depending on the number of sub-habitats present, the total number of areas sampled per lake ranged from 8–17. We used steel drop boxes (0.125 m² and 0.25 m²), on fine-medium-grained and cobble substrates, respectively) and a corer (0.025 m², where the roots of a species of Nuphar precluded sampling with the drop boxes). The substrate isolated by drop boxes was swept 6 times with a 900 µm mesh D-net. Catches from replicate sweeps in each drop box sample were washed and pooled. Core samples were taken to a depth of 10 cm and were similarly washed. The material was sorted in the laboratory from white trays. Any invasive mollusks were identified using the sources mentioned above and Jokinen (1992). Densities were expressed as individuals/m² substrate.

Voucher specimens of the species examined in this study are deposited in the Section of Mollusks at the Carnegie Museum of Natural History, Pittsburgh, as follows:

Actinonaias ligamentina: CMNH 74451; Lampsis siliquoidea: CMNH 74452; Utterbackia imbecillis: CMNH 74453; Pyganodon grandis: CMNH 74454; Lasmigona complanata: CMNH 74455; Liguina recta: CMNH 74456.

RESULTS

NATIVE UNIONIDS

A survey of the eight natural lakes resulted in a list of seven species of native unionids (Table 3). Pyganodon grandis (Say, 1829) was both the most broadly distributed, occurring in 5 of the lakes, and the most abundant, making up half of the individuals collected in all lakes. In New York State, there has been difficulty surrounding the taxonomy and identification of the closely related species Pyganodon cataractae, P. grandis, and P. laevis (Strayer and Jirka 1997). However, according to Strayer and Jirka (1997) and Strayer (Institute of Ecosystem Studies, personal communication, 2003), P. grandis is the only one of these three species to occur in the Ohio basin. Therefore, all Pyganodon collected in this study were identified as P. grandis even if the beak sculpture was obliterated or damaged and could not be used as a definitive identifying character. Utterbackia imbecillis (Say, 1829) was found in five of the lakes, but it made up less than 15% of all individuals collected. Lampsis siliquoidea (Barnes, 1823) was found in two lakes, and Liguina recta (Lamarck, 1819), Lasmigona complanata (Barnes, 1823), Actinonaias ligamentina (Lamarck, 1819), and Ambilona phicata (Say, 1817) were each found in only one lake. Lake LeBoeuf had the highest species richness with five species. No mussels were found in Crystal Lake.

In the 5 lakes where live unionids were present, they were found in low densities ranging from 0.01 individuals/m² in Conneaut Lake to only 0.03 individuals/m² in Canadohta Lake. In Pleasant and Sugar Lakes only valves were found. Unionid distributions and densities are shown for each lake in Tables 3 and 4.

DREISSENSIDS AND OTHER INVASIVE MOLLUSKS

All dreissenids in this study were identified as Dreissena polymorpha based on morphological characteristics outlined by Pathy and Mackie (1993) and confirmed by Mackie (University of Guelph, personal communication, 2003).

Living zebra mussels (D. polymorpha) were found only in Edinboro Lake and in Sandy Lake. In Edinboro
Table 2. Chemical characteristics of northwestern Pennsylvania lakes. P = phosphorus.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Spring total P (µg/L)</th>
<th>Carlson's trophic state index</th>
<th>Total alkalinity (mg/L)</th>
<th>Total dissolved solids (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canadota</td>
<td>26.9</td>
<td>52</td>
<td>39.0</td>
<td>80</td>
</tr>
<tr>
<td>Conneaut</td>
<td>18.6</td>
<td>46</td>
<td>73.0</td>
<td>120</td>
</tr>
<tr>
<td>Crystal</td>
<td>22.8</td>
<td>49</td>
<td>61.5</td>
<td>130</td>
</tr>
<tr>
<td>Edinboro</td>
<td>30.1</td>
<td>53</td>
<td>67.0</td>
<td>150</td>
</tr>
<tr>
<td>LeBoeuf</td>
<td>47.5</td>
<td>60</td>
<td>73.5</td>
<td>110</td>
</tr>
<tr>
<td>Pleasant</td>
<td>35.8</td>
<td>56</td>
<td>95.5</td>
<td>140</td>
</tr>
<tr>
<td>Sandy</td>
<td>13.6</td>
<td>42</td>
<td>66.5</td>
<td>140</td>
</tr>
<tr>
<td>Sugar</td>
<td>41.2</td>
<td>58</td>
<td>37.0</td>
<td>70</td>
</tr>
</tbody>
</table>

Lake, the mean density of *D. polymorpha* was 52 individuals/m² (s.e.=48) and the mean density in Sandy Lake was 442 individuals/m² (s.e.=137). *Dreissena polymorpha* was densely aggregated on scattered submerged wood, rocks, and on the shells of native unionoids. In Edinboro Lake, approximately 21% of the live unionoids and paired valves were fouled with *D. polymorpha* and an additional 42% had been recently fouled as evidenced by attached byssal threads. The average density of fouling *D. polymorpha* in Edinboro Lake was 1.4/unionoid (s.e.=1.1). In Sandy Lake, 78% of the live unionoids and paired valves were fouled with *D. polymorpha*, and an additional 22% had byssal threads only. The average density of fouling *D. polymorpha* here was 271/unionoid (s.e.=87).

The drop boxes yielded *D. polymorpha* valves in two other lakes. In Lake LeBoeuf shells were found in an artificially sandy area along the northwestern shore and probably were transported to the lake in beach sand dredged and imported from Lake Erie. In Canadota Lake, a few valves were found near the Pennsylvania Fish and Boat Commission access point. Prior to this study, several live *D. polymorpha* were found at this same location in 2001. These individuals probably represent a failed introduction inadvertently brought in by recreational boaters.

The drop box samples also revealed the invasive Asiatic clam, *Corbicula fluminea* (Müller, 1774), in Conneaut and Sandy Lakes. Like *Dreissena polymorpha*, the distributions were highly aggregated with mean densities in the two lakes of 454 (s.e.=251) and 216 (s.e.=87) individuals/m², respectively. In addition, the invasive snail *Cipangopaludina chinensis* (Reeve, 1863) was found in drop box samples from Canadota Lake and Lake Pleasant.

**DISCUSSION**

The unionid assemblages in northwestern Pennsylvania's natural lakes are species-poor and low in density when compared to the unionid assemblages in the region's rivers and streams. This stream fauna is also unique in that it contains endangered species such as *Pleurobema clava* and *Epioblasma torulosa rangiana*. In contrast, all of the taxa in our study lakes are ranked globally as "secure, common" by the Heritage ranking system and none have been granted special status under federal law or Pennsylvania code (NatureServe, 2005). In terms of within-state rankings by non-legislative groups, *P. grandis, U. imbecillus, L. siliquoidea, A. ligamentina* and *L. recta* all have Heritage state ranks of "secure" or "secure/vulnerable" (NatureServe, 2005) and have no state according to the Pennsylvania Biological Survey (2003). However, *L. complanata* has a Heritage state rank of "critically imperiled" (NatureServe, 2005) and is considered endangered in the state by the Pennsylvania Biological Survey (2003). Similarly, *A. plicata* has a Heritage state rank "imperiled" (NatureServe, 2005) and is considered threatened in PA by the Pennsylvania Biological Survey (2003).

It is difficult to determine if these two taxa of local concern (*L. complanata* and *A. plicata*) or any of the other taxa we found represent self-sustaining populations within our study lakes. Downing et al. (1993) found that in Lac de L'Achigan, Québec, complete fertilization failure occurs when *Elliptio complanata* (Lightfoot, 1786) is found at densities less than 10/m². In our study area, the density of all living unionoids is less than 0.03/m² and much lower for a given species, thus, successful sexual reproduction is unlikely. On the other hand, Strayer et al. (1981) found similar low densities of *Elliptio complanata* (0.032 individuals/m²) in oligotrophic Mirror Lake, and the size distribution of individuals there suggest regular recruitment. Frequent hermaphroditism may facilitate species survival in such low-density populations.

Past and present human impacts on unionid fauna of these lakes are possible since these waterbodies have

Table 3. Native Unionid species recorded from northwestern Pennsylvania lakes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Canadota</th>
<th>Conneaut</th>
<th>Crystal</th>
<th>Edinboro</th>
<th>LeBoeuf</th>
<th>Pleasant</th>
<th>Sandy</th>
<th>Sugar</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pyganodon grandis</em></td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td><em>Utterbackia imbecillus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Lampsilis siliquoidea</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Lasionigra complanata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Actinonaias ligamentina</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Ligumia recta</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Ambigonia plicata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total number of species</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 4. Densities of live unionids and paired valves. All densities are individual per m². Values in parentheses are standard errors.

<table>
<thead>
<tr>
<th></th>
<th>Canadota</th>
<th>Conneaut</th>
<th>Crystal</th>
<th>Edinboro</th>
<th>LeBoeuf</th>
<th>Pleasant</th>
<th>Sandy</th>
<th>Sugar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live unionids</td>
<td>0.030</td>
<td>0.011</td>
<td>0</td>
<td>0.029</td>
<td>0.014</td>
<td>0.023</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>(0.011)</td>
<td>(0.008)</td>
<td>(0.018)</td>
<td>(0.014)</td>
<td>(0.018)</td>
<td>(0.010)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paired empty valves</td>
<td>0.017</td>
<td>0</td>
<td>0</td>
<td>0.050</td>
<td>0.030</td>
<td>0.029</td>
<td>0.090</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>(0.012)</td>
<td>(0.008)</td>
<td>(0.014)</td>
<td>(0.019)</td>
<td>(0.028)</td>
<td>(0.008)</td>
<td>(0.014)</td>
<td>(0.011)</td>
</tr>
<tr>
<td>Combined</td>
<td>0.017</td>
<td>0.011</td>
<td>0</td>
<td>0.109</td>
<td>0.075</td>
<td>0.011</td>
<td>0.040</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>(0.019)</td>
<td>(0.008)</td>
<td>(0.019)</td>
<td>(0.039)</td>
<td>(0.028)</td>
<td>(0.008)</td>
<td>(0.014)</td>
<td>(0.011)</td>
</tr>
</tbody>
</table>

been subject to a variety of alterations such as cultural eutrophication, lakeshore development, fish stocking, water level modification, etc. However, it is difficult to ascertain whether the current density, richness, and taxonomic composition are typical for small, nutrient-rich lakes or if they represent the types of declines in richness/diversity and the alterations in taxonomic composition that have occurred in many unionid assemblages across the continent (e.g., Nalepa et al., 1991 on pre-Dreissena unionid declines in Lake Erie). Unionid densities in other small lakes (e.g., small Adirondack lakes, personal observation) can be much higher than found in our study area, but richness may naturally be low. For example, Strayer and Jirka (1997) found that small lakes in New York State usually contain five species or fewer. While we have some anecdotal basis for comparison, we lack models that predict unionid species richness or abundance for lotic systems. Predictors of lotic unionid richness that are potentially worth exploring include fish species richness and the area of oxygenated lake bottom (see Watters (1992) for an exploration of similar predictors in lotic systems).

Another way to assess the current status of unionidae in PA’s lakes would be to draw comparisons between past and present. We searched for historical records of the freshwater mussel fauna in these lakes from the Cleveland Museum of Natural History (Cleveland, Ohio), the Carnegie Museum of Natural History (Pittsburgh, PA), and from documents by key mussel collectors, primarily A.E. Ortmann, who surveyed for the Carnegie Museum in the early 20th century. Specific documents searched included Ortmann (unpublished, 1909, 1911, 1919). These efforts yielded only species lists in Ortmann (unpublished), a few specimens in the physical collections at the Carnegie Museum, and a few records in the Carnegie’s electronic database. These bits of information summed to an early 20th century, anecdotal account for Conneaut Lake and Edinboro Lake (then called “Conneauette” Lake in Ortmann, unpublished). Thus, overall, the dearth of quantitative and taxonomically clear information on the past mussel fauna of our study area makes inferences regarding human impacts speculative at best.

In any case, whether due to natural factors or human impacts, unionid assemblages in the glacial lakes of northwestern PA are currently low in density and low in species richness and the establishment of zebra mussels is likely to cause density and species richness to become even lower. The average number of fouling zebra mussel unionid specimen in Sandy Lake is well over 100 and models by Ricciardi et al. (1995) predict that this degree of fouling will result in greater than 90% unionid mortality. Whereas the average number of fouling Dreissena polymorpha/unionid specimen was only 1.4 in Edinboro Lake, this number is probably not an accurate indicator of the overall degree of fouling. Winter drawdown has been used at Edinboro Lake to manage dreissenid populations (Grazio and Montz, 2002) and the lake was drawn down approximately 1.5 m during the winter prior to this study. Thus many of the zebra mussels that were fouling unionids in depths shallower than 1.5 m were killed due to exposure, leaving only byssal threads on 42% of our specimens (22% of the specimens were fouled by byssal threads only in Sandy Lake). However, below the drawdown level, zebra mussels persist in field densities up to 727 individuals/m² and thus are likely to keep fouling unionids even if periodic drawdown is successful in reducing D. polymorpha in shallow depths.

Because the unionids in these lakes possibly do not represent self-sustaining populations, it is unlikely that D. polymorpha-induced losses within these waterbodies will contribute to any further decrease in richness or abundance on a regional scale. However, the potential spread of D. polymorpha from the lotic waterbodies of northwestern PA to nearby unionid-rich lotic systems is a potential threat to regional diversity. In addition, while not necessarily a threat to unionid populations, the presence of Corbicula fluminea in Conneaut Lake and Sandy Lake (Strayer, 1998) and the invasive snail Cipangopaludina chinensis in Lake Pleasant and Canadota Lake highlights the need for continued public education as to the causes and potential impacts of the spread of invasive species.

ACKNOWLEDGMENTS

We would like to thank T. Pearce for generous access to the unionid collections of the Carnegie Museum. D. Strayer and G. Mackie for confirming our identifications, A. McMillen for her capable field assistance and Pennsylvania Sea Grant for financial support.

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Replacement names and type material: examples from Hertlein and Strong (1940–1951) and Keen (1958)

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ABSTRACT
There is a sharp distinction between replacing a preoccupied name and describing a new species that is a synonym of such a name. We cite some examples of where this distinction has been misinterpreted with regard to type material of Hertlein and Strong and Keen taxa.

INTRODUCTION
The purpose of this paper is to establish the status of type material for some eastern Pacific Mollusca. The taxa discussed were re-catalogued, with presumed loss of their status as primary types, occasioned by what we consider to be a misunderstanding of the provisions of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, herein ICZN) Article 72.7 (ICZN, 1980) and its predecessors in prior editions of the Code (ICZN, 1961; 1964: Article 72d; ICZN 1985: Article 72e). These articles treat the "types of replacement nominal species" (1961, 1964), "name-bearing types of nominal species-group taxa bearing replacement names" (1985), and "name bearing types of nominal species-group taxa denoted by replacement names (nomen nova)" (1999). The four editions of the Code have minor differences in wording, but their intent and effect are identical. The version now in effect is:

72.7. Name-bearing types of nominal species-group taxa denoted by replacement names (nomen nova). If an author proposes a new species-group name expressly as a replacement (a nomen novum) for an earlier available one, then the two names are objective synonyms; both of the nominal taxa have the same name-bearing type despite any simultaneous restriction or application of the new replacement name (nomen novum) to particular specimens or any contrary designation of type, or any different taxonomic usage of the new replacement name. [emphasis supplied]

The key provision of this Article in all three editions of the Code, with only minor differences in wording, applies only to names proposed expressly as replacement names. There is an important distinction between proposing a replacement name and re-describing a species for which there is no available name that can be used, and it is the failure to appreciate that distinction that necessitates this paper.

If a species name is found to be preoccupied and there is no available synonym, a worker discovering that fact has two options:

1. The taxon can simply be renamed (nomen novum) with a simple statement such as "this name is proposed to replace the preoccupied _name_." Under this procedure nothing changes except that the replaced name becomes an objective synonym of the new name. The type material is identical for both the old and the replacement taxon, regardless of any contradictory statements.

2. The taxon can be described as if it were a new species, with types and type locality designated, with the former name that is a junior homonym becoming a synonym. In this case, the new taxon has the status of a new species with its own type material and locality, and the older name exists as a subjective synonym with its own type material, if any, and type locality. It is relevant only if at some future date it is discovered to not be conspecific with the newly proposed taxon.

There can be complications inherent in the first option, especially if the name to be replaced is from the old literature, and the location or even existence of type material is uncertain. Proposing replacement names for nomina for which there is incomplete information and/or no known type material was recently addressed by Rosenberg and Petit (2001). Description of a species as new provides accessible type material and other data. This procedure is often used when monographers wish to establish a firmer basis for the species involved than it would be possible by simple substitution for a new name.

Research Associate
The distinction between these two procedures is clear but, as with much systematic nomenclature, it can become clouded. Indeed, none of the four versions of the Code are completely clear for cases in which both the terminology (a) "new species" and (b) "replacement name" or "new name" are simultaneously present. However, the phrase "expressly as a replacement name" is a clear demarcation, especially the word "expressly" that appears in all versions of the applicable Article.

In each of the examples cited below, type material was set aside by the authors involved and catalogued as such, at the California Academy of Sciences for the Hertlein and Strong taxa and at Stanford University for the Keen taxa, with the latter subsequently transferred to the California Academy of Sciences [as CAS below] with the rest of the Stanford collection. Then, later, probably in the 1980s, all of the supposed type material was re-catalogued as non-type specimens.

Hertlein and Strong (1940–1951) and Keen (1958), in part motivated by the lack of type material on the West Coast and the difficulty either of visiting European or East Coast institutions or obtaining loans or photographs of type material, utilized a modification of homonym renaming. While stating that the motivation for their taxonomic actions was the presence of a situation of homonymy, they clearly stated their desire to propose new species with new type material. In other words, in the terminology of the Code published a few years later, they were trying to avoid having new taxa being interpreted merely as replacement names. Although their actions took place before the publication of the first of the "modern" Codes, the current Code makes clear that it and only it is the governing authority (ICZN 1999: Article 86.3). The notion of concern in this paper, and our judgment as to their type material, are:

**A. HERTLEIN AND STRONG PAPERS**

In their research on Panamic mollusks, Hertlein and Strong (1940–1951) found names they believed to be homonyms. In some cases discussed below, the names involved were mistakenly thought to be primary or secondary homonyms, raising different issues that are not discussed in detail here. The first two names below were proposed in a short note in *The Nautilus* written for the sole purpose of replacing the preoccupied names.

(1) *Lucina unduloides* Hertlein and Strong, 1945: 105.

"The species named *Lucina undata* by Carpenter ... requires a new name because of the prior use of that combination of names by Lamarck, 1819. The name *Lucina unduloides* is here proposed for the species described by Carpenter. Type in the California Academy of Sciences paleontology type collection, from Isthmus Cove, Espiritu Santo Island, Gulf of California."

The simultaneous designation of new type material and locality does not stand, and their type material does not have type status. It will elsewhere be demonstrated that this was not really a homonym in the first place and return to use of Carpenter's name for the eastern Pacific taxon will be recommended (Coan and Valentich-Scott, 2006, in preparation).

(2) *Tellina loria* Hertlein and Strong, 1945: 105.

"The combination of names, *Tellina panamensis* used by Li ... had already been used by Philippi in 1848. The name *Tellina loria* is here proposed for the species described by Li. Type in the California Academy of Sciences paleontology type collection, dredged off Mangleira Island, El Salvador, in the Gulf of Fonseca, in 16 fathoms."

As in the previous case, their new type material designation has no status as such. Moreover, the replacement name was unnecessary, because Li's species was originally spelled *T. panamensis*. (Li's species and Hertlein and Strong's replacement are both synonyms of *Tellina churruca* Haecky, 1844 [Coan and Valentich-Scott, prep.]).

In a series of papers on west Mexican mollusks published in *Zoologica*, Hertlein and Strong treated preoccupied taxa differently. The following seven examples (3–9) are different and in some cases more complex. Headings are as published.

(3) *Areta* (Areta) *fernandezensis* Hertlein and Strong, nom. nov.—(1943: 154)

This name was proposed as a replacement name for *Areta angulata* King and Broderip, 1832, non "Menschen, 1758" [an unavailable, non-binominal work]. We have not located an available use of *A. angulata* prior to 1832, concluding that this replacement was unnecessary, and that workers should return to the use of the King and Broderip name. It must be noted here that this new name is followed by the abbreviation "nom. nov.", (nomen novum), it is clearly a replacement name, and the authors did not attempt to designate new type material.

In six other cases, they referred to the new names as new species in addition to designating new type material.

(4) *Cardium (Americardia) guanacastense* Hertlein and Strong, sp. nov.—(1947: 140)

Their entry is headed "sp. nov." as shown. The shell is formally described in detail, with comparison and distribution, with new type material and a new type locality. In the discussion the authors stated "Sowerby's combination of names, *Cardium planicolatum*, has been used earlier by Sedgwick and Murichson; therefore a new name is required for *Cardium planicolatum* of Sowerby and the name *Cardium guanacastense*, based upon a type from Culebra Bay, Costa Rica, is here proposed."

The curatorial staff at the California Academy of Sciences decided that the type material had no type status, a determination here considered to be incorrect. However, as shown elsewhere (Coan, 2002), the homonym never existed and the correct name to use is *Americardia planicolatum* (G. B. Sowerby I, 1833).
(5) *Pitar (Pitarella) mexicanus* Hertlein and Strong, sp. nov.—(1948: 171)

This was also shown as a new species, with a complete description, comparisons, distribution and new type material and locality. In their discussion, the authors stated: "The species described as *Cytherea levis* by Conrad [1848] was referred to the genus "Pitaria" [= *Pitar*] by K. V. W. Palmer [1927]. This necessitates a new name for the west American species described under the name of *Pitar levis* by Pilsbry and Lowe [1932] and the name *Pitar mexicanus*, based on a specimen off Maldonado Point, Mexico, is proposed." The CAS staff determined that their type material had no type status.

(6) *Tellina (Moevella) recurvata* Hertlein and Strong, sp. nov.—(1949: 71)

Listed as a new species as shown, with a complete description, comparisons, distribution, and with new type material and locality. In this case, they only cited *Tellina (Augustus) recurvata* Dall, 1900, non Deshayes, 1855, in their synonymy. They did not use the words "new name", "replacement name", or "nom. nov." in their treatment. The CAS staff later determined that their type material has no type status.

(7) *Tellina (Merisca) proclives* Hertlein and Strong, sp. nov.—(1949: 83)

Treated as a new species, with a complete description, comparisons, distribution, and with new type material and locality. They said, "The use of the combination of names, *Tellina declivis* by Conrad, 1834, makes it necessary to propose a new name which is based on a new type specimen for the west American shell described under that name by Sowerby in 1868 which is here named *Tellina proclives*." (*Tellina proclives* C. B. Sowerby 1, 1868, proved to be a *Macoma* from another province; its actual provenance and identity with other taxa is as yet uncertain, and it is for the time being considered a *nonen dubium*.)

Hertlein (1968) later decided that this was the case of a replacement name, and he then named the eastern Pacific taxon *Tellina ulboana* based on the above type material. Depending on one's interpretation of this situation, the eastern Pacific taxon may now have two names, with Sowerby's unknown *T. declivis* remaining unreplaced, and it is that position that we endorse. This is an example of the dangers in simply renaming a junior homonym unless one can be positive about what exactly is being renamed! The CAS collection at present indicates that the type material of *T. proclives* has no type status under that name.

(8) *Lutrins mediamericanus* Hertlein and Strong, sp. nov.—(1951: 80)

Listed as a new species with a complete description, comparisons, distribution, and with new type material and type locality. They said, "The name *Turbinella castanea* was first proposed by Gray in 1839 for a shell which Melvill later referred to the synonymy of *Leneo-

zonie cingulifera* Lameck. . . . It therefore becomes necessary to propose a new name for Reeve's *Turbinella castanea* and the name *Lutrins mediamericanus* is here proposed." The staff at the CAS determined that their type material has no type status.

(9) *Muricopsis zeteki* Hertlein and Strong, sp. nov.—(1951: 85)

Listed as a new species, with a complete description, comparisons, distribution, and with new type material and locality. The chresonymy [a synonymy that includes misuses of names as well as true synonyms] begins with *Murix aculeatus* Wood, 1828, which is preoccupied by *M. aculeatus* Lamarck, 1822. Next listed is *M. dubius* Sowerby, 1841, which is a replacement name for *M. aculeatus* Lamarck. Hertlein and Strong stated that "The name *Murix dubius* which was applied to this species by Sowerby is not valid because that combination of names had already been applied to a different species by Dillwyn in 1817. We base the new name, *Muricopsis zeteki*, upon a specimen collected by Dr. James Zetek at Panama City, Panama." Nowhere is it stated that *Muricopsis zeteki* is a replacement name. However, the staff at the CAS determined that their type material has no type status.

B. Keen (1958)

Keen (1958) published a paper in which she named several new species because of underlying homonymy. In the abstract to that paper, it is stated that: "Six homonymous names are cited, of which four are replaced." In the Introduction to the paper, she said: "During the preparation of a handbook on tropical West American marine mollusks, it was perhaps inevitable that I should find a few homonyms, but I did not expect so many as six. . . . Therefore, the opportunity has been taken here to select new type specimens by treating the replacements not as mere new names but as new species. The new type specimens are deposited in museums that may be visited without the necessity of a trip abroad."

Each of her individual descriptions is clearly indicated as a new species description with the standard abbreviation n. sp. following each of the four new names. There were available synonyms for the other two of the homonyms she unearthed. The taxa are as follows:

(1) *Nuculana (Saccella) fastigata* Keen, n. sp.—(1958: 240)

*Nucula gibbosa* G. B. Sowerby I, 1833, non Fleming, 1828.

(2) *Adrana cultuata* Keen, n. sp.—(1958: 240)

*Nucula elongata* G. B. Sowerby I, 1833, non Bosc, 1801, non Defrance, 1825.

(3) *Macoma (Pomallama) clytriim* Keen, n. sp. (1958: 244)

*Tellina elongata* Hanley, 1844, non Dillwyn, 1823.
CONCLUSIONS

Our conclusion with regard to the last six examples from papers by Hertlein and Strong, and the four examples from Keen (1958) is that the clear intention of these authors was to propose new species. While they did so because they considered the only names available for these taxa to be preoccupied homonyms, they attempted to avoid their new taxa being interpreted as only being replacement names. The wording of their attempts to do so, in the absence of guiding Code language, may have been awkward in Hertlein and Strong papers, but the motivation is clear, and Keen’s intent is even more clearly expressed. Therefore, these taxa are, and should be interpreted as, new species and not replacement names, and the type material set aside by the authors should have type status. The types designated by the authors and currently in the collections of the CAS are here regarded as primary types.

As far as known now, this makes a difference on which name should be used only in the case of Tellina proctolvs, with that becoming the oldest name from the eastern Pacific taxon, rather than being a replacement name for a taxon from an unknown province.

We appreciate the advice of Gary Rosenberg and Rüdiger Bieler on this nomenclatural question.

LITERATURE CITED


Book Review

The Mollusks: A Guide to Their Study, Collection, and Preservation


Organizers and editors of books with many contributors will attest that it is not always easy to bring such projects to fruition. This may happen for distinct reasons. Different contributors will be inclined to allocate different levels of effort into the preparation of their chapters. Such unevenness may be enhanced when the book in question does not deal with cutting-edge research or alluring scientific breakthroughs. As a result of dissimilar levels of commitment from contributors, completion time and the depth at which subjects are treated may end up varying between the different chapters of the book.

Successful editors will be patient but persuasive, and must have a knack for inviting consistency and adding balance as one chapter flows into the next. In addition, as I know to be the case with the volume at hand, the budget for production and distribution may be very limited from the onset. If all these desiderati and parameters are brought into the equation, it is clear that Sturm, Pearce, and Valdés did a remarkable job in pulling together "The Mollusks," as I will try to show in this review.

The Mollusks aims to replace "How to Study & Collect Shells," a guide published in four editions between 1942 and 1974 by the American Malacological Union (AMU; now American Malacological Society, AMS). The concept for this new version of the AMU guide was to assemble a strong and diverse group of museum professionals, research malacologists, and serious collectors to contribute in different areas. As stated in the preface, the target audience will consist of “amateur and professional malacologists,” and the book shall “promote the educational mission of the American Malacological Society.”

Editor Sturm received the green light from the AMS council to proceed with the organization of the book during the 2000 annual meeting in San Francisco. In the few years that passed, some of the original contributors have left; new techniques in molluscan systematics were adopted; in particular those for sequencing and analyzing molecular data; the web, database technology, and digital photography grew by orders of magnitude and saw their status solidified as bona fide research tools. The resulting volume more than replaces the 1974 AMU guide. It consists of 445 pages (in contrast to 107 pages in 1974) of malacological information that may not be found in any other single publication. Twenty-nine contributors prepared 31 chapters covering topics from "Snorkeling and SCUBA Diving" to "Rearing Terrestrial Gastropoda," passing through "Donating Amateur Collections to Museums" and "Organizations, Meetings, and Malacology".

In addition to chapters on methods and techniques, the reader will find specific treatments of the seven main molluscan clades. There are chapters on "Aplacophora" (Amalie H. Scheltema), "Monoplacophora" (Clement L. Comts, III), "Polychaephora" (Enrico Schizhe and Andreas Wanninger), "Scaphopoda: The Tusk Shells" (Patrick D. Reynolds), and "Cephalopoda" (Frank E. Anderson). Gastropods are treated in four chapters, "Freshwater Gastropoda" (Robert T. Dillon, Jr.), "Terrestrial Gastropoda" (Timothy A. Pearce and Aydin Orstan), "Rearing Terrestrial Gastropoda" (Aydin Orstan), and "Marine Gastropoda" (Daniel L. Geiger), and bivalves in three ("Unionoida: Freshwater Mussels" (Kevin S. Cummings and Arthur E. Bogan), "Non-Unionoid Bivalvia" (Alexei V. Kornushin), and "Marine Bivalvia" (Eugene V. Coan and Paul Valenti-Scott).

Some contributions may be particularly valuable to collectors, collection managers, and biologists in general. "Archival and Curatorial Methods" (Charlie F. Sturm) discusses a plethora of data on problems that may arise when inadequate materials and preparations are involved in the curation of dry and preserved specimens. Sturm
provided a list of materials and suppliers that will prove handy both to amateur collectors and institutional collection managers. Two chapters on photography, "Digital Imaging: Flatbed Scanners and Digital Cameras" (Fabio Moretzsohn) and "Applied Film Photography in Systematic Malacology" (Daniel L. Geiger), better than adequately cover the topics with examples drawn from the authors’ obvious experiences. "The Molluscan Literature: Geographic and Taxonomical Works" (Sturm and collaborators) offers a brief overview of the malacological literature in which the main types of taxonomic works are discussed and a valuable list of regional publications provided. Other well-researched articles dealing with recent conceptual and methodological advances are "Computizing Shell Collections" (Gary Rosenberg), "Cladistics and Molecular Techniques: A Primer" (David Campbell), and "Issues in Marine Conservation" (Patrick Baker).

Are there any gaffes or omissions? Certainly, as one could expect from such a bold project. The resolution of halftone illustrations (known as "ruling" in typographical lingo) is very coarse, with evident loss of detail. In my copy of the book, a typo lingers in the title of Daniel Geiger’s article on “Applfield [sic] photography . . .”: I read “Monophacophora” on page 118, and “Xenoporidae” on page 120. I miss having access to a subject index at the end of the volume. Although I realize that the book is aimed at a very broad audience, I would have loved to see chapters on applications of electronic microscopy and georeferencing. At least some of these deficiencies and absences result from the need to keep production costs within budget, and I can appreciate that.

I am not proposing that this is the definitive tome on malacological techniques and methods because, now more than ever, techniques and methods change fast, rendering this type of guide obsolete at the blink of an eye (think digital imagery and techniques in molecular systematics, to cite only two examples). However, in preparation for inevitable obsolescence, the editors have assembled the book in a format that will easily lend itself to updates. If the editors, contributors, AMS, and the audience are willing to keep the project alive as demanded in fast-evolving times, then this will be the dynamic definitive guide. Until then, log onto the publishers site, get your copy, and encourage your colleagues, collecting buddies, librarians, and bookstore acquaintances to acquire and promote this great-value guide.

José H. Leal
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Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs, the Florida Arts Council and the National Endowment for the Arts.
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This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper)
John Slapcinsky

_Paryphanteopsis_ (Gastropoda: Pulmonata: Charopidae) from the Louisiade Archipelago of New Guinea ......................................... 119

Gerald E. Walsh

_Dordolochila_ lithica and _Dordolochila dorfeuilliana_ (Gastropoda: Polygyridae) in Arkansas, USA: morphology, distribution, and habitat .... 131

Brian F. Coles

_The Neogene history of Prisogaster_ Möreh, 1850 (Gastropoda: Turbinidae) in South America ............................................. 139

Thomas J. DeVries

_A new species of Hoplodoris_ Bergh, 1880 (Gastropoda: Opisthobranchia: Nudibranchia) from the Atlantic Ocean ............................. 150

Marta Dominguez

Frida Ben-Ami

_The Neocene history of Prisogaster_ Möreh, 1850 (Gastropoda: Turbinidae) in South America ............................................. 139

Francisco J. García

_The Neocene history of Prisogaster_ Möreh, 1850 (Gastropoda: Turbinidae) in South America ............................................. 139

Jesús S. Troncoso

_A new species of Hoplodoris_ Bergh, 1880 (Gastropoda: Opisthobranchia: Nudibranchia) from the Atlantic Ocean ............................. 150

First report of the invasive freshwater snail _Tarebia granifera_ (Lamareck, 1816) (Gastropoda: Thiariidae) from Israel ............................................. 156

Notice ................................................................................................................. 162
STATEMENT OF OWNERSHIP, MANAGEMENT, AND CIRCULATION

1. Publication Title, THE NAUTILUS.
3. Filing Date, October 1, 2006.
4. Issue Frequency, Quarterly.
5. No. of Issues Published Annually, Four.
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.
   Managing Editor, Linda Kramer, 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.

15. Extent and Nature of Circulation

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**Paryphantopsis** (Gastropoda: Pulmonata: Charopidae) from the Louisiade Archipelago of New Guinea

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**ABSTRACT**
Recent surveys (2003-2004) of the terrestrial snail fauna of the three largest islands in the Louisiade Archipelago, Misima, Rossel and Sudest have uncovered a remarkable radiation of *Paryphantopsis*, a diverse genus of charapid snails endemic to New Guinea and nearby islands. Previously, only one species, *Paryphantopsis louisiadarum*, here recognized as endemic to Rossel Island, was known from the Louisiade Archipelago. Three additional species were uncovered, all new and all appear to be endemic to single islands within the Louisiade Archipelago. The four species are described or redescribed using information on shell, genital and radular anatomy. The terrestrial mollusks of many of the other islands in the Louisiade Archipelago have never been sampled and it is likely that diversity of *Paryphantopsis* and other land snails is underestimated in the Louisiades.

*Additional Keywords*: Mollusca, mollusks, terrestrial, gastropods, land snails, endemism, Papua New Guinea.

**INTRODUCTION**
This is the second in a series of reports on the results of recent field surveys of terrestrial mollusks from Papua New Guinea. The first report (Slapcinsky, 2005) described six new species of the charapid genus *Paryphantopsis* from the eastern peninsula of mainland New Guinea; this, the second, reviews *Paryphantopsis* species collected during ten weeks of field surveys in January 2003 and April-May 2004 from the three largest islands in the Louisiade Archipelago: Misima (St. Aignan), Rossel (Yela), and Sudest (Vanatinai, Tagula). *Paryphantopsis*, a genus of charapid snails endemic to New Guinea, is comprised of twenty described species (Solem, 1970; Slapcinsky, 2005) that are distributed from Western Papua (Irian Jaya) to the Louisiade Archipelago. Only one species, *Paryphantopsis louisiadarum* (Möllendorff, 1899) was previously known from the Louisiade Archipelago; it is the type of the genus *Illoesta* (Iredale, 1911), later synonymized with *Paryphantopsis* (Solem, 1958).

The Louisiade Archipelago, a group of volcanic islands and coral islets, with a total area of approximately 1600 km², lies about 300 km east of the New Guinea mainland and 400 km west of the Solomon Islands (Figure 1). The archipelago is located on the southeastern extension of the Owen Stanley Terrane, part of the East Papua Composite Terrane (EPTC), a tectonic province composed of at least four separate geological units with differing ages, origins, and histories that appear to have assembled northeast of modern New Guinea during the Paleocene, 62-57 Myr ago, and fused to the main body of the island in the Late Oligocene to Early Miocene, 28-22 Myr ago. The Louisiades are at least 15-20 million years old and more likely were formed 40-60 million years ago and have apparently never had a land connection with the New Guinea mainland (Pigram and Davies, 1987). The Louisiades physical isolation and great age combine to provide considerable opportunity for the evolution of a distinctive fauna. However, this fauna is poorly sampled, especially for invertebrates, including terrestrial mollusks. Only approximately 30 species of land snails are known from the archipelago (Iredale, 1941); these were collected during brief surveys in the mid to late 19th Century. Nearly all of these species appear to be restricted to single islands. Low sampling intensity combined with anticipated high levels of endemism suggests that land snail diversity in the archipelago is underestimated.

**MATERIALS AND METHODS**
Specimens were hand-collected, drowned overnight, and preserved in 75% ethanol. Gross anatomical dissections were made in 75% ethanol using a dissecting microscope. Radulae were isolated from dissected buccal masses using a saturated KOH solution. Scanning electron micrographs of radulae were made using a Field Emission-SEM. Line drawings of the genital anatomy were made from digital images, and measurements were taken using an ocular micrometer. Shell and radular measurements were made as figured in Slapcinsky (2005). Whorl count was measured from the suture of the first whorl to the body whorl and fractions of a whorl were determined.
with the aid of a cardboard circle divided into ten equal parts of 36°. Spire diameter was the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture. Diameter was the greatest width of the shell perpendicular to the shell axis. Height was the greatest distance between the apex and the base of the aperture measured parallel to the shell axis. Spire height was measured from the top of the body whorl to the apex of the shell. Aperture width was the greatest distance from the columellar edge to the outer edge of the aperture. Aperture height was measured from the suture to the base of the aperture, parallel to the shell axis. The following abbreviations are used in figures of genital anatomy: AT = atrium; DI = diverticulum; EP = epiphallus; OV = free oviduct; PE = penis; PG = prostate gland; PP = penial pilasters; PR = penial retractor muscle; SD = spermathecal duct; SP = spermatheca; VA = vagina; and VD = vas deferens. Terminology of vegetation types follows Pijmans (1976). Specimens are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu (BPBM); Florida Museum of Natural History, Gainesville (UF); Natur-Museum Senckenberg, Frankfurt (SMF); Papua New Guinea National Museum, Port Moresby (PNGNM); Wroclaw University Museum of Natural History (MNHW); Queensland Museum (QM).

SYSTEMATICS

Family Charopidae Hutton, 1884
Genus Paryphantopsis Thiele, 1928

Type species: Flannulina (Paryphantopsis) lamellicerta Thiele, 1928, by original designation.

Paryphantopsis louisiadarum (Möllendorff, 1899)
(Figures 2-9, Table 1)

Figure 1. Distribution of Paryphantopsis in the Louisiade Archipelago, Papua New Guinea; L = P. louisiadarum, M = P. misimensis, V = P. canutensis, Y = P. yelensis, o = other sites sampled.
Ilonesta louisiadarum (Mollendorff, 1899).—Iredale, 1941: 92-93.
Paryphantopsis louisiadarum (Mollendorff, 1899).—Solem, 1955: 23; Solem, 1959: 156, pl. 12, figs. 10-11, pl. 13, fig. 6; Solem, 1970: 259-260.

Description: The adult shell is depressed globose and large for the genus, 9.3-11.9 mm (mean = 10.3, see Table 1 for sample size and standard deviation) in diameter and 6.7-9.0 mm (mean = 7.5) in height, with 2.7-3.0 (mean = 2.8) rapidly expanding whorls (Figures 2-4). The sutures are deeply impressed and the shell margin is...
evenly rounded. The spire is flat to slightly elevated 0.9–
0.2 mm (mean = 0.1). The body whorl descends slowly
near the aperture and the shell height/diameter ratio is
0.66–0.80 (mean = 0.73). The shell has 1.3 evenly
rounded protoconch (nuclear) whorls, sculptured with
spiral rows of small pits, approximately 15 rows can be
seen on the apex of adult shells. These spiral pits con-
tinue on the teleoconch (post-nuclear) whorls eventually
merging into incised spiral striae that weaken towards
the aperture. The teleoconch whorls are also sculptured
with weak growth lines that are not accentuated by pe-
rriostacial extensions; these are strongest on the body
whorl near the aperture. The protoconch and teleoconch
whorls are brown. The suture is darker brown and
the body whorl is usually irregularly maculated with darker
brown. The umbilicus is closed by a reflection of the
peristome. The aperture is large, compressed ovate, with
an aperture-width to aperture-height ratio of 0.91–0.98
(mean = 0.95).

The body color is bright yellow with green-black pig-
ment on the head and eyestalks extending in two lateral
bands to the posterior of the foot (Figure 5). These bands
are irregularly maculate anteriorly and extend ventrally,
often visible as spots on the sole of the foot. The yellow
defades to creamy-white in specimens preserved in ethanol.
The vas deferens remains narrow to the slightly swollen
head of the epiphallus (Figure 6). The epiphallus does
not bear a diverticulum. The penis is 0.70 the length of
the epiphallus and is apically robust, about 3 times the
width of the epiphallus at their junction, and tapers rap-
idly towards its base. Penis is sculptured with four plas-
ters two of these are wide and two narrower. Each pil-
aster is regularly plicated perpendicular to the length of
the penis (Figure 7). The penial retractor muscle origi-
nates from the diaphragm and inserts on the basal 0.30 of
the epiphallus. The spermathecal duct is robust, narrow-
g Gradually from the basal 0.25 to the apical 0.25 and
remaining narrow until joining the ovary spermatheca.
The free oviduct joins the short vagina just above the
spermatic.

The central teats of the radula (Figure 8, center row)
are tricuspid, 12–13 μm wide and 15–16 μm long, rough-
ly the same shape as, but smaller than, the first
lateral teeth, which are 16–17 μm wide and 19–20 μm
long. The mesocones of both the centrals and first lat-
erals are blade shaped, apically robust, widest slightly
above their mid-point, and narrowing basally, joining the
rectangular basal plates close to, but not on, their poste-
rior edge. The mesocones of the central teeth do not
project beyond the anterior edge of the basal plates,
those of the lateral teeth project beyond the edge. The
ecocones are trigonal and short only 0.30 of the height of
the mesocones, joining the posterior edge of the basal
plates. The lateral teeth are barely asymmetrical, their
endocones are only slightly taller than their ectocones.
The endocones of the lateral teeth are slightly larger but
otherwise of similar shape to their ectocones. The first
ten teeth to the left and right of the central row are
similar to the first laterals, the next four teeth on either
side are about the same height as the mesocones and the
ecocones vary from less than 0.50 to nearly 0.70 the height of
the mesocones. The endocones and mesocones of the marginal
teeth occasionally bear small notches or cusps near their
apices.

Lectotype: SMF 137274.

Paralectotype: SMF 165564 (1 specimen).

Remarks: Möllendorff’s description of Paraphanta
louisiana (1902) included a single set of measurements; ma-
jor diameter 9.5 mm, minor diameter 6.5 mm, and alti-
tude 6 mm. However, these measurements are difficult to
match to either of the two now slightly broken shells
of P. louisiana donated from his collection to Natur-
Museum Senckenberg, Frankfurt, and originally cata-
logued as SMF 137274. One specimen has pat-
tterns of missing periostracum similar to the shell figured
by Möllendorff and Kohl (1902–1905). Labeling with
this shell indicates it was separated from the other speci-
men and marked “Lectotype” based on its similarity to
the shell figured by Möllendorff; later, Solen (1970) for-
mally published this lectotype designation. The other speci-
men in the lot, now the paralectotype, was re-
cataloged as SMF 165564. Möllendorff’s specimens of
Paraphanta louisiana came from Strubell, who also

Table 1. Measurements in mm of undamaged adult shells of four species of Paraphanta. N = sample size, H = height, D =
diameter, SH = spire height, SD = spire diameter, AH = aperture height, AD = aperture width, W = number of whorls.

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<th>D</th>
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<th>SD</th>
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<th>AD</th>
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<td>P. louisiana</td>
<td>50</td>
<td>7.5 ± 0.7</td>
<td>10.3 ± 0.7</td>
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<td>6.0 ± 0.3</td>
<td>8.0 ± 0.5</td>
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sent specimens to Fulton. These specimens were distributed to other collections that eventually found their way into museums, and are the source of UMMZ 127616 and ANSP 109257.

**Type Locality:** Louisiaden (Louisiade Archipelago).


**Habitat:** Observed above 250 meters altitude in mixed hill forest and mixed lower montane forest, active during the day crawling on trees and shrubs from near ground level to 2 m height.

**Remarks:** Within *Paryphantopsis*, *P. louisiadanum* is similar only to *P. globosa*, *P. misisnus*, *P. ubranus*, and *P. vanatinius* in lacking all traces of periostracal extensions on the growth lines. *Paryphantopsis louisiadanum* differs from *P. globosa* in being smaller, having a closed umbilicus and fewer whorls and differs from *P. misisnus* and *P. vanatinius* in having a penis that is robust apically and narrow basally. It further differs in body color pattern with two broad lateral bands not present in *P. misisnus* that extend to the sole of the foot unlike those of *P. vanatinius*. The shell of *P. louisiadanum* is usually irregularly maculated with darker pigment unlike the more uniformly colored *P. misisnus* and *P. vanatinius*. *Paryphantopsis ubranus* differs from *P. louisiadanum* in having a more tightly coiled shell with a higher spire and an apical diverticulum on the epiphallus.

*Paryphantopsis misisnus* new species (Figures 10–12, Table 1)

**Description:** The adult shell is globose, large for the genus, 7.2–8.7 mm (mean = 8.0, see Table 1 for sample size and standard deviation) in diameter and 5.7–6.6 mm (mean = 6.0) in height, with 2.3–2.7 (mean = 2.5) rapidly expanding whorls (Figures 10–12). The suture is deeply impressed and the shell margin is evenly rounded. The spire is flat to slightly elevated, 0.0–0.3 mm (mean = 0.1), the body whorl descends slowly and regularly. Shell height/diameter ratio is 0.65–0.81 (mean = 0.75). There are 1.3 evenly rounded protoconch whorls, sculptured with spiral rows of small pits; approximately 13 rows can be seen on the apex of adult shells. Rows of spiral pits are continued on the teleoconch, becoming weaker and eventually merging to become incised spiral striae. Spiral striae weaken becoming nearly obsolete on the final 0.25 of the body whorl where shell sculpture becomes predominated by weak and somewhat rounded growth lines that do not bear periostracal extensions. The protoconch and teleoconch whorls are uniformly brown, except for some darker pigmentation in the suture. The umbilicus is closed by a reflection of the peristome. The aperture is large, ovate, with an aperture-width to aperture-height ratio of 0.87–1.02 (mean = 0.97).

The body color is uniform yellow that fades to cream in specimens preserved in ethanol; there are no lateral bands on the foot or pigment on the eyestalks (Figure 13). The vas deferens narrows rapidly after the prostate gland and remains narrow until entering the slightly swollen head of the epiphallus (Figure 14). The epiphallus is robust, especially basally where it is twice the diameter of its mid-point, it does not bear a diverticulum, and is 1.25 times penis length. The penial retractor muscle originates on the diaphragm and is inserted near the mid-point of the epiphallus. The penis is robust throughout its length, approximately 0.25–0.30 longer than the base of the epiphallus. Penis is sculptured with two massive smooth pilasters (Figure 15). The spermatheca is ovate, its duct is narrow throughout its length expanding only slightly at the junction with the free oviduct at the short vagina only slightly above the atrium.

The central teeth of the radula (center row) are tricuspid, 9–10 µm wide and 16–17 µm long, smaller than the first lateral teeth, which are 13–14 µm wide, 21–22 µm long (Figure 16). The mesocones of the central teeth do not project beyond the basal plate while those of the lateral teeth do. The ectocones of the central and lateral teeth are about 0.30 the height of the mesocones. The laterals are tricuspid and slightly asymmetric with the endocone of each lateral tooth slightly taller than the ectocone. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones and both point towards their mesocones. The first seven teeth to the left and right of the central row are similar to the first lateral teeth, the next five teeth on either side are of a different height and difficult to classify as either lateral or marginal teeth. The last six are clearly marginal teeth and are dorsoventrally compressed and tricuspid, without accessory cusps, 11–12 µm wide and 15–18 µm long (Figure 17). The endocones of the marginals are 0.70 the height of the mesocones while the ectocones are shorter, only 0.50 the height.
Figures 10-17. *Paryphantopsis misimensis.* 10-12. Photographs of shell, Holotype UF 308234, diameter 8.4 mm. 13. Photograph of live animal. 14-15, camera lucida drawing of genitalia, UF 353422, maximum width 9.3 mm. 16-17, Scanning electron micrograph of radula, UF 353422, field width of central and lateral teeth 73 μm, marginal teeth 64 μm.

Paratypes: BPBM 268735 (2 specimens), PNGNM 005-002 (5 specimens), UF 303579 (19 specimens), UF 303580 (7 specimens), UF 353421 (1 specimen), UF 353422 (2 specimens), type locality, F. Kraus, 17 January 2003.

Type Locality: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Misima Island, Oya Tan, 1014 meters altitude, 10.660° S, 152.629° E.

Habitat: Active during the day on trees and shrubs within 2 meters of the ground in mixed lower montane forest near the summit of Oya Tan.

Etymology: Named for Misima Island where this species is presumed to be endemic.

Remarks: Paraphantopsis misinensis is similar only to P. globosea, P. louisiadarum, P. ubcamensis, and P. vanatinensis in lacking all traces of periostracal extensions on the growth lines. Paraphantopsis misinensis differs from P. globosea in being smaller, having a closed umbilicus and fewer whorls and differs from P. louisiadarum and P. vanatinensis in having a penis that is robust throughout its length, not having dark lateral bands on the foot, and having narrower radial teeth with endocones and ectocones that point towards the mesocones. Paraphantopsis ubcamensis differs from P. misinensis in having a more tightly coiled shell with a higher spine and an apical diverticulum on the epiphrallis.

Paraphantopsis vanatinensis new species
(Figures 18-25, Table 1)

Description: The adult shell is globose, larger than average for the genus, 7.0–9.6 mm (mean = 7.9; see Table 1 for sample size and standard deviation) in diameter and 5.1–6.9 mm (mean = 5.8) in height, with 2.4–2.9 (mean = 2.6) rapidly expanding whorls (Figures 18-20). The suture is deeply impressed and the shell margin is evenly rounded. The spire is flat to slightly elevated, 0.0–0.3 mm (mean = 0.1). Teleoconch whorls descend slowly and regularly until the final 0.70 of the body whorl where it descends more rapidly. Shell height/diameter ratio is 0.77–0.91 (mean = 0.85). There are 1.3 evenly rounded protoconch whorls sculptured with spiral rows of small pits; approximately 13 rows can be seen on the apex of adult shells. These pits become larger and less regular on the teleoconch whorls eventually fusing to form incised spiral strie. Spiral strie weaken slightly on the final 0.25 of the body whorl where shell sculpture becomes predominated by weak and somewhat rounded growth lines that do not bear periostracal extensions. Protoconch and teleoconch whorls are uniformly brown except for some darker pigmentation near the aperture. The umbilicus is closed by a reflection of the peristome. The aperture is large, ovate, with an aperture-width to aperture-height ratio of 0.92–1.12 (mean = 1.01).

The body color is bright yellow with green-black pigment on the eyestalks and in two weak mid-lateral bands on the anterior of the foot and two stronger mid-lateral bands on the posterior half of the foot (Figure 21). These bands are solid, not maculate, do not extend to the central edge of the foot, and can not be seen on the sole of the foot. In some individuals the anterior bands are lacking. The yellow fades to creamy-white in specimens preserved in ethanol. The vas deferens narrows slightly to the junction with slightly inflated cylindrical head of the epiphrallis (Figure 22). The epiphrallis is approximately 0.50 the diameter of the penis, narrows only slightly basally and does not bear a diverticulum. The penial retractor muscle is short, originating from the diaphragm, and inserted at the basal 0.30 of the epiphrallis. The penis is about the same length as the epiphrallis, and sculptured with several rows of regularly plicate plasters (Figure 23). The atrium is moderate in size and of consistent width. The spermathecal duct is robust remaining wide for basal 0.50 then tapering gradually to the junction with the ovate spermatheca. The free oviduct is about 0.50 the diameter of the spermathecal duct where they join. The vagina is of moderate length about the same length as the atrium.

The central teeth of the radula (middle row) are symmetrically tricuspid, 13–14 μm wide and 17–18 μm long. The slightly asymmetrical lateral teeth are otherwise similar in shape to the central teeth but are slightly wider, 15–16 μm wide, and nearly identical in length, 17–18 μm long (Figure 24). The bluntly concave and erect mesocones of the central and lateral rows join their basal plates near the posterior edge and project to or slightly beyond the anterior of their basal plates. The ectocones of both the central and lateral rows are trigonal and short, about 0.50 of the height of the mesocones, and join the posterior edge of their basal plates. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The first ten teeth to the left and right of the central row are clearly lateral teeth; the next five on either side grade in shape and are difficult to classify as either laterals or marginal teeth. The last five are clearly marginal teeth and are dorsoventrally compressed, tricuspid, about 11–14 μm wide and 13–19 μm long (Figure 25). The endocones are a bit more than 0.70 the height of the mesocones while the ectocones are slightly shorter, about 0.70 the height of the mesocones.


Type Locality: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Sudest Island (Vanatinai, Tagula), Emua Peak, just W of the summit of Mount Riu (Mount Rio), 725 meters altitude, 11°50′ S, 153°43′ E.

Habitat: Found active during the day on trees and shrubs from near ground level to 2 meters in mixed hill forest and mixed lower montane forest from 120 meters to 725 meters altitude.
Etymology: Named for Vanatinai Island where this species is presumed to be endemic.

Remarks: Paraphantopsis canattinaeus is similar only to P. globosa, P. louisiadarum, P. misiineus, and P. ndvaneusis in lacking all traces of periostracal extensions on the growth lines. Paraphantopsis canattinaeus differs from P. globosa in being smaller, having a closed umbilicus and fewer whorls and differs from P. louisiadarum and P. misiineus in having a penis that is relatively narrow throughout its length and having dark lateral bands that are not maculate and do not extend to the sole of the foot. Paraphantopsis ndvaneusis differs from P. canattinaeus in having a more tightly coiled shell with a higher spire and an apical diverticulum on the epiphalus.

Paraphantopsis yelenis new species (Figures 26–32, Table 1)

Description: The adult shell is globose to depressed globose, small for the genus, 3.6–4.5 mm (mean = 3.9, see Table 1 for sample size and standard deviation) in diameter and 2.4–3.1 mm (mean = 2.7) in height, with 2.7–3.0 (mean = 2.7) rapidly expanding whorls (Figures 26–28). The shell is wider and slightly angular below the mid-point and its suture is deep, sometimes appearing nearly adnate. The spire is flat to elevated, 0.0–0.2 mm (mean = 0.1). Teleoconch whorls descend regularly and shell height/diameter ratio is 0.62–0.73 (mean = 0.68). There are 1.2 rounded protoconch whorls; approximately 13 rows of spiral lames can be seen on the apex of adult shells. These lames are crossed by stronger sharp axial lines forming a lattice pattern. The teleoconch is sculptured with spiral rows of pits that become less regular malleations on the final third of the body whorl. This shell sculpture is somewhat obscured by periostracal extensions approximately every 0.7–9 growth lines that are accentuated with processes at the angled shell margin. These processes are often worn and can be missing from some adult shells. The protoconch and teleoconch whorls are uniformly brown. A reflection of the peristome closes or nearly closes the umbilicus. The aperture is large, nearly circular except at the angled periphery and has an aperture-width to aperture-height ratio of 0.69–0.93 (mean = 0.80).

In life the body color is bright yellow, there are no lateral patches on the foot, the eyestalks are dark black-brown, the yellow fades to cream in specimens preserved in ethanol. The vas deferens narrows toward the junction with the inflated spherical head of the epiphalus. Immediately below the head of the epiphalus there is a finger shaped apical diverticulum that is roughly 1/2 the length of and nearly the same diameter as the epiphalus (Figure 29). The epiphalus is approximately the same length as the penis. The penial retractor muscle is long, originating from the diaphragm, and inserted just below the mid point of the epiphalus. The epiphalus is roughly half the diameter of the penis. The penis is widest 0.30 of the way down from the apex and narrows slightly towards the apex and towards the base where it is 0.70 the diameter of the atrium at their junction. Penis sculptured with a narrow pilaster that widens basally (Figure 30). The atrium is average to short, about 0.50 the length of the relatively long vagina. The spermathecal duct, free ovi- duct, and vagina are all of similar diameter at their junction. The spermathecal duct is relatively narrow basally and tapers slowly and evenly until joining the spherical spermatheca.

The central teeth of the radula (center row) are tricuspid, 7–8 μm wide and 12–13 μm long, of similar shape and length but slightly narrower than the first lateral teeth, 8–9 μm wide and 12–13 μm long (Figure 31). The mesocones of both the central and first lateral teeth are relatively short and blunt, not tapering until the rounded tip of the cusp and not extending beyond their basal plates. They appear particularly short because they project nearly perpendicularly from their basal plates and not as much anteriorly. Mesocones of the central and lateral teeth are attached toward the middle of their basal plates. The ectocones of the central teeth and the nearly symmetric ectocones and endocones of the laterals are trigonal and about 0.50 the height of the mesocones. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The first five teeth to the left and right of the central row are similar to the first lateral teeth, the next three on either side grade in shape and are difficult to classify as either laterals or marginal teeth. The last five are clearly marginal teeth and are dorsoventrally compressed and tricuspid, 7–9 μm wide and 7–8 μm long (Figure 32). The ectocones of the marginal teeth are only slightly shorter than their endocones, which are only slightly shorter than their mesocones.


Type Locality: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Yela Island (Rossel Island), Lipuopua at Lipu River, 320 meters altitude, 11.346° S, 154.221° E.

Habitat: All specimens were collected in mixed hill forest from 275 to 285 m altitude. Individuals were observed active during the day on boulders that were densely encrusted with algae, mussels and lichens, and, less commonly, on dead logs and twigs near the ground.

Remarks: *Paryphantopsis yelensis* differs from all other *Paryphantopsis* from the Louisiades, *P. laotis*, *P. misimensis*, and *P. vanatinensis*, and from the lowland species from the mainland, *P. lebouii* and *P. gowii*, in having an apical diverticulum on the epiphallus.

*Paryphantopsis yelensis* differs from all other species of *Paryphantopsis* other than *P. globosa* and *P. striata* in having protoconch sculpture of axial and spiral lirae rather than spiral pits. However, *P. globosa* and *P. striata* have roughly equal axial and spiral lirae while *P. yelensis*
has stronger axial sculpture. Of the species for which the radial morphology is known, the origin of the mesocones from the center of the basal plate in the central and lateral teeth of P. yelensis is similar only to P. lebasii and P. yucu.

**Etymology:** Named for Yela Island where this species is presumed to be endemic.

**DISCUSSION AND CONCLUSIONS**

New Guinea lies at the leading edge of the Australian plate and is geologically complex, with much of the eastern and northern edge of the island and nearby satellite islands being composed of accreted terranes (Pigram and Davies, 1987). This complex geology has promoted the development of a unique and diverse biota that is still being discovered. Terrestrial invertebrates including snails are especially poorly known, being both inadequately sampled and diverse as evidenced by recent collecting in eastern Papua New Guinea. Recent collecting has uncovered high diversity and endemism in the genus *Paryphantopsis*, with all isolated mountains sampled having unique suites of endemic and previously undescribed species (Slapcinsky, 2005).

The islands off New Guinea including the Louisiades are also rich in endemic *Paryphantopsis* species, although only one of these, *P. louisidarium*, was previously described (Möllerodt, 1899) and later localized to Rossel Island (Solem, 1958) where it appears to be endemic. The Louisiades are also very poorly sampled with only approximately 30 species of terrestrial snails previously known from the archipelago (Iredale, 1941). The ongoing brief surveys of a small portion of the three largest islands in the Louisiade Archipelago have increased the known diversity of *Paryphantopsis* in the Louisiades by 300%. In addition to *Paryphantopsis*, species from several other characid genera and other families were also collected; these will be treated in later publications. The family Charopidae, previously considered to be a minor component of the terrestrial mollusk fauna of New Guinea, with relatively few species and genera (Solem, 1955), may be among the most diverse families on New Guinea and its satellite islands, rivaling the spectacular radiations exhibited by this family in the oceanic Pacific (Solem, 1983).

Two groups of *Paryphantopsis* appear to have colonized the Louisiade Archipelago. One group, *P. louisidarium, P. misiensis, and P. vanuatusis* share similar large, globose shells that have nearly flat spires and large apertures, are sculptured with spiral rows of pits that fuse to form incised spiral striae, and do not bear periostracal extensions or processes on the growth lines. A second group includes only *P. yelensis* a small species with strong axial sculpture on the protoconch and periostracal extensions with marginal processes on the growth lines of the teleoconch and with an apical diverticulum on the epiphallus. The relationship of both Louisiade clades with species from mainland Papua New Guinea is not clear. The three large species from the Louisiades, *P. louisidarium, P. misiensis, and P. vanuatusis* lack periostracal extensions on the growth lines similar only to *P. globose* and *P. utinatensis* from mainland Papua New Guinea; however, they also lack an apical diverticulum similar only to *P. lebasii* and *P. yucu* from the adjacent Papuan Peninsula. The relationship of *P. yelensis* to mainland species of *Paryphantopsis* is equally cryptic. The radula in this species has central and lateral teeth with mesocones that originate from near the center of the basal plates, a trait that is thus far known only from *P. lebasii* and *P. yucu*; however unlike those species, *P. yelensis* possesses an apical diverticulum. Although anatomic evidence suggests two origins for *Paryphantopsis* in the Louisiade Archipelago, additional anatomic and/or genetic characters would be necessary to determine the relationships of these species to those from mainland New Guinea.

**ACKNOWLEDGMENTS**

I thank the landowners of Aractha, Tcheme, Damien, and Liak for permission to work on their land and for field assistance; F. Kraus, F. Malesa, D. Mitchell, and G. Shea for additional field assistance; G. Kuka and D. Mitchell of Conservation International for providing logistical support and advice; Papua New Guinea National Museum and Art Gallery for providing in-country collaborative assistance; Papua New Guinea Department of Environment and Conservation, Papua New Guinea National Research Institute, and Milne Bay Provincial Government for permission to work in Milne Bay Province; K. Kelley, Electron Microscopy Core Laboratory, University of Florida for imaging radulae; E. Neubert for photographing labels and type material of *Paryphantopsis louisidarium*; L. Appleton, P. Callomon, R. Jennison, D. Potter, and M. Shea for facilitating my study of specimens in their care; and J. Worisford for sharing bibliographic information. Fieldwork for this research was supported by National Science Foundation grant DEB 0103794 and the University of Florida Foundation, McGinty Endowment, F. Kraus, T. Pearce, F. G. Thompson, and an anonymous reviewer suggested improvements to earlier drafts of this manuscript.

**LITERATURE CITED**


Daedalochila lithica and Daedalochila dorfeuilliana (Gastropoda: Polygyridae) in Arkansas, USA: morphology, distribution, and habitat

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ABSTRACT

Shell and genital morphology, geographic distribution, and habitat of two polygyrid species, Daedalochila lithica and Daedalochila dorfeuilliana in Arkansas are described. The two species have been confused because their shells are similar and the anatomy of D. lithica has not been previously described. In this paper, the genital anatomy of D. lithica is described and shell and genital anatomy of the two species are compared. No statistically significant differences were found in 15 shell-morphometric characters. The only constant difference in shell morphology was in the upper palatal lamella of D. lithica, which is less immersed than that of D. dorfeuilliana. Anatomically, the species differed in diameter of the penis, ventral growth of the epiphallus, thickness of the vas deferens at its junction with the prostate gland, ratio of vagina length to diameter. Genital anatomy indicates that both species belong to the Daedalochila plicata group. They are found in oak-hickory forest: D. lithica in areas where vegetation has been cut; D. dorfeuilliana in undisturbed old-growth forest. These data support the view that D. lithica is a taxon distinct from D. dorfeuilliana and other polygyrid species.

INTRODUCTION

Daedalochila dorfeuilliana (L. Lea, 1838) is a widely distributed land snail of the Ozark and Ouachita Mountain regions of Arkansas, Oklahoma, and Missouri, extending into Louisiana, Texas, Kansas and Illinois (Pilsbry, 1903; Pilsbry and Ferriss, 1906; Hubricht, 1955). The species is placed in the Polygyra plicata group of the Polygyridae. Polygyrinae (Pilsbry, 1940), and is distinguished from other members of the group by its geographical range, and by the palatal and basal apertural lamellae of approximately equal size (Pilsbry, 1940). Until Hubricht’s description of Daedalochila lithica (Hubricht, 1961), variation of shell morphology within this diagnosis had been accepted as falling within the range of variation of D. dorfeuilliana (Branson, 1970). The distribution of D. lithica, extending from north central and west central Arkansas into southeastern Oklahoma (Hubricht, 1955), falls entirely within the range of D. dorfeuilliana. Hubricht (1961) described D. lithica as related to D. dorfeuilliana but differing in details of the apertural lamellae: “Polygyra lithica is related to Polygyra dorfeuilliana, differing in the teeth. The parietal tooth is lower and is rounded rather than square. The lip teeth are smaller and are not deeply immersed.”

Hubricht (1955) described D. lithica and D. dorfeuilliana as “calciphenes found under logs, rocks, and leaf litter in dry upland woods” but they are never found together.

Hubricht (1961) did not report the anatomy of D. lithica. However, Pratt (1951b) placed the species in the genus Millereix Pratt, 1951 “because of its position as a precise intermediate between Polygyra nooreana and Polygyra dorfeuilliana in shell characters.” Both Daedalochila mooreana (Binney, 1857) and D. dorfeuilliana having been assigned to Millereix on the basis of shell characters and genital anatomy (Pratt, 1981a, b). Subsequently, Emberton (1995) placed all members of the Polygyra plicata group into Millereix, separating the species of Millereix semison Pratt, 1981b, from other members of the genus by erection of the sub-genus Prattelix Emberton, 1995. Coles and Walsh (2006) dissected the well-defined species of the Polygyra plicata group and expressed doubt as to the validity of placing all members of the group in Millereix because of the inconsistency of diagnostic generic features. Consequently, the species were referred to the senior genus Daedalochila (Beck, 1837). However, D. lithica was not dissected by Coles and Walsh (2006) because wet-preserved type material did not exist and because of the uncertainty of identification of new material as noted above. The dissected specimen of D. dorfeuilliana illustrated in Coles and Walsh (2006) came from outside the range of D. lithica as given by Hubricht (1955). We were unable to examine material from the type locality of D. dorfeuilliana because that locality is unknown (Pilsbry, 1940).
We have used type material of *D. lithica* plus material identified by Hubricht as *D. dorfeuilliana* and *D. lithica* to examine Hubricht's (1961) concept of the two species in more detail. Live material was obtained for study of the anatomy and habitat preferences so as to identify which characters of the shell and anatomy can be used to define *D. dorfeuilliana* and *D. lithica* and to clarify the relationship of the two species within the *Daedalochila plicata* group.

**MATERIALS AND METHODS**

**Material Examined:** *Daedalochila lithica*: one lot of four adult (based on development of the aperture and apertural lamellae) paratype shells from the University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Catalog Number UMNZ 205889; 19 lots (291 specimens of adult shells) collected between 10 April 1936 and 1975 (no day/month given) from the Hubricht Collection at the Field Museum of Natural History (FMNH), Chicago, Catalog Numbers FMNH 256348–256362 and FMNH 256369–256370; 14 lots (182 specimens of adult shells) collected by the senior author between 10 April 1996 and 14 September 2000 from seven Arkansas counties. *Daedalochila dorfeuilliana*: 50 lots (299 adult shells) from the Hubricht Collection of the FMNH, Catalog Numbers FMNH 255102–255148 and FMNH 256377–256381; 26 lots (142 adult shells) collected by the senior author between 12 June 1985 and 24 March 2000 from nine Arkansas counties.

**Shell Measurements:** Shell characters that were measured are shown in Figures 1–4, except body whorl height, which was measured immediately behind the outer lip of the aperture. Measurements were made to the nearest 0.01 mm with an electronic digital caliper, accuracy of ± 0.03 mm. Ratios of shell height/diameter, number of whorls/shell diameter, inside diameter of aperture/outside diameter of aperture, width of parietal tooth/height of parietal tooth and diameter of umbilicus/ diameter of shell were calculated. Student's two-sample t test was conducted for each shell variable and box plots graphed on a Texas Instruments TI-84 Plus graphing calculator coupled with a Power Macintosh G3 desktop computer.

**Genital Anatomy:** Specimens were drowned overnight in sealed containers of degassed (boiled and cooled) water and preserved in 70% ethanol. Dissections were performed at 20–40× magnification. The shell was removed from the body, the animal opened from near the genital pore to the lung, and the tissues teased apart while submerged in 70% ethanol. The right ocular retractor muscle was cut and partially removed to aid viewing the basal penis. The penis was opened with a sharpened spear-point needle from near its junction with the atrium/vagina to the attachment of the penial retractor muscle. Sections of the penis were obtained by cutting the opened penial tubes where indicated in the figures and allowing the remaining tissues to reform to their approximate original cylindrical form. Drawings were made by eye, taking particular care to ensure that relative proportions of the organs were accurately reproduced, and with reference to an appropriate scale.

**Dissected Specimens:** *Daedalochila lithica* (Figures 5–16), eight specimens from the following Arkansas localities: Boone County, Buffalo National River, Rush Mountain Trail, 29 April 2004, G. Walsh, UF 376769, two specimens dissected and measured (Figures 5–7, 14); Boone County, Stonington Road, NE of New Hope, 2.1 miles N of Highway 114, 22 September 2004, G. Walsh, UF 376765, one specimen dissected and measured (Figure 16); Carroll County, Lake Leatherwood Park, 13 April 2004, G. Walsh, UF 376816, two specimens dissected, one measured (Figures 12, 13); Madison County, Withrow Springs State Park, 22 September 2004, G. Walsh, UF 376766, two specimens dissected and measured (Figures 8–10, 15); Marion County, Buffalo National River at Buffalo Point, B. Coles, 20 January 2003, UF 376767, one specimen dissected and measured (Figure 11). *Daedalochila dorfeuilliana* (Figures 17–24), seven specimens from the following Arkansas localities were dissected and measured: Hempstead County, Lake Millwood at Saratoga Landing, B. Coles, 5 January 2003, FMNH 293240, one specimen (Figures 17, 18) and UF 376768, one specimen (Figures 19, 20); Faulkner County, River Plantation Golf Course (Highway 365), Morgan, B. Coles, 10 October 2005, NMWZ.2005.011.03298, one specimen measured and illustrated (Figures 21, 22); NMWZ.2005.011.03296,
two specimens, Faulkner County, as above (dissected but not illustrated); Carroll County: Beaver Dam Overlook, 15 and 20 March 2005, G. Walsh, UF 376770, two specimens (Figures 23, 24).

**Distribution and Habitat:** Geographical distributions of *D. lithica* and *D. dorfeuilliana* in Arkansas were compiled from the Hubricht collection at the FMNH and the authors’ collections. Environmental conditions were noted for each collection site visited by the authors.

**Disposition of Specimens:** All shells of the senior author have been deposited in the FMNH. These include 7 lots of *D. lithica* (FMNH 308144–308150) and 40 lots of *D. dorfeuilliana* (FMNH 308104–308143). Collections of the junior author have been deposited in the Florida Museum of Natural History (UF), Gainesville, Florida, and the National Museum of Wales (NMW), Wales; catalog numbers are presently available only for critical dissected material given below.

**RESULTS**

**Shell Characters:** Visual examination of Hubricht’s material of *D. lithica* and *D. dorfeuilliana* in the FMNH confirmed the general features of his description of *D. lithica* and its comparison with *D. dorfeuilliana* (Hubricht, 1961). Thus, shells of the two species are similar in apical and umbilical views (Figures 25–28), and the structure of the apertural lamellae of many examples of *D. lithica* (e.g., Figure 29) shows the low, rounded palatal lamella and conical “not deeply immersed” apertural lip lamellae that conform to Hubricht’s (1961) description of the species; however, detailed examination of the several hundred shells of *D. lithica* and *D. dorfeuilliana* that comprise the material identified by Hubricht showed that there was considerable variation in the form of the apertural lamellae. For example, a higher, less rounded palatal lamella was often present in specimens identified as *D. lithica* (Figure 30), the shape being similar to the “squarish” palatal lamella of *D. dorfeuilliana* (Figure 31) as described by Pilsbry (1940). Conversely, the palatal lamella of *D. dorfeuilliana* (Figure 32) was often similar to that of *D. lithica*. In addition, the basal lamellae of both species were similar, i.e., conical and not deeply placed within the aperture (Figures 29–32), and did not appear to offer reliable diagnostic characters. Thus, of Hubricht’s description of *D. lithica*, the depth of immersion of the palatal lamella appears to provide the only consistent shell character for separation of the two species (Figures 29–32). The palatal lamella of *D. lithica* is always placed more superficially on the lip, whereas that of *D. dorfeuilliana* is always well below the lip.

Reexamination of Hubricht’s material confirmed that specific assignments could be made on this basis. Similarly, shells in the collection of the authors showed similar variation of form of the apertural lamellae, but all (including wet preserved material) could be assigned to *D. lithica* or *D. dorfeuilliana* on the basis of the depth of the palatal lamella.

The results of a more formal analysis of variation of shell parameters are shown in Figures 33–47, and the Arkansas counties from which specimens were taken for this analysis are shown in Figures 48–49. Both species showed considerable variation in all shell parameters measured, with overlap of the ranges of the values, and no statistical differences were found (P>0.05).

**Genital Anatomy:** *Daedalochila lithica:* Atrium short, approximately twice the diameter of the basal penis (Figures 5, 12, 14–16); vagina of similar length, as broad in diameter as the basal penis (Figures 14, 16) or slightly inflated (Figures 5, 12, 15), its length approximately equal to its diameter (Figure 16); free oviduct approximately half the length of the penis (Figures 5, 12, 14–16); penis elongate, tapering to a weakly defined, variably flexed (Figures 5, 14–16) or coiled (Figure 12) epiphallus, without appendix or flagellum; length 2.63–3.59 mm (mean = 3.44 mm±0.53 mm, n = 7) including the epiphallus; maximum width at mid-length, but basal penis only slightly narrower; width/length of penis 0.67–0.18 (mean = 0.15±0.04, n = 7); penial retractor muscle terminal, variable in length and form; internally, the penis bears two fleshy pilasters that become weak in the terminal penis/epiphallus (Figures 7, 9–11); in the terminal 1/10 of the penis there is a minute papilla approximately 0.05 mm long attached to the penial walls and pilasters by thickenings of the tissues (Figures 10, 11); presence of a papilla was not confirmed for all dissected specimens; vas deferens narrow, expanding from approximately mid length to reach its maximum diameter (approximately twice its minimum diameter) proximally, at the junction with the prostate gland (Figures 6, 13); no other papillae, glandular regions, colored regions or additional features were visible in the penis at 40× magnification.

The genital anatomy of *D. dorfeuilliana* has been described and illustrated for specimens from Tulsa County, Oklahoma, Pratt (1981a, reproduced in Emberton, 1995) and Hempstead County Arkansas (Coles and Walsh, 2006). Dissection of additional material is given in Figures 19–24, including a specimen from within the range of *D. lithica* (Figures 23, 24). These dissections confirm the features of the genital anatomy of *D. dorfeuilliana* as described by us (Coles and Walsh, 2006); notably the penis widest in mid length where the pilasters are well-developed, with a narrow base, penis length (including epiphallus) 2.15–3.77 mm (mean 2.52±0.68 mm, n = 4), width/length 0.13–0.15 (mean 0.15±0.01, n = 4), and the proximal vas deferens at the junction with the prostate gland greatly enlarged, approximately fourfold its minimum diameter (Figures 21, 23). In addition, the length of the vagina is approximately twice its diameter (Figure 21), and a minute papilla approximately 0.05 mm long was found in the terminal 1/10 of the penis of a specimen from Lake Milwood (Figures 19, 20), although this was not confirmed for other specimens. The well-differentiated and strongly reflected terminal penis (referred to here as the epiphallus, Figures 17, 23, 24) was
regarded previously by us as a specific character (Coles and Walsh, 2006). However, this was not evident for the three specimens from Faulkner County (Figure 21), although these conformed in other respects to the description given here.

Habitats: Geographic distributions of *Daedalochila lithica* and *D. dorfeuilliana*, by Arkansas counties, are similar (Figures 48, 49). Both species were found in oak (Quercus spp.)-hickory (Carya spp.) forest. However, *D. lithica* is found under stones and fallen logs and on bare ground in open, dry areas where trees and underbrush have been cut and where regeneration by young oak, hickory and juniper (Juniperus ashei Buchholtz, 1930) is occurring. *Daedalochila dorfeuilliana* lives in humid conditions under stones and fallen logs on undisturbed forest floor but can also extend into areas of scrub where trees have been cut and on exposed limestone outcrops.

**Figures 5-24.** Genital anatomy of *Daedalochila lithica* (Figures 5–10) and *Daedalochila dorfeuilliana* (Figures 17–24) from Arkansas, 5. *D. lithica* Boone County, 29 April, 2004, UF 375676. 6. Same, detail of junction of vas deferens (vd) and prostate gland (pt). 7. Same, penis opened to show the two pilasters and the papilla (p) in the terminal penis. 8. *D. lithica*, Madison County, 22 September 2004, UF 375677, showing a stout penis (p) and a short penial retractor muscle (pr). 9. Same, detail of penis opened to show the terminal retractor muscle. 10. Same, apical penis opened to the penial retractor muscle, showing oblong apical pilasters and detail of terminal penial papilla. 11. *D. lithica*, Marion County, 29 January 2004, UF 375678, apical penis, opened, showing oblong apical pilasters and detail of terminal penial papilla. 12. *D. lithica*, Carroll County, 3 April 2004, UF 375616, distal genitalia showing narrow, coiled penis (p) and sections of penis as indicated in A and B. 13. *D. lithica*, Carroll County, 3 April 2004, UF 375616 (second specimen), detail of junction of vas deferens and prostate gland. 14–15. *D. lithica*, distal genitalia showing variation of penis. 14. From Boone County, 29 April 2004, UF 375617 (second specimen). 15. From Madison County, 22 September 2004, UF 375616 (second specimen). 16. From Boone County, 29 August 2004, UF 375675. 17. *D. dorfeuilliana*, Hempstead County, 5 January 2003, FMNH 293210 (reproduced from Coles and Walsh, 2006, fig. 55*), distal genitalia and penial sections. 18. Same, opened to show pilasters (reproduced from Coles and Walsh, 2006, fig. 56*). 19. *D. dorfeuilliana*, UF 375618 (second specimen), apical penis opened to penial retractor muscle to show the terminal end of the pilasters, with oblong extension into the vas deferens and the terminal penial papilla. 20. Same, view of papilla from the side showing stalked form. 21. *D. dorfeuilliana*, Faulkner County, 10 October 2005, NMOZ 2005.011.03(251), showing enlarged proximal vas deferens (vd) and vagina (vag) approximately twice as long as diameter. 22. Same, penis opened to show pilasters. 23. *D. dorfeuilliana*, Carroll County, 10/15 March 2005, UF 375670, distal genitalia showing enlarged vas deferens. 24. Same, detail of penis. Abbreviations: ag, albumen gland; at, atrium; ep, epiphallus; fo, free ovul duct; hd, hermaphroditic duct; pa, penial papilla; p, penis; pr, penial retractor muscle; pt, prostate gland; s, spermatheca; sd, spermatheca duct; u, uterus; vd, vas deferens; vag, vagina. * Reproduced by permission of the American Malacological Bulletin.

**Figures 25-32.** Shells of *Daedalochila lithica* (25, 27, 29, 30) and *Daedalochila dorfeuilliana* (26, 28, 31, 32) from Arkansas. 25. Apical view, *D. lithica*, paratype, UNMZ 203595, 5.0 mm diameter, six miles east of Mountain View, Stone County. 26. *D. dorfeuilliana*, FMNH 305109, 5.2 mm diameter, Buffalo National River, Tyler Bend, Scary County. 27. Umbilical view, *D. lithica* same as above. 28. *D. dorfeuilliana*, same as above. 29. *D. lithica*, paratype, FMNH 256372, 7.5 mm diameter, six miles east of Mountain View, Stone County. 30. *D. lithica*, paratype, FMNH 256372, 7.5 mm diameter (same lot as 29 above). 31. *D. dorfeuilliana*, FMNH 305114, 5.2 mm diameter, Dogwood Trail at Beaver Dam Overlook, Carroll County. 32. *D. dorfeuilliana*, FMNH 305119, 5.0 mm diameter, Buffalo National River, Rush Historic Area, Marion County. Scale bars: figures 25–28 = 2.0 mm; figures 29–32 = 0.5 mm. Arrows indicate the slightly immersed palatal lamella of *D. lithica* (Figures 29, 30) and the more deeply immersed palatal lamella of *D. dorfeuilliana* (Figures 31, 32).
Figures 33–47. Box plot diagrams of shell measurements and ratios: *Dactalochila dorfeuilliana* (n=441) (above); *Dactalochila lithica* (n=427) (below). The 25th–50th percentiles of data fall within the boxes, the 10th–90th percentiles fall within the error bars, and data outside these ranges are plotted individually. The median value is shown within each box, or if not shown, falls at the lower 25%. Figures 33, 39, 41 (*D. dorfeuilliana*), 45 or upper 50% (Figure 41 *D. lithica*) limit of the boxes. No significant difference was indicated between the means of corresponding pairs of characters (P<0.05). Student’s t values are given in parentheses. 33, Number of whorls (5.32). 34, Diameter of shell, mm (6.89). 35, Height of shell, mm (1.46). 36, Body whorl height, mm (10.93). 37, Outside diameter of aperture, mm (8.90). 38, Inside diameter of aperture, mm (7.19). 39, Width of aperture, mm (4.31). 40, Height of parietal tooth, mm (15.62). 41, Width of parietal tooth, mm (8.55). 42, Diameter of umbilicus, mm (5.12). 43, Height of shell diameter/diameter of shell (6.65). 44, number of whorls/diameter of shell (9.89). 45, inside diameter of aperture/width of aperture (3.66). 46, width of parietal tooth/height of parietal tooth (5.21). 47, diameter of umbilicus/diameter of shell (12.63).
DISCUSSION

Comparison of the shells of Daedalochila lithica and D. dorfeuilliana show few consistent differences between them: only the depth of the palatal lamellae within the aperture provides a differential specific character (Table 1). Specimens selected on this basis show consistent differences in their genital anatomy (Table 1) that are as marked as between other members of the D. plicata group that have distinct shell morphology. For example, Daedalochila peregrina (Rehder, 1932) differs from D. lithica in its penis being of approximately uniform width throughout its length, an obsolete epiphallus, and pilasters anastomosed (Coles and Walsh, 2006). The penis of Daedalochila bisonites (Coles and Walsh, 2006, is similar in shape to that of D. lithica, but differs in the pilasters being more abruptly developed in the mid penis (Coles and Walsh, 2006). Other species in the group, Daedalochila plicata (Say, 1821), Daedalochila fastigiata (Say, 1829), Daedalochila jacksoni (Bland, 1866) and Daedalochila troostiana (Lea, 1839), are distinct in the highly developed apical pilasters or associated features (Coles and Walsh, 2006). Thus, these new data support Hubricht’s view that D. lithica is a taxon distinct at specific level from D. dorfeuilliana and other Polygyridae of the USA.

Position of Daedalochila lithica and D. dorfeuilliana in the D. plicata group: In our earlier study of the D. plicata group (Coles and Walsh, 2006), we abandoned the concept of Millerelix (Pratt, 1981b) and the subgenera Millerelix sensu stricto and Prattelix (Emberton, 1995) because of the lack of, or variability of, the diagnostic generic and subgeneric features. In part, this decision was made because the anatomy of D. dorfeuilliana as we described (Coles and Walsh, 2006), and confirmed here, disagreed with that described by Pratt (1981b), particularly with respect to the diagnostic generic features of Millerelix: an elongate penis (width/length<0.06), and the presence of a pendant conical projection in the apical penis (Pratt, 1981a,b; Emberton, 1995; Coles and Walsh, 2006). The dissections presented here show that these features are variable between individuals for both D. lithica and D. dorfeuilliana. For example, both species show considerable variability of penis width/length, and both possess a minute papilla in the terminal penis. The papilla was not found in all dissected specimens, but because of the fragility of the tissues of the epiphallus/terminal penis, we cannot be certain

Table 1. Consistent differences between Daedalochila lithica and Daedalochila dorfeuilliana.

<table>
<thead>
<tr>
<th>Feature</th>
<th>D. lithica</th>
<th>D. dorfeuilliana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palatal lamella of aperture</td>
<td>not immersed (Figures 29, 30)</td>
<td>immersed (Figures 31, 32)</td>
</tr>
<tr>
<td></td>
<td>approximately uniform in diameter from base</td>
<td>widest at mid length where the pilasters are</td>
</tr>
<tr>
<td></td>
<td>to mid length (Figures 5, 12, 14–16)</td>
<td>well developed, with a narrow base (Figures 17, 21, 24)</td>
</tr>
<tr>
<td>Penis</td>
<td></td>
<td>greatly enlarged, approximately 4 times its</td>
</tr>
<tr>
<td></td>
<td></td>
<td>minimum diameter (Figures 21, 23)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>approximately 2 (Figure 21)</td>
</tr>
<tr>
<td>Proximal vas deferens</td>
<td>not greatly enlarged, approximately twice its</td>
<td></td>
</tr>
<tr>
<td></td>
<td>minimum diameter (Figures 6–13)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vagina length/diameter</td>
<td>approximately 1 (Figures 12, 14–16)</td>
<td></td>
</tr>
</tbody>
</table>
whether it is variable in development or was destroyed during dissection. Nevertheless, its presence agrees with Pratt’s description of the anatomy of D. dorefuliana (Pratt, 1981b) and appears to be a “derivative” of the apical, pendant, conical projection (Emborton, 1995). It was not observed by us previously because several aspects of Pratt’s (1981a, b) description discussed in Coles and Walsh (2006) led us to believe that this feature was more prominent than it is. It should also be noted that Pratt (1981a, b) regarded the epiphallus (of D. lithica?) as that portion of the narrow terminal penis extending from the papilla to the penial retractor muscle (i.e., being approximately 1/10 the length of the penis), whereas we have regarded the epiphallus as the abrupt penial narrowing (e.g., Figure 24) observed in D. dorefuliana (i.e., the papilla is in the epiphallus). Other species of the D. plicata group were examined for papillae or similar features through the opened terminal penis (i.e., to the penial retractor muscle) but none was observed (Coles and Walsh, 2006). Using Emborton’s (1995) classification of Millerelix and the anatomy as described by us, D. lithica would be placed in the subgenus Millerelix on the basis of the elongate, narrow penis and the lack of a greatly enlarged proximal vas deferens, whereas D. dorefuliana would be placed in the subgenus Prattelix because of the wider penis and greatly enlarged vas deferens (Emborton, 1995). Thus, these data give some support to the concepts of Millerelix as used by Pratt (1981a,b) and modified by Emborton (1995), but they do not change our conclusions concerning the inappropriate use of Millerelix for all members of the D. plicata group.

ACKNOWLEDGMENTS

We are grateful to Jochen Gerber for providing shells from the Hubricht collection deposited at FMNH, Liath Appleton for providing shells from UMMZ, and to the staff of the Buffalo National River, Greg Butts of the Arkansas State Parks, Douglas Zollner of the Arkansas Field Office of the Nature Conservancy, Cindy Osborne of the Arkansas Natural Heritage Commission, the staff of the Arkansas Game and Fish Commission and the staff of the Ozark Saint Francis and Ouachita National Forests.

LITERATURE CITED


The Neogene history of Prisogaster Mörch, 1850 (Gastropoda: Turbinidae) in South America

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ABSTRACT

Prisogaster Mörch, 1850, is the sole genus of the turbinid subfamily Prisogasterinae Hickman and McLean, 1990, and is represented by only one extant species, the western South American P. niger (Wood, 1828). Two new fossil species from southern Peru (P. valenciiai new species and P. nelsoni new species) extend the record of Prisogaster to the middle late Miocene and reveal its turbinid ancestry. A major morphological transformation during the late Miocene produced the modern taxon, which is heavier and more streamlined than its Mio-Pliocene forebears, and thus probably better suited to the higher energy environments that characterize the present-day Peruvian and Chilean coastline.

INTRODUCTION

Prisogaster Mörch, 1850, has rightly been called "enigmatic" by Hickman and McLean (1990) in their study of trochoidian systematics. The genus has only one species, the extant Prisogaster niger (Wood, 1828), a gastropod with a sturdy purple-black shell and calcareous operculum. The species is endemic to western South America and has a fossil record not older than the middle Pliocene [Herm, 1969; not late Pliocene (Hickman and McLean, 1990)]. Individuals of Prisogaster live amongst wave-battered intertidal rocks and tide pools (Marine, 1973; Guzman et al., 1985), niches more typically occupied by trochids than turbinids (Hickman and McLean, 1990). Its perplexing suite of characters has led Prisogaster to be placed in Phasianellinae Swainson, 1840 (Thiele, 1929; Weinz, 1935). Turbininae Rafinesque, 1815 (Knight et al., 1960), and, most recently, Prisogasterinae (Hickman and McLean, 1990).

This paper describes two new fossil species of Prisogaster from southern Peru, P. stuechi new species and P. valenciiai new species. Specimens of the former were found near Sacaco in middle upper Miocene and lower Pliocene well-sorted cross-beded sandstones. Specimens of the latter were encountered farther south near Chala in upper lower Pliocene or upper Pliocene bioclastic gravels. These new taxa demonstrate a dramatic shift in morphology and niche of the living species, P. niger, from its Mio-Pliocene predecessor.

GEOLOGY

The Neogene stratigraphy of forearc basin deposits between Pisco and Camaná (Figure 1) was reviewed by DeVries (1998). Upper Miocene and Pliocene marine strata of the Pisco and La Planchada formations include fine-grained tuffaceous and diatomaceous sandstone, which are attributed to outer shelf environments, and coarse-grained massive tuffaceous sandstone from closer to shore (Muizon and DeVries, 1985). Lying disconformably on crystalline basement rocks are cross-bedded and lenticular bioclastic conglomerates, remnants of littoral

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deposits that lapped onto pre-Eocene erosional platforms or against precipitous Andean foothills. An excellent example of the latter is seen southeast of Chala, where the Panamerican Highway descends in tight curves towards the beach at Playa Huacllaco (Figure 2). Seventy meters of sediment were deposited in high-energy foreshore and intertidal environments that once flanked rugged cliffs (DeVries, 2003). The age of the Huacllaco beds is constrained by basal beds with specimens of Concholepas nodosa Hupe, 1854, Acanthina triangularis DeVries, 2003, and Hermionespis mirabilis (Moricke, 1896), which collectively indicate an early late Pliocene age (DeVries and Frassinetti, 2003), and the uppermost and oldest of several marine terraces, whose 200 m elevation and largely extant taxa suggest a latest Pliocene age (Muizon and DeVries, 1985).

**MATERIALS AND METHODS**

Specimens described in this study were found by the author. Comparative material was studied at the Los Angeles (California) County Museum of Natural History (LACM). Locality and sample descriptions are listed in the appendix. "DV" locality numbers refer to the author’s field notes. Lengths (L) and widths (W) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Figured specimens viewed from oblique angles may be listed with a “maximum viewed width” (m.v. width) measured at right angles to the axis. Some figured specimens are coated with ammonium chloride. Types and numbered specimens are deposited at the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, in Lima, Peru (MUSM INV) and University of Washington’s Burke Museum of Natural History and Culture in Seattle, Washington (UWBM).

**SYSTEMATICS**

Family Turbinidae Rafinesque, 1815
Subfamily Prisogasterinae Hickman and McLean, 1990

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**Figure 2.** Type localities of *Prisogaster valenciai* new species (locality-samples DV 1254-Bal 6, Bal 8, and Bal 10) and *P. stucchii* new species (DV 573-1). Also shown are lower Pliocene locality-samples near Yauca (DV 1629-1, DV 1635-1, DV 460-1, DV 1598-1) and Sacaco (DV 380-2, DV 573-1) with *P. mcleani* and an upper Pliocene/lower Pleistocene marine terrace southeast of Chala with *P. niger* (DV 1629-1).
Section above Playa Huacllaco

Figure 3. Huacllaco section southeast of Ciah with stratigraphic position of type specimens of *P. valenciai* new species and other horizons with *Prisogaster* material.

Genus *Prisogaster* Möh., 1850

*Anuya F. H. Troschel, 1852 (objective synonym)

Type species: *Turbo niger* Wood, 1828. Type locality not specified.

Discussion: Möh (1850, p. 21) did not describe *Prisogaster*, but simply applied the new genus name without comment to *Turbo niger* Gray (= *Turbo niger* Wood, 1828), itself introduced with only a drawing and one-word description, “black” (Wood, 1828, p. 18). Hickman and McLean (1990) implicitly defined *Prisogaster* by their description of *Prisogasterinae*. Diagnostic non-anatomical characters include an incomplete peristome (also present in Turbininae) and an operculum with a “thick, convex exterior calcareous pad” (Hickman and McLean, 1990, p. 52). Other distinguishing shell characters included the black color of the outer shell layer, an oblique aperture, the absence of an umbilicus in adult specimens, a predominance of spiral sculpture, and an inner nacreous layer. New fossil data show that the black color is not diagnostic of the entire genus. The morphology of the operculum is distinctive for the subfamily and genus, however, as is the quadrupartite structure of the columella described in this paper.

*Prisogaster niger* (Wood, 1828)

(Figures 4–10, 13, 14)

*Turbo niger* Wood, 1828, p. 18, pl. 6, fig. 1; d’Orbigny, 1840, 5:411–412, vol. 9 (Mollusca), pl. 55, figs. 9–11.

*Turbo niger* Gray, 1839, p. 143, pl. 36, fig. 1; Hupé, 1854, p. 140.

*Turbo* (Prisogaster) *niger* Wood.—Dall, 1899, p. 238.

*Prisogaster niger* Wood.—Möh, 1850, p. 21; Carcelles and Williamson, 1951, p. 268; Dell, 1971, p. 197; Marincovich, 1973, p. 24, fig. 41; Osorio et al., 1979, p. 18, fig. 15; Ramírez, 1981, p. 130, fig. 154; Alamo and Valdivieso, 1997, p. 15, fig. 30; Guzmán et al., 1995, p. 37, fig. 27; Forcelli, 2000, p. 64, fig. 102; Aldea and Valdivinos, 2005, p. 300, fig. 841.

*Prisogaster niger minor* Möh, 1850, p. 21.

*Turbo* (Prisogaster) *niger* Hupé, 1854, p. 146, Malacologia, pl. 4, figs. 4, 4a, 4b.

Diagnosis: Spiral cords and interspaces purple-black. Whorls slightly angulate anteriorly. Spiral sculpture of 13 to 24 primary spiral cords, including six to ten cords on base.

Description: Shell thick, up to 30 mm long, globose, variably compressed axially. Spire variably elevated, about one-quarter to one-third of shell length. Protoconch unknown; teleoconch with about five whorls. Whorls broadly rounded posteriorly, very weakly angulate or biangulate anteriorly; periphery anterior to axial midpoint of body whorl. Sutures usually appressed, sometimes slightly impressed. Exterior purple-black, spire usually corroded, nacreous. Axial sculpture absent. Spiral sculpture of 13 to 24 primary spiral cords, including six to ten on base; cord widths vary irregularly two-fold. Most posterior spiral cord wider, flatter, forming collar against preceding whorl. Interspaces narrower.
than spiral cords, shallow, sometimes crossed by strongly prosocline colabral growth-line lamellae. Aperture oblique, diagonally ovate, with incomplete peristome. Umbilicus absent in juveniles and adults. Outer lip thick, strongly prosocline, with weak inflection posteriorly and salient adjacent to suture; inner edge smooth, nacreous. Parietal and umbilical areas weakly excavated, nacreous; sometimes with weak anal canal without sinus. Columella with innermost white column ending anteriorly at slight inflection near columellar base; medially with slightly ex-
Excavated, curved, nacreous band alongside innermost column, narrowing anteriorly, then broadening at base of aperture to join nacreous inner layer of outer lip; also with weakly sinuous white ridge outboard of nacreous band, extending toward base of aperture and coalescing with interspace between second and third basal spiral cord to form a blunt tooth; first tooth separated from second blunt tooth abaxially by short groove inside aperture; and with shallow, white, elongate excavation bordering ridge at outer margin of columellar area.

Operculum: Exterior convex, steeper posteriorly and adaxially; basal rim smooth, remainder of surface pustulose, more so peripherally than centrally. Two subaxially elongate, adaxially-anteriorly converging creases on adaxial side of diagonal bulge, inner crease extending to adaxial posterior corner; sinusoid growth lines present on adaxial side. Interior nearly planar, coiled, changing from multispiral to puncispiral; all coils with long growing edge. Subsurface texture reticulate with elongating "cells" perpendicular to growth lines.

Material Examined: MUSM INV, 113, DV 461-1, latest Pliocene, L 13.6, W 15.6; MUSM INV, 114, DV 461-1, middle Pleistocene, L 22.8, W 22.0; MUSM INV, 115, DV 463-1, late Pleistocene, L (21.7), W 25.7; MUSM INV, 116, DV 1629-1, latest Pliocene, L 15.3, W 17.9; MUSM INV, 117, DV 1629-1, L 12.7, W 14.1; UWBM 97828, DV 398-1, Recent, L 18.3, W 17.4; UWBM 97829, Pisco Bay, Recent, L 18.4, W 19.1; UWBM 97830, Pisco Bay, Recent, L 14.6, W 15.1; UWBM 97831, DV 461-1, L 16.3, W 15.5; UWBM 97832, DV 464-1, L 21.0, W 21.6; UWBM 97833, DV 463-1, L (23.5), W 27.0; UWBM 97834, DV 720-1, Holocene, operculum, L 5.1, W 4.4; UWBM 97835, DV 1629-1, L 16.0, W 19.1; UWBM 97836, DV 1629-1, L 13.5, W 14.2; UWBM 97837, DV 1629-1, operculum, L 8.9, W 7.1; Devries collection: 1pm, Chile, Recent, lot of one; Caldera region, northern Chile, from eight meters deep on sand and rocks, Recent, lot of two; DV 461-1, lot of two; DV 463-1, lot of six; DV 720-1, lot of twelve; DV 730-1, Holocene, lot of one and one operculum; DV 1252-1, latest Pliocene, lot of 3.

Distribution: Ecuador (7°N) to northern Peru; LACM collections. Recent, north-central Peru; Holocene. Recent, Southern Peru: latest Pliocene, early Pleistocene, middle Pleistocene, late Pleistocene. Recent, Chile: middle Pleistocene to Recent (Hern, 1969; Valdivinos, 1999).

Remarks: Modern specimens of *Prisogaster niger* vary in the number of spiral cords and height of the spire. The oldest specimens of *P. niger* from southern Peru have only 13 to 15 primary spiral cords between the columella and suture (e.g., Figures 13, 14), about as few as the youngest specimen of the older *P. valenciensi*. Specimens of *P. niger* differ from those of *P. valenciensi* by lacking any vestige of cream-colored banding of cords or interspaces. The modern range of *Prisogaster niger* extends from 7° N to 41° S (LACM collections) and beyond to the Straits of Magellan (Osorio et al., 1979; Valdivinos, 1999), a distribution more extensive than ascribed to the species by Dall (1909) or Alano and Valdivieso (1997). The Pleistocene record is limited to southern Peru and Chile, with no records from the marine *tablazos* of northern Peru (DeVries, 1985). The late Pleistocene record is still more restrictive, with only southern Peruvian specimens known, including the oldest, which were found southeast of Calla (DV 1629-1) in the uppermost cope (Unit IV) of the Hualcoelco section (Figure 3), a shell bed dominated by thick disarticulated valves of the bivalve, *Mulinia edulis* (King, 1851).

A second modern species assigned to *Prisogaster* has been the Chilenan *P. elevatus* (Eyoud and Souleyet, 1852) (Souleyet, 1852, v. 2, p. 594, pl. 37, figs. 15-19; Nicosia and Gaete, 2003). The original figures of *"Turbo elevatus,"* however, nor the deep lunate columellar/parietal excavation, is characteristic of Chilenan *Tricolla*, but rather suggest the Chilean trochid, *Diloma nigerrima* (Gmelin, 1791). The generic assignment of *"Turbo elevatus"* remains in doubt.

*Prisogaster valenciensi* new species

(Figures 15-19, 22)

Diagnosis: Compressed axially; sculpture of five to 14 broadly rounded charcoal-gray primary spiral cords, including two to four on the base; one or more interspaces cream-colored.


Type Material: UWBM 97838, DV 1254-Bal 8, holotype, late Pliocene, L (13.3), W 15.9; UWBM 97839, paratype, DV 1254-Bal 6, L (13.8), W 15.5; MUSM INV...
Type locality: Roadside along the Panamanian Highway, 10 km southeast of Chala. Locality-samples DV1254-Bal 6, DV1254-Bal 8, DV1254-Bal 10, late Pliocene, in section at 35.12, and 47.5 meters, respectively, above crystalline basement (Figures 2, 3). 13°52' S, 74°10' W (Chala 1:100,000 quadrangle).

Other Material Examined: UWBM 97840, DV 1031-1, late early Pliocene, L (12.2); W 13.0.

Distribution: Southern Peru: late early Pliocene to late Pliocene.

Etymology: Named in honor of Dr. Niels Valenciano Chacón, director of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

Remarks: The incomplete specimens of Prisogaster valenciæi preclude a complete description, but the shape, size, and spiral sculpture clearly mark them as examples of Prisogaster. These specimens differ from P. niger by having one or more cream-colored interspaces and generally fewer and more clearly differentiated primary spiral cords. The oldest known specimen of P. valenciæi is from the Pliocene section above Playa Huacaclaco (Unit II, DV 1254-Bal 6); it has several broad dark spiral cords alternating with cream-colored bands that sometimes encompass a spiral cord and interspace (Figures 18, 22). A specimen from several kilometers away (DV 1031-1) has very few spiral cords, all gray, and equally wide interspaces, all cream-colored (Figures 16, 17, 19).

Most specimens of Prisogaster valenciæi were found in Unit II and the lower part of Unit III of the Huacaclaco section (DV 1254; Figure 3) in cobbly barnacle-rich bioclastic gravel and poorly sorted coarse-grained sandstone thought to have been deposited intertidally or at very shallow subtidal depths. Associated molluscan taxa include Acanthina spp. Concholepus spp. Choromytilus choris (Molina, 1782); and a new species of Xantochorida Fischer, 1884 (DeVries, 2005a).
Type Material: UWBM 97841, DV 571-1, holotype, middle late Miocene, L 13.9, W 15.4; UWBM 97842, DV 571-1, paratype, middle late Miocene, L 21.1, W (18.5); UWBM 97843, DV 571-1, paratype, L 17.9, W 19.3.

Type Locality: Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona (= El Jahnay locality of Muizon and DeVries, 1985). Shell banks on south-facing slope, 15°26′57″ S, 74°52′06″ W (Acari 1:100,000 quadrangle).

Material Examined: MUSM INV 120, DV 1598-1, L 12.4, W 12.1; MUSM INV 121, DV 1598-1, L 11.1, W 11.5; MUSM INV 122, DV 1635-1, early Pliocene, L 9.4, W 11.0; MUSM INV 123, DV 460-1, lot of two; MUSM INV 124, DV 573-1, L 12.7, W 14.5; MUSM INV 125, DV 571-1, L 17.8, W 16.0; UWBM 97844, DV 1598-1, early Pliocene, L 9.4, W 8.2; UWBM 97845, DV 1598-1, L 12.1, W 12.7; UWBM 97846, DV 460-1, early Pliocene, L 5.9, W 10.3; UWBM 97847, DV 573-1, early Pliocene, L 12.0, W 13.0; UWBM 97848, DV 573-1, operculum, L 8.7, W 7.8. DeVries collection: DV 1598-1, lot of four; DV 423-3, middle Pliocene, lot of two; DV 1029-1, early Pliocene, lot of two; DV 806-1, late Miocene, lot of one; DV 380-2, early Pliocene, lot of one.

Distribution: Southern Peru: middle late Miocene, early Pliocene.

Etymology: Named after James H. McLean, malacologist, Natural History Museum of Los Angeles County.

Remarks: Specimens of Prisogaster stucchi differ from those of P. niger by being uncompressed axially, by having an outer calcitic layer that is thin, sometimes with brown mottling and prosocline axial stripes, and by having spiral cords that are narrower and higher, with broader interspaces. The complex structure of the columella, however, is identical with that of P. niger, as is the operculum. Prisogaster melani exhibits considerable variation in spiral ornamentation, with specimens from the same horizons being alternatively densely sculptured with 15 spiral cords (Figures 24, 30), moderately sculptured with eight primary and two secondary cords (Figure 26), and lightly sculptured with ten subordinated cords that barely rise above the neighboring wide interspaces (Figures 31, 32). Some Miocene and younger Pliocene juvenile specimens (Figures 28) have a pronounced biaugulate profile produced by two strong primary spiral cords posterior to the suture, a feature shared with juveniles of many turbinine species (Hickman and McLean, 1990).

The oldest specimens of Prisogaster melani were found near Alto Grande (DV 571-1) in middle upper Miocene beds with an estimated age of about 9 Ma (Muizon and DeVries, 1985). Lower Pliocene specimens from Sacaco (DV 350-2) and Yanca (DV 1598-1, DV 1635-1) are identical with the Miocene specimens.

DISCUSSION

The extant Prisogaster niger, which appeared about two million years ago, has changed little in either its pattern of low rounded spiral cords or its uniformly purple-black color. Prisogaster melani, in contrast, resident on southern Peruvian coasts from 9 Ma to 3 Ma, has highly variable spiral sculpture and coloration. Some specimens (Figures 24, 28, 30) exhibit the high spires, impressed sutures, numerous primary spiral cords, and bicarinulate juvenile whorls that characterize many members of Turbinellinae. These similarities strengthen the case of Hickman and McLean (1990) that Prisogasterinae and Turbinellinae are sister taxa and that Prisogaster arose from an advanced turbinine.

Prisogaster probably appeared in southern Peru during the early late Miocene, since no turbinines have been found in middle Miocene or older beds in southern Peru. Its arrival coincided with that of other taxa that constituted the core of a late Miocene-early Pliocene mollusc fauna in southern Peru and northern Chile (DeVries, 2002). The route by which Prisogaster or its predecessor arrived in Peru is unclear. No medium-sized or large turbinids are known from Miocene deposits of Chile (Philippi, 1887; Tavera, 1979; Nielsen et al., 2004). The only Miocene turbinid from northern Peru (Spiekier, 1922) is probably related to two northern Peruvian Recent species of Turbo (Taeniaturbo) Gray, 1850; the modern species have opercula with strong and complex external spiral relief very unlike the sculpture on the opercula of fossil and Recent species of Prisogaster. The pustulose convex opercula and multizipitate columellae of some species of Turbo (Marmarostoma) Swainson, 1829, do resemble those of Prisogaster, although opercula of the former are more broadly convex and not scored by diagonal grooves, and the columellae of the shell do not have a well differentiated ridge and groove structure toward the periphery of the columellar area. Modern species of Turbo (Marmarostoma) have an Indo-Pacific distribution, suggesting that Prisogaster might be a trans-Pacific immigrant, as other western American taxa have been (Emerson, 1978), including, it appears, the trochid species Diloma nigerrima (Gmelin, 1791) (Donald et al., 2005).

The transition from the globular tan-colored and brown-mottled Prisogaster melani to the axially compressed purple-black P. niger occurred during the time represented by Units II and III of the Huacallico section (Figure 3), i.e., latest early Pliocene to late Pliocene, in the guise of P. valenciae. The oldest specimen of P. valenciae (Figures 18, 22; DV 1254-Bal 6) show the first appearance of broad black spiral cords and the persistence of thin cream-colored interspaces, the latter of which become reselected to spire whorls on the youngest specimens (Figure 15; DV 1254-Bal 10).

The late Pliocene appearance of a purple-black external calcite layer in Prisogaster is an odd event that nonetheless is repeated in western South American Diloma Philippi, 1845 (Marincovich, 1973; Nielsen, 2003). The significance of these purple-black outer layers in Quaternary turbinids and western South American trochids [Miocene-Pliocene undescribed species of Tegula (Chlo-
rnostoma) Swainson, 1840; Tegula (Chlorostoma) atra (Lesson, 1830); T. (C.) leucos (d’Orbigny, 1841); T. (C.) tridentata (Potiez and Michaud, 1836); and, incipiently, in T. (C.) quadricostata (Gray, 1828), as well as trochoids from mid- and high-latitude northern Pacific and South African shorelines, merits further investigation.

Occurrences of most modern and Pleistocene specimens of Prisogaster aiger are consistent with a high-energy intertidal and shallow subtidal habitat with rock- and gravel substrates (e.g., DeVries collection, Recent, juveniles, eight meters deep, northern Chile; DV 720-1, Holocene, gravel beach ridge, northern Peru; DV 1629-1, upper Pliocene; 250 m marine terrace, southern Peru). The same is true for upper Pliocene occurrences of specimens of P. valenciæi, which are found in bioclastic coarse-grained sandstones and gravel deposited within 150 meters of a mountainous paleo-shoreline. In contrast, specimens of the older P. melecani are found in well-sorted hummocky cross-beded sandstones with shell banks of large venerid bivalves, as well as bioclastic sandy gravels, suggesting that the habitat of the late Miocene-early Pliocene species also included intertidal environments with lower energies than typical for intertidal environments.

The late Pliocene was a time of morphological novelty for Mos-Pliocene taxa in Peru other than Prisogaster: Acmaelithine Fischer von Waldheim, 1867 (DeVries, 2003), Concholepas Lamark, 1799 (DeVries, 2000), Xanthochonus Fischer, 1854 (DeVries, 2005a), and Tegula Lesson, 1835 (DeVries, unpublished data). It was during this time that the molluscan fauna of the Mo-Plumaian Faunal Province was undergoing the second phase of a local species-level mass extinction (DeVries, 2001) that coincided or at least overlapped with increased rates of tectonic uplift in northern and southern Peru (DeVries, 1986, 1988; Ortlieb et al., 1995) and the transport of greater quantities of gravel and rounded cobbles of Andean andesitic rock to the southern Peruvian coast (DeVries, 2003).

CONCLUSION

With the discovery of two new fossil species in southern Peru, the “enigmatic” turbinid Prisogaster now has a pedigree extending back to the middle late Miocene. Miocene and early Pliocene specimens with turbinid features suggest Prisogaster did arise from a middle Miocene species of Turbo, a possibility raised by Hickman and McLean (1960). The place from which Prisogaster or its turbinine ancestor immigrated is uncertain, but based on some similarity in key characters with some species of Turbo (Marmarostoma), the Indo-Pacific region seems as likely as the Magellanic or Panamic regions. The Prisogaster shell underwent a rapid transformation during the late Pliocene, including an axial compression, a streamlining of sutural contacts, a thickening of the shell, a broadening and smoothing of primary spiral cords, and the development of a purple-black outer shell layer. Some of these changes might be construed to have improved the strength of Prisogaster shells to more successfully withstand attacks from clawed predators, which seem to have been a common hazard for individuals of P. melecani (see Figures 20, 24, 30, 31). Alternatively, a stronger and more stable shell may have enabled individuals of P. aiger to survive on rockier, higher-energy, intertidal substrates. Such environments became the norm for coastal Peru when much of the coast underwent a 200 m uplift during the latest Pliocene and protected embayments became few and much smaller (DeVries, 2001).

ACKNOWLEDGMENTS

I would like to thank M. Urbina, R. Salas, and M. Stucchi of the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima, Peru, for their hospitality and help in the laboratory and field. Helpful suggestions for improving the manuscript were offered by C. Hickman and S. Nielsen. Support for field research was provided in part by a Fulbright scholarship in 1999.

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APPENDIX

Locality-samples:

DY 380-2 Sacaco, in cross-bedded sandstones just below farmhouse, 15°32’29” S, 74°43’53” W (Acari 1: 100,000 quadrangle), Lower Piocene.

DY 398-1 Playa Caumestos, Bahía de la Independencia, Peru (Punta Grande 1:100,000 quadrangle), Recent.

DY 423-1 Terrace deposit capping Miocene strata west of Quebrada Huancacangua, 14°55’29” S, 75°17’54” W (Palpa 1:100,000 quadrangle), Piocene.

DY 160-1 Roadcut along Panamerican Highway, de-
scent from north into Yauca. Shell beds, 15°39'49" S, 74°31'50" W (Yauca 1:100,000 quadrangle). Lower Pliocene / lowermost Pleistocene. [Note: This locality was mistakenly referred to as Morro Abra de los Chaparrinos (the "Huacllaco section" of DV 1254) in DeVries (2005a, b.)]

DV 1252-1 Quebrada de la Vaca, roadcut along Panamerican Highway, south of south wall, uppermost terrace above non-marine deposits, 15°48'56" S, 74°18'50" W (GPS; Chala 1:100,000 quadrangle), uppermost Pliocene.

DV 1254-Bal 6 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco, 35 meters above basement rocks in measured section (see Figure 3), 15°53'25" S, 74°09'52" W (GPS; Chala 1:100,000 quadrangle), upper lower Pliocene.

DV 1254-Bal S Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco, 42 meters above basement rocks in measured section (see Figure 3), 15°53'25" S, 74°09'52" W (GPS; Chala 1:100,000 quadrangle), upper Pliocene.

DV 1254-Bal 10 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco, 47.5 meters above basement rocks in measured section (see Figure 3), 15°53'25" S, 74°09'52" W (GPS; Chala 1:100,000 quadrangle), upper Pliocene.

DV 1598-1 Roadcut along Panamerican Highway, descent from north into Yauca. Shell beds, 15°39'49" S, 74°31'50" W (Yauca 1:100,000 quadrangle), lower Pliocene.

DV 1629-1 Section above Playa Huacllaco, ten km southeast of Chala, uppermost coquina beds (Unit IV; see Figure 3), 15°52'47" S, 74°10'13" W (GPS; Chala 1:100,000 quadrangle). Uppermost Pliocene / lowermost Pleistocene.

DV 1635-1 Yauca Depression, west of Panamerican Highway. 15°39'33" S, 75°34'54" W (GPS; Yauca 1:100,000 quadrangle), lower Pliocene.
A new species of *Hoplodoris* Bergh, 1880 (Gastropoda: Opisthobranchia: Nudibranchia) from the Atlantic Ocean

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ABSTRACT

Discodorid nudibranchs belonging to the genus *Hoplodoris* Bergh, 1880 have not been recorded previously from Atlantic waters. In the present paper a new species found in Ilha de Cabo Frio (Cabo Frio Island), Brazil (Arraial do Cabo, State of Rio de Janeiro), is described and illustrated. The new species is compared with other species of *Hoplodoris*. The new species can be distinguished from other species by its distinctive body color pattern and by characters of the reproductive system and radial morphology.

Additional Keywords: Brazil, southwestern Atlantic, sea slug, Discodorididae, *Hoplodoris hansrosaorum*.

INTRODUCTION

Up to now, seven species of *Hoplodoris* Bergh, 1880 are known (Falvey and Gosliner, 2003). Some species have been previously assigned to the genus *Carminodoris* Bergh, 1889. The original descriptions of the genera *Hoplodoris* and *Carminodoris* were done by Bergh (in 1880 and 1889, respectively). However, the incomplete descriptions of type species and the lack of additional specimens since the original descriptions are some of the reasons for the difficulties in undertaking taxonomic research in this group (Falvey and Gosliner, 2003). Since the 1980s, different authors have compiled a list of the distinguishing characters of *Hoplodoris* (Thompson, 1975; Miller, 1991; Valdés, 2002). Falvey and Gosliner (2003) examined discodorid specimens from the type localities and concluded that the genus *Carminodoris* is a junior synonym of *Hoplodoris*; however, later, Dayrat and Gosliner (2005) retained both genera.

The genus *Hoplodoris* has thus far only been found in the Indian and Pacific Oceans. The present study is the first record of *Hoplodoris* from the Atlantic Ocean.

An abbreviation used in the text is MZUSP, for Museu de Zoologia da Universidade de São Paulo (Brazil).

SYSTEMATICS

Family Discodorididae Bergh, 1891
Genus *Hoplodoris* Bergh, 1880

*Hoplodoris hansrosaorum* new species

(Figures 1–14)


Buccal Armature (Figures 3–13): Radular formula 24×31,0,31. Lateral teeth hook-shaped with denticles along outer margin of cusp (Figure 3, 9). Middle radial teeth with a more elongate cusp with approximately 14 denticles. Inner side of cusp devoid of denticles (Figure 8). Approximately eight outermost lateral teeth usually flat, shaped as elongate plates; plates closely packed together (Figure 10, 11). Each plate surrounded by very fine denticles, plates becoming smaller toward external side of radula (Figures 4, 12). Labial cuticle with elongate jaw rodlets, some rodlets with rounded tips and other irregularly tipped (Figures 5, 13).

Reproductive System (Figures 6, 7, 14): Bulbous ampulla folded into itself. Prostate rounded, lying next to ampulla, narrowing into deferent duct. Deferent duct widening into penial bulb. Bursa copulatrix large, ovate.
Figure 1-2. *Hoplodoris hansrosaorum*. Living holotype; 27 mm length. 1. Dorsal view. 2. Ventral view.

Figures 3-7. *Hoplodoris hansrosaorum*. 3. Middle lateral tooth showing the denticles. 4. The three outer lateral teeth. 5. Jaw rodlets. 6. Reproductive system (*ag*: accessory gland; *amp*: ampulla; *bc*: bursa copulatrix; *dd*: deferent duct; *fg*: female gland; *ga*: genital atrium; *hd*: hermaphrodite duct; *pb*: penial bulbus; *pr*: prostate; *rs*: receptaculum seminis; *st*: stylet; *vd*: vaginal duct). 7. Detail of the accessory gland duct with the stylet. Scale lines (3-5) = 10 μm; (6) = 0.5 mm.

Bursa about three times as large as receptaculum seminis. Vaginal duct emerging from base of bursa, thick and looped. (Dissection of the only available specimen did not reveal the presence of genital armature.) Large, elongate accessory gland present, opening into genital atrium. Gland has narrow duct armed with long, tapering stylet (Figures 7, 14).

**Holotype:** MZUSP 52190, 27 mm length, colls. Jesús S. Troncoso and Francisco J. García, 28 July 1999.

**Type Locality:** Collected in the intertidal zone at Ilha de Cabo Frio (Cabo Frio Island), Arraial do Cabo, State of Rio de Janeiro, Brazil.

**Etymology:** The species is named after Hans Bertsch, great friend and malacologist, and his wife Rosa.

**DISCUSSION**

Several characters allocate the species into the genus *Hoplodoris*: species in this genus are characterized by
Table 1. Diagnostic characters in species of *Hoplodoris*

<table>
<thead>
<tr>
<th></th>
<th><em>H. hansrosaorum</em></th>
<th><em>H. armata</em></th>
<th><em>H. bifurcata</em></th>
<th><em>H. bramale</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Distribution</strong></td>
<td>Brazil</td>
<td>Japan</td>
<td>Hawaii, Japan, Philippines and Okinawa</td>
<td>Pacific Coast of Costa Rica</td>
</tr>
<tr>
<td><strong>Ground color of dorsum</strong></td>
<td>Brown orange central dorsum, and whitish orange towards the mantle edge</td>
<td>Yellowish gray with some brown flecks</td>
<td>Gray with mottled shades of darker grays and reddish-browns. Central red-brown band</td>
<td>Brown or tan</td>
</tr>
<tr>
<td><strong>Tubercle color</strong></td>
<td>Brown orange, with a white ring at the base</td>
<td>Brown with a white ring basally. Some specimens prominently capped with chocolate brown</td>
<td>With a white ring at the base, followed by a reddish-brown or tan ring, and a white tip</td>
<td>Brown with a white ring at the base</td>
</tr>
<tr>
<td><strong>Tubercles morphology</strong></td>
<td>Rounded</td>
<td>Rounded of different sizes</td>
<td>Large, round and tapered</td>
<td>Large and rounded</td>
</tr>
<tr>
<td><strong>Rhinophore color</strong></td>
<td>Orange with cream tip</td>
<td>Dark yellowish gray</td>
<td>Tan color with white tip</td>
<td>Brown with a white tip</td>
</tr>
<tr>
<td><strong>Branchial leaf color</strong></td>
<td>Anterior leaves, yellow and middle and posterior leaves orange</td>
<td>Darker yellowish gray leaves</td>
<td>Tan with whitish flecks the anterior leaves. Red-brown the posterior</td>
<td>Light tan</td>
</tr>
<tr>
<td><strong>Radula</strong></td>
<td>Formula: 24 × 31.0.31. Middle lateral teeth with about 14 denticles. The eight outermost lateral teeth are elongated plates with denticles. No hamate.</td>
<td>Formula: 45 × 50-60, 0.50-60. Smooth teeth</td>
<td>Formula: 25 × 31.0.31. Innermost lateral teeth bifid. Middle radular teeth with 5-8 denticles. Two or three outermost teeth shorter and denticulate</td>
<td>Formula: 28 × 38, 0.38. Innermost and middle teeth smooth. Two outermost teeth smaller and denticulate</td>
</tr>
<tr>
<td><strong>Jaw roddets</strong></td>
<td>With rounded and irregular tip</td>
<td>Fibrous</td>
<td>Irregularly tipped</td>
<td>Irregularly tipped and with irregular edges</td>
</tr>
<tr>
<td><strong>Accessory gland</strong></td>
<td>One long large gland</td>
<td>Two glands</td>
<td>One large and bulbous gland</td>
<td>Two bulbous glands</td>
</tr>
<tr>
<td><strong>Receptaculum seminis</strong></td>
<td>Much smaller than the bursa copulatrix</td>
<td>Small and elongate</td>
<td>Much smaller than the bursa copulatrix</td>
<td>About the same size as the bursa copulatrix</td>
</tr>
<tr>
<td><strong>Ampulla</strong></td>
<td>Bulbous, doubled on itself</td>
<td>Elongated</td>
<td>Long, thin and tubular</td>
<td>Long, thin and tubular</td>
</tr>
</tbody>
</table>

presence of simple, rounded tubercles covering the dorsum, head with two conical oral tentacles, anterior border of the foot grooved and notched, labial armature armed with jaw elements, radula composed of denticulate hamate teeth, and reproductive system with a large and pedunculated accessory gland armed with copulatory spine (Valdés, 2002).

*Hoplodoris hansrosaorum* new species is externally similar to *H. bramale* Fahey and Goshiner, 2003, and *H. grandiflora* (Pease, 1860) from Indo-Pacific. The mantles of both *H. bramale* and *H. grandiflora* are brown and have tubercles surrounded by a white ring, but *H. hansrosaorum* has a brown-orange central dorsum and is white-orange towards the mantle edge. *Hoplodoris bramale* and *H. grandiflora* have tan or brown rhinophores and gill leaves, whereas the rhinophores of *H. hansrosaorum* are orange and the gill leaves are cream and orange.

Internally, *H. hansrosaorum* differs from *H. bramale*, particularly in relation to their radular teeth. *Hoplodoris hansrosaorum* has teeth with denticles on the outer margin, and jaw elements with rounded tip, whereas *H. bramale* has teeth devoid of denticles, except for the two outermost ones; the jaw roddets are irregularly tipped and have irregular edges. Differences in the reproductive system also distinguish the two species. *Hoplodoris bramale* has long and tubular ampulla, two accessory glands, and the receptacular seminis is about the same size as the bursa copulatrix. However, *H. hansrosaorum* has a thick ampulla, one accessory gland, and the receptacular seminis is about a third the size of the bursa copulatrix.

The radular teeth of *H. hansrosaorum* and *H. grandiflora* are similar. Both species have lateral teeth with up to 14 denticles on the outer edge of the cusp, and the outer lateral teeth have small denticles. *Hoplodoris hansrosaorum* has approximately eight outermost lateral teeth as plates, which are very close to each other, and each plate is surrounded by very fine denticles. However, *H.
Table 1. Continued.

<table>
<thead>
<tr>
<th><strong>H. estrellado</strong></th>
<th><strong>H. flamma</strong></th>
<th><strong>H. grandiflora</strong></th>
<th><strong>H. nodulosa</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gosliner and Behrens, 1998; Fahey and Gosliner, 2003</strong></td>
<td>Fahey and Gosliner, 2003</td>
<td>Fahey and Gosliner, 2003</td>
<td><strong>Eastern Australia, Western Australia and New Zealand</strong></td>
</tr>
<tr>
<td><strong>Philippine Islands, Western Australia, Vietnam, Indonesia, Marshall Islands, Solomon Islands, Coral Sea</strong></td>
<td>Indonesia</td>
<td><strong>Hawaii, Philippines, Tanzania, Palau, Mauritius, Kerama Island and Madagascar</strong></td>
<td>Gray to yellows and reddish-browns, with mottled shades of darker hues. Color more distinct on the central dorsum. On the central dorsum the tubercles have the same coloration of mantle. Tubercles with white ring at base towards the mantle edge. Large, round and tapered</td>
</tr>
<tr>
<td><strong>Tan with brown and white specks</strong></td>
<td>Reddish-mottled brown or tan. Bright red central dorsum, with white areas around them</td>
<td><strong>Brown or tan. Some specimens with dark spots near the mantle edge. Others with a dark ring of tubercles on dorsum</strong></td>
<td><strong>Tan with a white tip</strong></td>
</tr>
<tr>
<td><strong>White patch with yellow center, surrounds a medial group of brown tubercles. Some white, and tan tubercles.</strong></td>
<td>Bright red in the center of the dorsum, with white ring at the base. Reddish-brown tubercles along the mantle edge, some of them with white tip.</td>
<td><strong>Large and rounded</strong></td>
<td><strong>Tan anterior leaves with whitish flecks. The posterior leaves can be a darker color</strong></td>
</tr>
<tr>
<td><strong>Large tapering tubercles</strong></td>
<td>Large and rounded</td>
<td><strong>Light tan with white tip</strong></td>
<td><strong>Formula: 25 x 53.0.53.</strong> Smooth innermost and middle teeth. Four outermost lateral teeth short and denticulate</td>
</tr>
<tr>
<td><strong>Reddish brown with white specks</strong></td>
<td><strong>Tan and brown with white tip</strong></td>
<td><strong>Light tan with white tip</strong></td>
<td><strong>Irregularly tipped</strong></td>
</tr>
<tr>
<td><strong>Tan with brown and white specks</strong></td>
<td><strong>Light gray with tan tips</strong></td>
<td><strong>Light tan with frosted tips</strong></td>
<td><strong>Irregularly tipped</strong></td>
</tr>
</tbody>
</table>

**H. grandiflora** has outer lateral teeth with small denticles, and the two or three penultimate lateral teeth are hamate and much shorter than the rest. The reproductive system of the two species are similar, but the ampulla and the accessory gland of **H. grandiflora** are long and tubular (bulbous in **H. hansrosaorum**).

There are differences between **Hoplodoris hansrosaorum** and other **Hoplodoris** species. For example, the coloration of **Hoplodoris bifurcata** (Babs, 1993) is complex and variegated (Fahey and Gosliner, 2003). The background color in this latter species is gray with mottled shades of darker grays and reddish-browns scattered over the mantle, whereas **H. hansrosaorum** has whitish-orange background color. **Hoplodoris bifurcata** has a red-brown band of color band on the central dorsum, which is lacking in **H. hansrosaorum**. Both species have a white ring at the base of the dorsal tubercles, but **H. bifurcata** has also a red-brown or tan ring on the tubercles and a white tip. **Hoplodoris bifurcata** has tan and white rhinophores, the anterior gill leaves are tan with whitish flecks of color, and the posterior leaves are red-brown. This coloration differs from that of **H. hansrosaorum**, because the rhinophores are orange with a pale cream tip, and the gill leaves are yellow-cream and orange. Further, the radial morphology differs between these species. The innermost lateral tooth of **H. bifurcata** is bifid, the middle teeth have a cusp with 3–8 denticles, and the 2–3 outermost lateral teeth are denticulate plates. **Hoplodoris hansrosaorum** has an innermost lateral tooth with one cusp, the middle teeth have a cusp with about 14 denticles, and the eight outermost lateral teeth are denticulate plates.
The background color of *Hoplodoris nodulosa* (Angas, 1864) ranges from gray to yellow and reddish-brown; a white ring may be present at the base on the tubercles. That species differs from *H. hansrosaorum* by its tannicolored rhinophores and tan gill leaves with whitish flecks. Furthermore, the four outermost radular teeth of *H. nodulosa* are dentilicate (the rest are smooth), and there are two accessory glands in the reproductive system.

Main internal and external morphological characters that can be used to distinguish among the species of *Hoplodoris* are compiled in Table 1.

In relation to geographic distribution, the species *H. grandiflora*, *H. bifurcata*, *H. nodulosa*, *H. bramale*, *H. estrelidade* Gosliner and Behrens, 1998, *H. flammea* Fahey and Goslin, 2003, and *H. armata* (Baba, 1993), are known only from the Pacific and Indian Ocean. Therefore, *H. hansrosaorum* is the first record of *Hoplodoris* from the Atlantic Ocean.

ACKNOWLEDGMENTS

The authors are very grateful to Dr. Paulo Marcio Costa and Dr. Renata Gomes for assistance in collecting nudibranchs; the Rear-Admiral Napoleão Gomes, director of the Instituto de Estudos do Mar of the Brazilian Navy, for facilitating the transport by boat in the zone of Arraial do Cabo, and Jesus Méndez for the scanning electron micrographs at CACTI of Vigo University. This paper has been partially supported by the projects PHB2002-0045-FC and CGI2004-20366-E/IBOS, of the Ministerio de Educación y Ciencia (MEC, Spain).

LITERATURE CITED


First report of the invasive freshwater snail *Tarebia granifera* (Lamarck, 1816) (Gastropoda: Thiaridae) from Israel

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ABSTRACT

An invasive operculate gastropod, the freshwater snail *Tarebia granifera*, is reported for the first time from Israel. In a survey of 52 freshwater sites populations of *T. granifera* were discovered at four sites, in abundance at two of them, one of which included individuals infected with the trematode *Philophthalmus*, sp. In both sites *T. granifera* outnumbered its close native relative and potential competitor, the triad *Melanoidea tuberculata*, in abundance and mean embryo counts, and in one of the habitats almost excluded it. This invasion may have important public health implications, due to *T. granifera*’s role as an intermediate host of the human eye flukes. Furthermore, evidence of long-distance dispersal or multiple invasion sites may facilitate the host’s and parasite’s spread to other water bodies used for agriculture and fish ponds.

Additional Keywords: Melanoidea tuberculata, Philophthalmus, biological invasion.

INTRODUCTION

Biological invasions threaten terrestrial, marine and freshwater biodiversity, as increased replacement of native species by highly competitive generalist invaders may lead to biotic homogenization (Prenter et al., 2004). In particular, agricultural trade has broken down many natural dispersal barriers (Kolar and Lodge, 2001) and facilitated the invasions of many exotic species, with dramatic effects on ecosystem functioning (Carlsson, Brommark, and Hansson, 2004). Among the most notorious invaders are mollusks, which cause extensive economic loss and disturbance because of their detrimental impact on indigenous fauna and their intermediary role in transmitting parasitic diseases to humans (Pointier, 2001). Among gastropods, the freshwater snail *Melanoidea tuberculata* (Müller, 1774), which is native to the Middle East (Pointier, 1999), has invaded North America (Muray, 1984; Murray, 1971). South America (Pointier et al., 1994; De Marco, 1999; Giovannoni, Vieira, and da Silva, 2005), East Africa (Genner et al., 2004), the French Polynesia (Pointier and Marquet, 1990) and the islands of the Pacific (Cowie, 2001b).

Another invasive freshwater snail is *Tarebia granifera* (Lamarck, 1816) (Thiaridae). It is native to Southeast Asia, from India and Ceylon eastward to the Philippines and Hawaii, northward to southern Japan, and southward to the Society Islands (Abbott, 1952), where it is found in a wide variety of habitats including rivers, streams, lakes, drainage ditches, irrigation canals, cement ponds and swamps (Chaniotis et al., 1980b), though shallow, fast-flowing freshwater streams seem to be its preferred habitat (Lachner, Robins, and Courtenay, 1970). *Tarebia granifera* can survive in a wide range of temperatures (7–10°C), can be kept out of water for several days under relative humidity of 80–100% (Chaniotis et al., 1980c) and is even capable of surviving in polluted habitats (Chaniotis et al., 1980b). It feeds on algae, associated microorganisms and small particles of organic matter (Oglesby, 1977). *Tarebia granifera* is ovoviviparous and reproduction is mainly by parthenogenesis (Morrison, 1954), although male presence varies from total absence in populations from Florida and Guam (Abbott, 1952) to frequencies of 22.7% in Puerto Rico (Chaniotis et al., 1980a).

*Tarebia granifera* serves as an intermediate host of numerous trematodes that cause parasitic diseases in humans. Among these are representatives of the superfamilial Heterophyidae, which are vectors of intestinal flukes of animals and humans, e.g. *Metagonimus yokogawai* (Murray and Stewart, 1968). Other trematodes include *Philophthalmus megaharum* (family Philophthalmidae), which affects the vascular membrane of aquatic birds (Jacobson, 1975). As part of the life cycle of the trematodes, a second intermediate host, such as a freshwater crayfish or crab, is necessary and for human infection to be successful, the infected crustacean must be eaten raw (Lachner et al., 1970).
This study documents the first record of T. granifera from Israel and discusses the possible implications of its invasion on public health and on the native freshwater molluscan fauna.

MATERIALS AND METHODS

A survey of 52 freshwater sites was conducted in Israel during July–August 2004 (Figure 1). At each site five random samples were taken by dredging with a square-framed net (50×50 cm, 1 mm mesh) and each sampled scanned for the snails retrieved. Additionally, at two sites that included T. granifera, all snail species found within twenty random squares (20×20 cm) were collected and shell height was measured to an accuracy of 0.01 mm. Most snails were returned to the site. However, to quantify embryo numbers and infection prevalence, 100 randomly chosen individuals of T. granifera and M. tuberculata were transported alive to the laboratory. The number of embryos in each brood pouch was counted and trematode infection determined by examination of the gonad and digestive gland under a light microscope. Individual snails were defined as adults if they measured more than 7 mm in shell height and treated as juveniles if their height did not exceed 7 mm. This definition is based upon the dissection of 266 snails in which embryo presence was scored against shell height.

For statistical analysis, SPSS for Windows version 12.0.2 (SPSS Inc., 2004) was used. Means ±SD were determined and all probabilities discussed are two-tailed. Frequency data were analyzed either with the χ² test or Fisher’s exact test, when possible. An analysis of covariance (ANCOVA) was used to compare mean embryo counts among habitats and species (see Table 1 for details).

RESULTS

Tarebia granifera was only found at four of the 52 sites, all in the Jordan Valley and within a radius of 1.5 km: En Taynon, En um Sidra, En Saharon and Avoka (Figure 1). Since only three T. granifera individuals were found in En Taynon and two individuals in En um Sidra, no further studies were undertaken beyond recording these observations. In En Saharon (n=1386) and Avoka (n=1740) four relatively abundant snail species were found: T. granifera, M. tuberculata, Melanopsis sauleyi (Bourguignat, 1853) and Theodoxus jordani (Sowerby, 1836) (Figure 2). Additionally, there were two species of which only a few individuals were found: Helicobia contempta (Dautzenberg, 1894) and Melanopsis buccinoides (Olivier, 1901).

Species abundances differed significantly between En Saharon and Avoka (χ²=380.3; df=5; P<0.001). Specifically, T. granifera (Fisher’s exact test; P<0.001), M. buccinoides (Fisher’s exact test; P=0.004), T. jordani (Fish-

Figure 1. Distribution of sampling sites in Israel: (1) En Taynon, (2) Avoka, (3) En um Sidra and (4) En Saharon. Due to the resolution of the map, some data points represent more than one sampling site.

er’s exact test; P<0.001) and H. contempta (Fisher’s exact test; P=0.006) were significantly more abundant in Avoka, whereas M. tuberculata (Fisher’s exact test; P<0.001) and M. sauleyi (Fisher’s exact test; P<0.001) were more common in En Saharon.
The size distribution of *T. granifera* in En Saharon was highly bimodal, with the majority of individuals in the sample being young (56.5%) and with an average shell height of 2.8±1.4 mm, compared to 43.5% of adults with mean shell height of 18.2±3.4 mm (Figure 3A). In Avoka, however, size distribution was unimodal and skewed towards adults (78.8%; average height of 10.6±2.5 mm), in contrast to 21.2% of young with mean shell height of 5.0±1.8 mm (Figure 3B).

The size distribution of *M. tuberculata* in both sites was unimodal and skewed towards adults. The En Saharon sample consisted of 74.1% of adults with an average shell height of 12.6±3.4 mm and 25.9% of young with mean shell height of 4.2±1.8 mm (Figure 4A). Similarly, in Avoka there were 67.9% of adults with an average shell height of 8.9±1.7 mm and 32.1% of young with mean shell height of 5.8±0.8 mm (Figure 4B).

The juvenile-adult ratio differed significantly between *T. granifera* and *M. tuberculata* in En Saharon ($\chi^2=56.0; df=1; P<0.001$) but not in Avoka ($\chi^2=1.9; df=1; P=0.165$).

Mean embryo counts of *T. granifera* were 28.1±21.5 (n=100) in En Saharon and 9.6±9.3 (n=100) in Avoka. The mean number of embryos per *M. tuberculata* female was 20.5±17.6 (n=101) in En Saharon and 1.1±1.7 (n=7) in Avoka. Mean embryo counts were significantly higher in En Saharon than in Avoka for both species, but did not differ significantly between species (Table 1).

Infected snails were found only in En Saharon. The brood pouch of six *T. granifera* individuals (6%) was infected by both miracidia and cercariae stages of *Philophthalmus* sp. One *M. tuberculata* individual (1%) was infected by *Centrocestus* sp. In both species infected snails were not carrying embryos.

The National Mollusc collection of Israel has no records of *T. granifera* from Israel. It is also absent from the rich fossil deposits of the Jordan Valley, currently under investigation (J. Heller, personal communication).

**DISCUSSION**

This is the first report of *T. granifera* from Israel, where it was found in four freshwater springs in the Jordan
Table 1. Analysis of covariance testing the effects on female fecundity (number of embryos), with habitat and species as fixed factors and shell height as covariate ($R^2 = 0.463$). Embryo counts were Bio-Cox transformed prior to analysis to meet the normality assumption. The homogeneity of variances criteria was also met using Levene's test of equality of error variances $F = 2.6; df_{1,2} = 5262; P = 0.054$. 

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>F-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole model</td>
<td>1</td>
<td>23585.5</td>
<td>56.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shell height</td>
<td>1</td>
<td>9142.4</td>
<td>87.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Habitat</td>
<td>1</td>
<td>1587.6</td>
<td>45.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species</td>
<td>1</td>
<td>34.3</td>
<td>0.3</td>
<td>ns</td>
</tr>
<tr>
<td>Habitat x Species</td>
<td></td>
<td>213.4</td>
<td>2.0</td>
<td>ns</td>
</tr>
<tr>
<td>Error</td>
<td>261</td>
<td>27344.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Valley. The mode of introduction is unknown but it is likely that, as in Martinique (Pointier et al., 1998), T. granifera arrived via the trade in aquatic plants and pet fish. The invasion of T. granifera into Israel poses an ecological threat to native freshwater mollusks. In particular, T. granifera is likely to compete with other thiarids, notably M. tuberculata (Pointier et al., 1998), as these two species are similar in form and occupy a closely similar microhabitat of soft mud substratum.

The density of T. granifera in Avoka (1139 snails/m²; 52.4%) was more than twice that in En Saharon (511 snails/m²; 29.5%), whereas the density of M. tuberculata in Avoka (35 snails/m²; 1.6%) was almost tenfold less than in En Saharon (290 snails/m²; 1.6%). This may suggest that in sites where T. granifera reaches high densities, it competitively excludes M. tuberculata. The bimodal size distribution of the T. granifera population in En Saharon, consisting of adults and very young individuals, may suggest that in this site T. granifera is still in the midst of the establishment process. It could perhaps indicate that the life-history of T. granifera is different, i.e. adults breed only at a certain time of year and the small size class represents a new cohort of young snails. If that is the case, since M. tuberculata reproduces throughout the year (Ben-Ami and Heller, in press), the T. granifera population must compensate for shorter breeding periods via increased reproduction or reduced juvenile mortality. This may in turn explain the relative success of the M. tuberculata population in En Saharon, whereby the population structure represents the stage in which both species can share the habitat, without competitively excluding each other. Although only a long-term survey of multiple invasion sites in Israel can unravel the exact nature of the competition between the two species, a similar situation was observed in Martinique where T. granifera quickly outnumbered M. tuberculata, though it did not exclude it entirely (Pointier et al., 1998).

The mean number of embryos was larger (though not significantly) in T. granifera than M. tuberculata females at both sites, which in part may explain the competitive advantage of T. granifera over M. tuberculata. Alternative nonexclusive factors, which may explain the competitive advantage of T. granifera, include higher survival rates of juveniles or lower susceptibility to predators, although the latter is less likely because there are no specific molluscs in either site. Additionally, field observations reveal that M. tuberculata occurs only along the banks of rapidly flowing rivers, whereas T. granifera is distributed over the entire river bed, suggesting that the latter species can withstand faster currents and resist dislodgement.

The invasion of T. granifera into Israel may also influence public health, as it was found to be infected by Philophthalmus eye flukes. These parasites are known in Israel from both M. tuberculata, which hosts Philophthalmus distomatus (Radev, Kaney, and Gold, 2000) and M. buccinoides, which hosts P. palpebrarum (Gold, Lang, and Lengy, 1993). Although a case of human infection by P. palpebrarum in Israel was documented almost thirteen years ago (Lang et al., 1993), the genus Philophthalmus appears to be very rare and has not been found in Israel since then (D. Gold, personal communication). Given that six T. granifera individuals (6%) of our sample were found to be infected, and that the parasite's lifecycle requires only two hosts (a snail, and a bird or mammal), this may suggest that Philophthalmus could spread relatively easily. However, in this study M. tuberculata and Melanopsis buccinoides were not found to be infected with Philophthalmus. Since T. granifera has been found to host Philophthalmus megaherms in Cuba (Jacobson, 1975), it may very well be that the T. granifera population found in Israel is infected with a new or another Philophthalmus species, the spread of which depends solely on the invasion success of T. granifera. This may in turn also affect the parasite fauna in the Jordan Valley (Torchin, Byers, and Huspeni, 2005).

Tachebia granifera has a long history of invasion. It was introduced to Florida and Texas in the 1940s via aquatic plants (Abbott, 1952; Murray, 1964; Murray and Wopshall, 1965). It was recorded from Puerto Rico by Harry and Aldrich (1958) and then spread quickly throughout the Caribbean, reaching the Dominican Republic by 1967 and Cuba, Grenada, and Venezuela in 1970 (Jaume, 1972; Chrosteczewski, 1973; Jacobson, 1975; Ferguson, 1977; Pointier et al., 1994). In 1991 T. granifera was discovered in the Charpentier River, Martinique, where it rapidly spread from its introduction site and had already colonized thirteen river systems by 1997 (Pointier et al., 1998). In places where it invaded it quickly became dominant in numbers and competed with native mollusks (Murray, 1971; Jacobson, 1975; Oglesby, 1977; Channotis et al., 1980b). It has also been suggested that T. granifera is responsible for the disappearance of the endemic freshwater snail Heminsius eubandaus (d’Orbigny, 1841) in Cuba (Pointier, 1999). A recent report from South Africa suggests that T. granifera has been present in a reservoir since at least 1996 (Appleton and Nadason, 2002).
Despite its invasiveness or perhaps because of the competitive capabilities of T. granifera, it has been used as a biological control agent against the small host of schistosomiasis, Biomphalaria glabrata (Say, 1818) and B. straminea (Dunker, 1848) (Butler et al., 1990; Michelson, 1992; Pointier, 2001). Gomez et al. (1990) suggested that T. granifera probably produces chemical factors that reduce the fecundity of B. glabrata, Perez et al. (1991) found that T. granifera competed with B. glabrata not for food or vital space but for chemical substances or by physical contact with a large number of individuals. Cañete et al. (2004) found a negative association between T. granifera and Fossaria cubensis (Pfeiffer, 1839) abundances, but a positive correlation with Pseudosuccinea columella (Say, 1817) densities, both of which are intermediate hosts of the liver fluke Fasciola hepatica. This only emphasizes that the safety and effectiveness of snails as biocontrol agents remains questionable (Civeyrel and Simberloff, 1996, Covic, 2001a).

The dispersal of an alien freshwater snail species following invasion could occur through two non-exclusive processes. The first is invasion to a single site, followed by diffusion into neighboring sites at a rate depending on the local intrinsic rate of population increase and the diffusion coefficient (Pointier et al., 1998). The second is long-distance dispersal by means of an agent of dispersal, such as birds (Boag, 1986), mammals (Madsen and Frandsen, 1989) or human activities (Pointier et al., 1998).

The four sites at which T. granifera was found are isolated from each other. This suggests the occurrence of either long-distance dispersal or multiple (separate) invasions, though only genetic studies will be able to distinguish these. Both sites flow naturally into the Jordan River, which drains many other water bodies, including water used for agriculture and fish ponds, and thus could further spread T. granifera. Hence, the dispersal patterns of T. granifera throughout the Jordan Valley are difficult to predict and only a long-term survey can estimate the impact of the invasion.

ACKNOWLEDGMENTS

J. Heller, J. P. Pointier, N. Sivan and an anonymous reviewer provided valuable comments that improved the manuscript. I am grateful to D. Gold for assistance during the identification of the parasites, to N. Sivan for preparing the map, and to R. Ben-Yosef and Y. Sever for helping with the sampling. Specimens for this study were collected under permit 6004 from the Israeli Authority for Nature Reserves and National Parks. This study was supported by a Horwitz Foundation Fellowship to FBA and by grant 665/02 of the Israel Science Foundation to J. Heller.

LITERATURE CITED


Notice

AMS 2007—Antwerp, Belgium
15–20 July 2007

The American Malacological Society (AMS) will hold its 73rd annual meeting in Antwerp in July 2007 as part of the next World Congress of Malacology. Sessions of contributed papers and posters are planned as usual, as are six exciting symposia:

- "Molluscan models: advancing our understanding of the eye" organized by Jeanne Serb and Laura Robles [sponsored by AMS]
- "Sexual selection" (Ronald Chase and Joris Koene)
- "Micromolluscs" (Daniel Genger)
- "Mollusks as models in evolutionary biology" (Matthias Glaubrecht and Thomas von Rintelen)
- "Inventoring the molluscan fauna of the world" (Philippe Bouchet and Somsak Panha)
- "Neogastropod origins and evolution" (Jerry Harasewych)

Our venue is the Groenenborger Campus of University of Antwerp (UA), hosted by Thierry Backeljau, President of Unitas Malacologica (UM). Campus facilities include most of our meeting rooms and a cafeteria under one roof. The conference begins with a Sunday afternoon icebreaker. Scientific presentations are in four parallel sessions on Monday, Tuesday, Thursday, and Friday. Wednesday is open for you to join one of the suggested tours, discover historical Antwerp, or visit a nearby museum collection. During the Tuesday evening session we will enjoy Belgian food, wine, and beer. A banquet will conclude the Congress on Friday evening.

On Thursday evening, we will host the traditional AMS Auction of molluscan books and paraphernalia (no specimens) open to all Congress participants. This annual event raises the necessary funds for our student programs, in addition to providing a fun-filled evening for all involved (even if you don’t buy anything!). Paul Callomon will return as our auctioneer—this is not to be missed! Because we are meeting overseas, transporting books and other items for the auction presents us with a challenge. For this reason, I am asking each attending member to bring at least one item for the auction in his/her luggage. Please dig deep and generously—surely everyone has an unneeded book or something malacologically silly to contribute! Please help AMS present its best face to the world!

Early registration ends 30 April 2007. Registration for AMS members who are not also UM members is €280 = $221 [see your favorite online currency converter for current rates] (students €160); a discounted price applies to those who are also UM members. The registration fee includes the abstract volume, event refreshments, and all lunches.

Airfare from the US to Brussels International Airport is relatively affordable. From there, buses and trains to Antwerp are easy and inexpensive. Dormitory accommodations are offered at UA (200 single and 20 double rooms, each with linens and washbasin but shared toilets/showers) at €20.27 per person/night, including breakfast. Hotel rooms are available in Antwerp city center, very near the railway station and bus terminals. Room prices range from €17.5 (single) to €155 (4 persons) per night, including breakfast. Buses travel from the city center to campus in about 20 minutes. Alternatively, the organizers recommend a rental bicycle—the vehicle of choice in Antwerp for young and old alike!

Student travel grants will be offered by both AMS and UM. Watch the AMS (http://www.malacological.org/meetings) and WCM websites for details and application forms. There will also be student awards at the Congress for best oral and poster presentations.

Full details about the Congress are available at http://www.ucd.ie/zooloogy/unitas/congress.html#content.

Please join us in Antwerp!

Paula M. Mikkelsen
AMS President
NEW TAXA PROPOSED IN VOLUME 120 (2006)

GASTROPODA

Hoplodoris hansrosaorum Domíngues, García, and Troncoso, 2006, new species (Discodorididae) ................................................................. 150
Humboldtiana corruga Thompson and Mejía, 2006, new species (Humboldtianidae) ................................................................. 25
Humboldtiana icersoni Thompson, 2006, new species (Humboldtianidae) ................................................................. 21
Humboldtiana sylavia Thompson and Mejía, 2006, new species (Humboldtianidae) ................................................................. 28
Margaretia inulotil Vilvens and Sellanes, 2006, new species (Trochidae) ................................................................. 19
Mureocypraea ormenoi DeVries, Groves, and Urbina, 2006, new species (fossil, Cypraeidae) ................................................................. 103
Onuphis dysis Squires and Saul, 2006, new species (fossil, Buccinidae?) ................................................................. 71
Otukaia cristulum Vilvens and Sellanes, 2006, new species (Calliostomatidae) ................................................................. 16
Paryphantopsis misimensis Slapcinsky, 2006, new species (Charopidae) ................................................................. 123
Paryphantopsis vanatinensis Slapcinsky, 2006, new species (Charopidae) ................................................................. 125
Perrilliata Squires and Saul, 2006, new genus (fossil, Fasciolariidae?) ................................................................. 74
Perrilliata califa Squires and Saul, 2006, new species (fossil, Fasciolariidae?) ................................................................. 74
Prisogaster melzani DeVries, 2006, new species (fossil, Turbinidae) ................................................................. 145
Prisogaster valenciai DeVries, 2006, new species (fossil, Turbinidae) ................................................................. 143
Sasakiconcha Geiger, 2006, new genus (Anatomidae?) ................................................................. 45
Sasakiconcha elegansisima Geiger, 2006, new species (Anatomidae?) ................................................................. 46
Satituberosa Squires and Saul, 2006, new genus (fossil, Fasciolariidae?) ................................................................. 72
Satituberosa jons Squires and Saul, 2006, new species (fossil, Fasciolariidae?) ................................................................. 72
Scaphella cariae Landau and Silva, 2006, new species (fossil, Volutidae) ................................................................. 89
Typhipropia cardalognathae Houart and Hertz, 2006, new species (Typhinae) ................................................................. 56
Lesleigh Anderson
T. David Bass
Alan G. Ben
Rüdiger Bieler
Arthur E. Bogan
Philippe Bouchet
Roberto Cipriani
Alfonso Correa Sandoval
Robert H. Cowie
Robert T. Dillon, Jr.
Shireen J. Fahey
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Charles Powell
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Ned Streat
Sven Nielsen
Fred G. Thompson
Ángel Valdés
G. Thomas Watters
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Diego Zelaya

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INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of $8\frac{1}{2} \times 11$-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized; for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized; use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author’s name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be abbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. In doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

Illustrations: Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). “Tall” page-width illustrations should be avoided, square or “landscape” formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution files at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, …, NOT Figures 1A, 1B, 1C, …, NOR Plate 1, Figure 1, …). In illustrations with more than one figure, make sure that blank areas between figures is kept to a minimum, thereby allowing for more area for each individual figure.

Compressed files (e.g., .jpg) may be used to facilitate transmission of files during original submission, but may not be acceptable at final submission (see below).

Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly encouraged, as is the deposition of representative voucher specimens for all other types of research work.

The Editorial Process: Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for THE NAUTILUS. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers’ recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers’ comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

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