THE NAUTILUS

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May 30, 2006
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to malacology.

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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 inauspicious 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 (16.5×14 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 19×13 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 15.2×8.2 cm flyer (Figure 2) published sometime in the early 1890s. The flyer proffered: "Its scope is broad, including

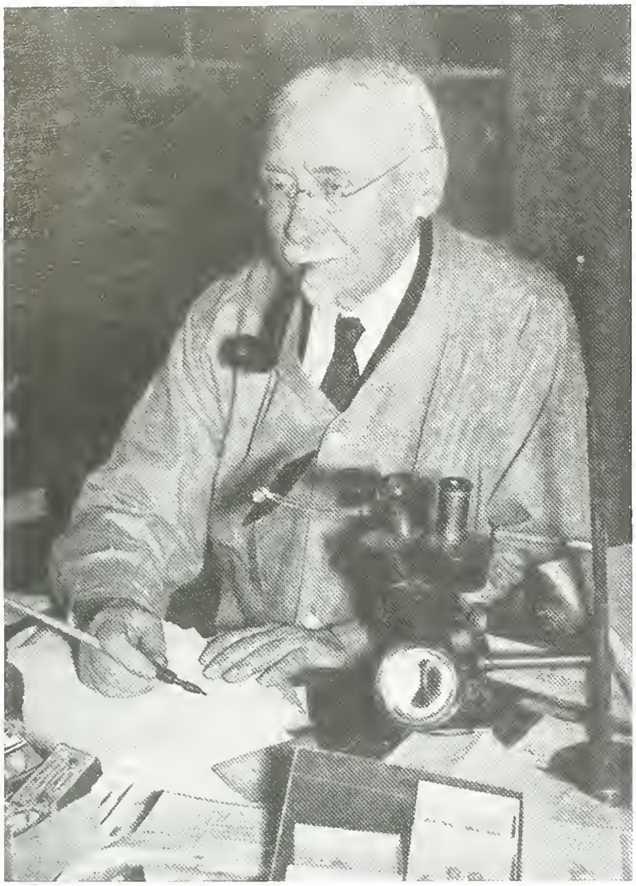
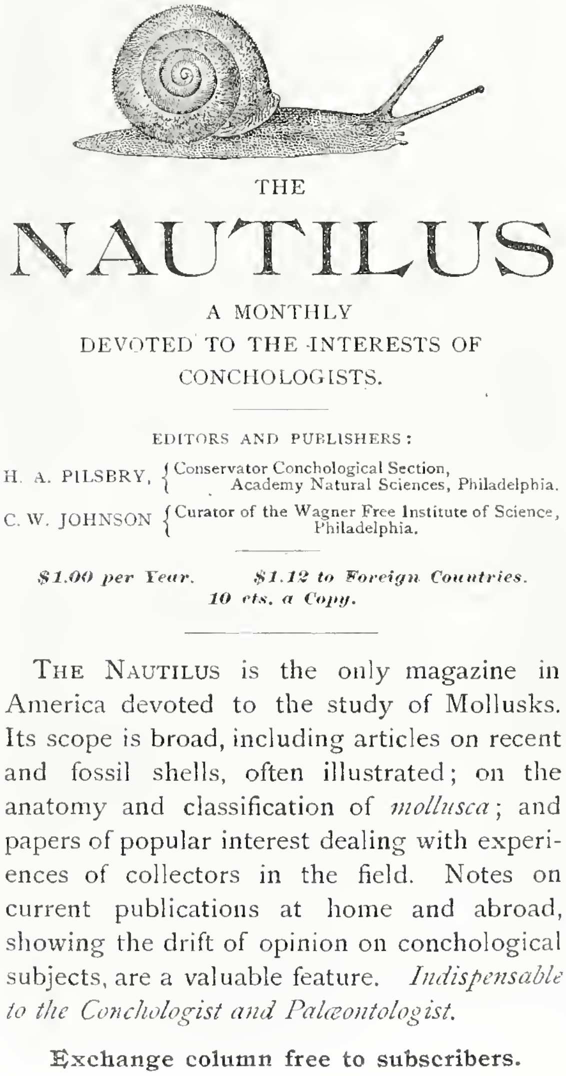


Figure 1. Henry Augustus Pilsbry, 1862–1957; editor 1889–1957. Photo *The Nautilus* archives.

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 subcribers." 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.'"



THE

NAUTILUS

A MONTHLY
DEVOTED TO THE INTERESTS OF
CONCHOLOGISTS.

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 Palæontologist.*

Exchange column free to subscribers.

Figure 2. Promotional flyer, circa early1890s. Note emphasis on scientific aspects combined with appeals to the non-professional audience of the journal. The line drawing portrays North American land snail *Xolotrema denotatum* (Férussac, 1821). The same drawing appeared earlier, as *Helix palliata* Say, in Binney (1857), Binney and Bland (1869), and Teator (1890).

EARLY BUSINESS MANAGEMENT

Pilsbry was aided for most of his career as editor of *The Nautilus* by Charles Willison Johnson (1863–1932) (Figure 3). Johnson was curator at the Wagner Free Institute

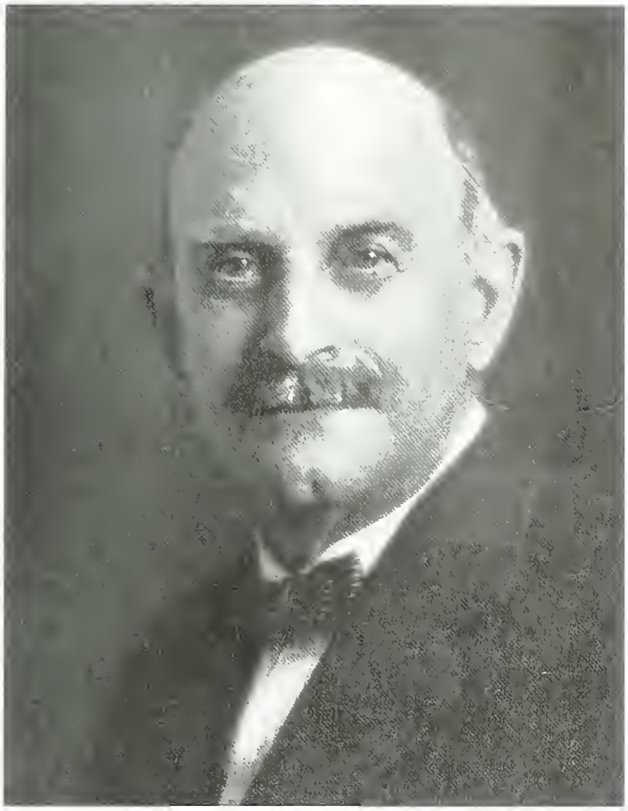


Figure 3. Charles Willison Johnson, 1863–1932; business manager 1890–1932. Photo Museum Comparative Zoology, Harvard University.

of Philadelphia between 1888 and 1903; from 1903 to his death in 1932 he was principal curator of the Boston Society of Natural History. Early in his career as curator at the Wagner Institute, Johnson replaced W. D. Averell in 1890 as business manager of *The Nautilus*.

New England malacologist Arthur Fairfield Gray (Gray, 1932) remarked about Johnson's role with *The Nautilus*: "[Pilsbry's] choice was most fortunate; Johnson established the most cordial relations with subscribers and contributors. During extended periods, when Dr. Pilsbry was away on collecting trips, he acted as editor as well as business manager." Gray commented on the personal relation between the two editors: "In those days *The Nautilus* was a monthly. This co-partnership and intimate friendship continued for forty-two years, until terminated by Mr. Johnson's death." Figure 4 portrays a sample of Johnson's ledger work in the early 20th Century as business manager of *The Nautilus*.

Horace Burrington Baker (1889–1971) (Figure 5), Professor of Zoology at the University of Pennsylvania and a specialist in terrestrial gastropods, became business manager of the journal upon the death of Charles W. Johnson in 1932. Baker served as an associate editor for 25 years. Abbott and Wurtz (1971) remarked that Baker "was one of America's outstanding land mollusk anatomists." He was also an excellent illustrator, as attested by the exquisite anatomical drawings in his works.

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 was 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).

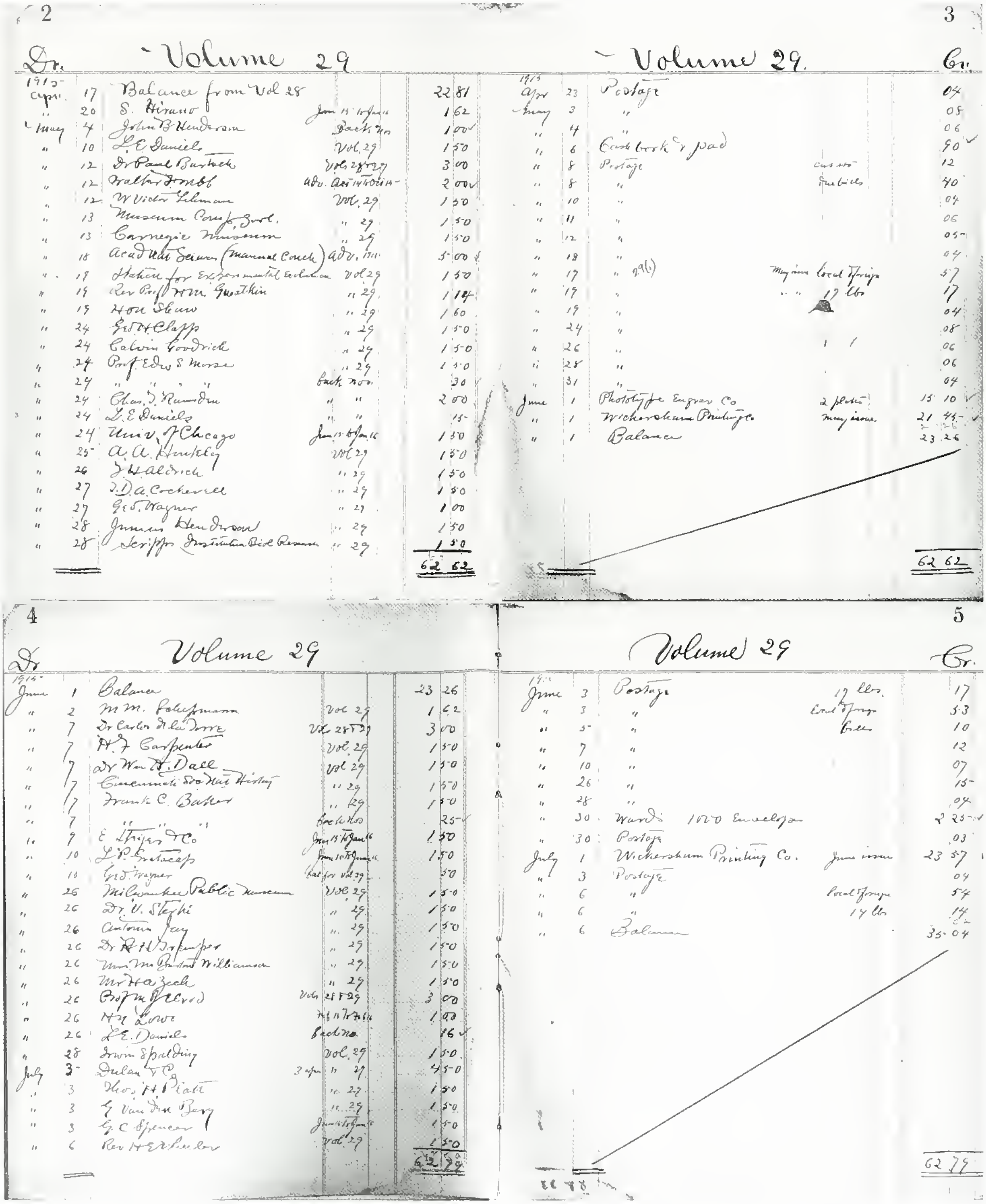
R. Tucker Abbott was initially in charge of marine mollusks, Wurtz was responsible for mailing issues and became editor for fresh water mollusks and ecology, and Bernadine B. Baker ("Mrs. Horace B. B.") tended to the finances and subscriptions. Baker added: "Since the Bakers and *The Nautilus* can afford 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 1968, 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 Du 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-



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Dr. Volume 29

1915 Apr.	17	Balance from Vol 28		22 81
"	20	S. Hirano	Jan 15 to Jan 16	1 62
May	4	John B Henderson	Back Nos	1 00
"	10	L. E. Daniels	Vol. 29	1 50
"	12	Dr Paul Bartsch	Vols 28 & 29	3 00
"	12	Walter F. Webb	adv. Apr 14 to Oct 14	2 00
"	12	W Victor Tileman	Vol. 29	1 50
"	13	Museum Comp. Zool.	" 29	1 50
"	13	Carnegie Museum	" 29	1 50
"	18	Acad Nat Sciences (Manual Conch)	adv. [illegible]	5 00
"	19	Station for Experimental Evolution	Vol 29	1 50
"	19	Rev Prof Wm. Gwatkin	" 29	1 14
"	19	Hon Shaw	" 29	1 60
"	24	Geo H Clapp	" 29	1 50
"	24	Calvin Goodrich	" 29	1 50
"	24	Prof Edw S Morse	" 29	1 50
"	24	" " " "	back nos	30
"	24	Chas. T. Ramsden	" "	2 00
"	24	L. E. Daniels	" "	15
"	24	Univ. of Chicago	Jan 15 to Jan 16	1 50
"	25	A. A. Hinkley	Vol 29	1 50
"	26	J. H. Aldrich	" 29	1 50
"	27	T. D. A. Cockerell	" 29	1 50
"	27	Geo. Wagner	" 29	1 00
"	28	James Henderson	" 29	1 50
"	28	Scripps Institution Biol Research	" 29	1 50
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Volume 29. Cr.

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Dr Volume 29

1915 June	1	Balance		23 26
"	2	M. M. Schepman	Vol 29	1 62
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"	7	H. F. Carpenter	Vol. 29	1 50
"	7	Dr Wm H. Dall	Vol 29	1 50
"	7	Cincinnati Soc Nat History	" 29	1 50
"	7	Frank C. Baker	" 29	1 50
"	7	" " "	back Nos	25
"	7	E. Steiger & Co.	Jan 15 to Jan 16	1 50
"	10	L. P. Gratacap	Jan 15 to Jan 16	1 50
"	10	Geo. Wagner	bal for Vol 29	50
"	26	Milwaukee Public Museum	Vol 29	1 50
"	26	Dr. V. Sterki	" 29	1 50
"	26	Antonio Jay	" 29	1 50
"	26	Dr R H [illegible]	" 29	1 50
"	26	Mrs. Mc[illegible] Williamson	" 29	1 50
"	26	Mr H A Zeck	" 29	1 50
"	26	Prof M. J. Elrod	Vols 28 & 29	3 00
"	26	H N Lowe	Feb 15 to Feb 16	1 00
"	26	L. E. Daniels	Back No.	16
"	28	Irwin Spalding	Vol. 29	1 50
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"	3	Thos. H Platt	" 29	1 50
"	3	G. Van der Berg	" 29	1 50
"	3	G. C. Spencer	Jan 15 to Jan 16	1 50
"	6	Rev H E Wheeler	Vol. 29	1 50
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Volume 29 Cr.

1915 June	3	Postage	17 lbs.	17
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				62 79

Figure 4. First four pages of the ledger for 1915 in Charles W. Johnson's longhand. Pages correspond to the initial batch of subscriptions for Volume 29. List of subscribers is a who's who of American and international malacology of the period. Included are, among others, John B. Henderson, Paul Bartsch, William F. Clapp, Calvin Goodrich, Edward S. Morse, M. M. Schepman, Don Carlos de la Torre, William H. Dall, Frank C. Baker, and Victor Sterki. Some institutions listed (e.g., Museum of Comparative Zoology, Carnegie Museum, and University of Chicago) have been loyal subscribers through the entire 20th Century and to the present day.

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 26.5×20.5 cm. He added a gray protective cover (each number in the preceding 85 years started with a contents

Figure 5. Horace Burrington Baker, 1889–1971; editor 1958–1968. Photo *The Nautilus* archives.

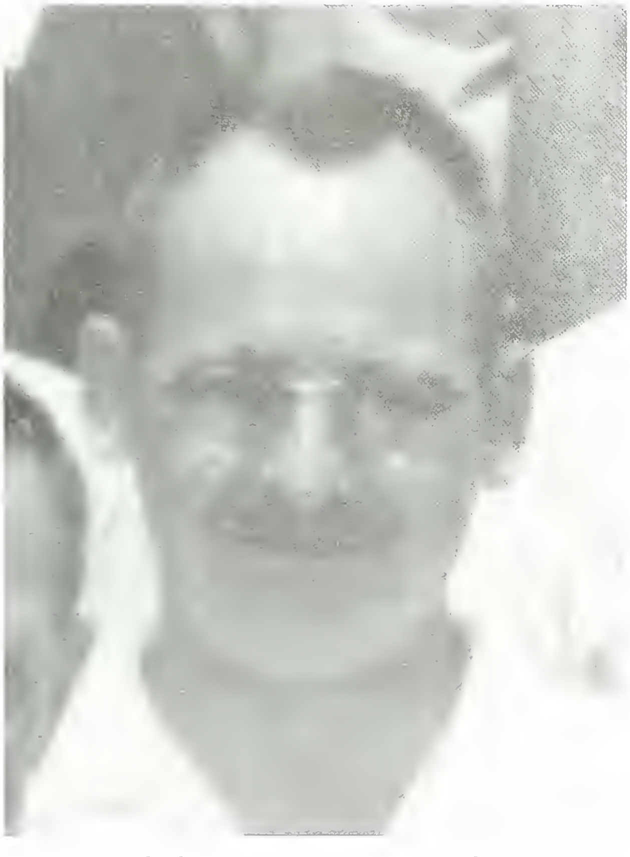


Figure 6. Charles B. Wurtz (1916–1982) at the AMU meeting at Haverford College in 1959. Photo from the American Malacological Society archives.

Figure 7. Robert Tucker Abbott, 1919–1995; editor 1968–1985. Photo *The Nautilus* 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".

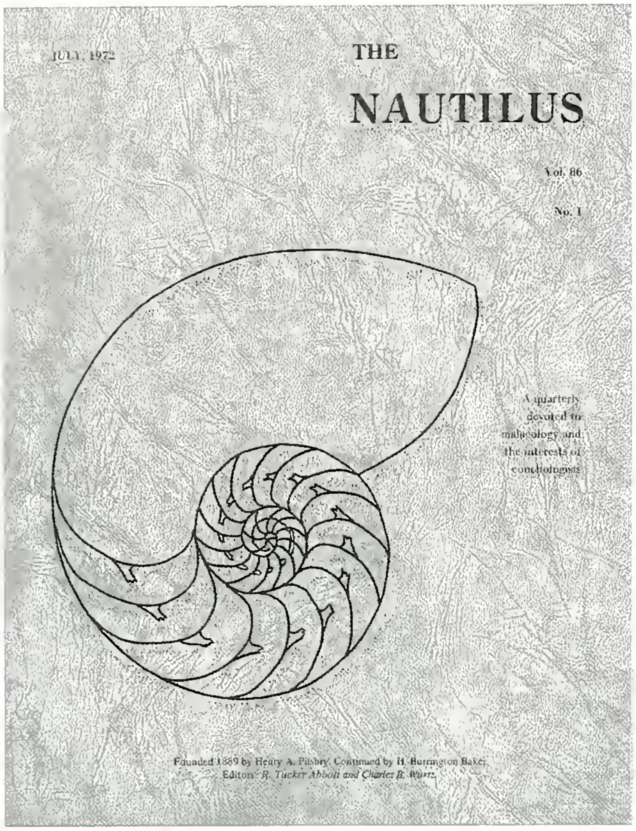
Another advance introduced in the same number was the addition of an editorial committee composed of 13 professionals representing a wide swath of American malacology. These were Arthur H. Clarke, Jr., William J. Clench, William K. Emerson, Morris K. Jacobson, Aurèle La Rocque, James H. McLean, Arthur 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 87 (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



JULY, 1972

THE
NAUTILUS

Vol. 86

No. 1

A quarterly
devoted to
malacology and
the interests of
conchologists

Founded 1889 by Henry A. Pilsbry. Continued by H. Burrington Baker.
Editors: *R. Tucker Abbott and Charles B. Wurtz.*

Figure 8. Cover with new design introduced by Robert Tucker Abbott in July, 1972.

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 Mollusca 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 Trophon 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.

Figure 9. M.G. (Jerry) Harasewych, born 1949; editor 1985–1998. Photo courtesy M.G. Harasewych.

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.

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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 specimens 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-lamellar with an inner prismatic layer. The additional presence of a (vestigial?) outer prismatic layer dorsal to the ligament area, the pustular 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.

INTRODUCTION

Philobrya brattstromi Soot-Ryen, 1957, belongs to a small but rather successful arcoid family, the Philobryidae, 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 Philobryidae emphasizes the importance of prodissoconch and postlarval hinge characters (e.g., Bernard, 1897; Dell, 1964; Hayami and Kase, 1993; Malchus and Warén, 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; Ramorino, 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 redescribe the main shell features in a modern interpretational context and to clarify the type status of the specimens.

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 3894) 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.

In addition to the literature, my own data on the following eleven species of *Philobrya* were used for comparisons: *Philobrya crispa* Linse, 2002; *P. laevis* Thiele, 1912; *P. magellanica* Stempell, 1899 ; *P.* cf. *olstadi* Soot-Ryen, 1951, *P. quadrata* Pfeffer, 1886 (in Martens and Pfeffer, 1886); *P. sublaevis* Pelseneer, 1903; *P. wandelensis* Lamy, 1906; *P. meleagrina* Bernard, 1897 (type

Table 1. Data for the five lots of *P. brattstromi* from the Swedish Museum of Natural History (SMNH).

SMNH number	Station	Date	Locality	Depth, substrate
3894	M24	16 Dec. 1948	Seno Reloncavi, S of Isla Guar, 41°44′ S, 72°45′ W	70 m, sand with shells
74831	M17	14 Dec. 1948	Golfo de Ancud, Canal Calbuco, 41°46′ S, 73°06′ W	30 m, grey sand and small stones
74832	M48	3 Feb. 1949	Seno Reloncavi, bay of Puerto Montt, 41°28′ S, 72°56′ W	30 m, ?
74833	M92	3 May 1949	Golfo de Ancud, Bahia Ilto, 41°53′ S, 73°10′ W	45 m, sand with dead algae
74834	M103 (M104?)	5 May 1949	Canal Chacao, N of Punta Soledad, 41°48′ S, 73°31′ W	40 m, stones and polychaete tubes

series) and *P. olstadi* Soot-Ryen, 1951 (type series); *Philobrya* ?new species from New Zealand identified as *P. meleagrina* (SMNH specimens) (I also included comparisons with some species of *Adacnarca* and *Lissarca*).

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* (Muséum national d'Histoire naturelle, Paris) and *P. olstadi* (Zoological Museum, Oslo).

Specimens of *Philobrya 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 FLIII stereo microscope equipped with a Planapo 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, 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).

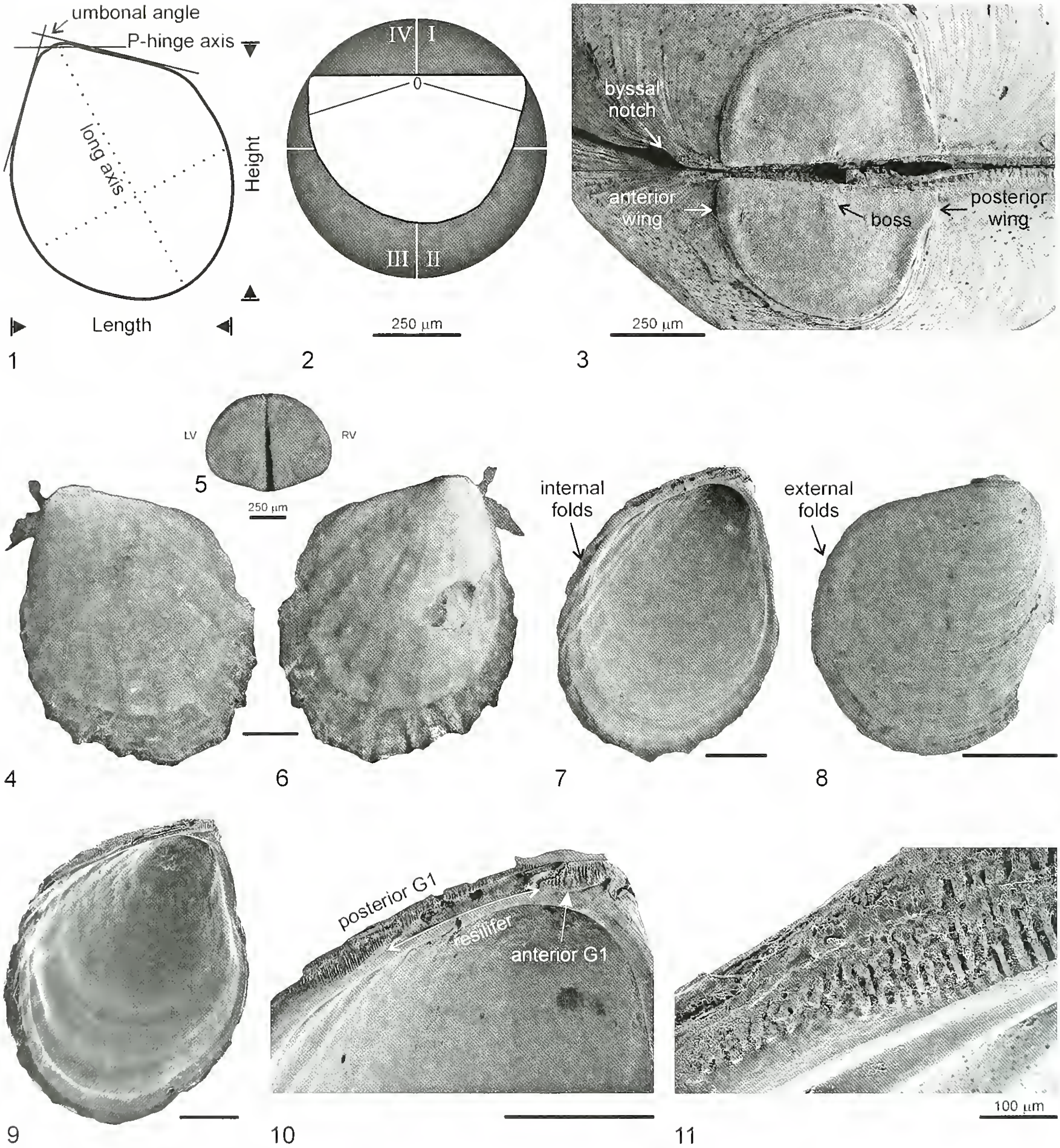
Table 2. Dimensions of some prodissoconchs and adult shells from the collection. (1) identifies adult shell dimensions without periostracum. Abbreviations: AV, articulated valves; LV, left valve; RV, right valve, n/d, not determined.

SMNH number	Notes	Prodissoconch L × H (μm)	Adult L × H (mm)
3894	AV (holotype)	659 × 414	4.2 × 5.5
	LV + RV	649 × 409	4.5 × 5.3
	AV	n/d	3.3 × 4.0
	AV	n/d	3.0 × 3.3
	AV	n/d	2.3 × 2.8
74831	RV fragment	620 × 442	n/d
	AV (1)	591 × 403	2.6 × 3.1
	LV (1)	614 × 421	3.8 × 4.8
	AV	n/d	3.6 × 4.6
	AV	n/d	3.0 × 2.5
	AV	n/d	2.3 × 2.7
74833	AV	n/d	4.0 × 5.2
	AV	n/d	3.3 × 3.8
74834	AV	n/d	3.0 × 3.5

The lengths of the larval and postlarval shells were measured as the longest anterior-posterior distance parallel to the straight hinge axis of the prodissoconch 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 umbonal 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 1959. 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 *Lyonsia elegantula*, which directly follows the diagnosis of *Philobrya brattstromi* in that paper. This value changed to 15 mm



Figures 1–11. Definitions, terms, and general shell features. Scale bars = 1mm (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 Warén, 2005, fig. 5). **3.** Prodissoconchs of right valve (top) and left valve of an articulated specimen (SMNH 74831). **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 74831). **9.** Left valve of paratype (SMNH 3894). **10.** Close-up of hinge of specimen in Figure 7 (SMNH 74831). **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 (<10mm), 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 pustules in larger adults and then unlikely functional (e.g., *Philobrya sublaevis*); primary, "larval" ligament (L1) within primary resilifer 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 duplivincular, 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, 1969; Tevesz, 1977; own observations; based also on Malchus and Warén, 2005; Morton, 1978; Prezant, 1990):

Discussion: Recent studies leave little doubt that the postlarval first generation of hinge teeth and the ligament/resilifer of philobryids are homologous with the larval to early postlarval hinge teeth and larval ligament/resilifer of planktotrophic Pteriomorphia. Similarly, the second generation of hinge teeth (e.g., *Lissarca*) is homologous with the adult tooth series as found in the majority of arcoid bivalves (Malchus, 2004a, b; Malchus 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 duplivincular adult ligament are deemed to indicate paedomorphic evolution (Malchus 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 tear-drop-shaped with a pointed umbo capped by prodissoconch, umbonal angle from 90° to 120° (between antero-dorsal and posterodorsal 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 *Adacnarca* 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 *Adacnarca* but incorrectly included *Philobrya wandelensis* 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 *Dacrydium* hinge; Malchus and Warén, 2005: figs. 1-2 of various Limopsidae; among many others). For this reason, Nicol's concepts of *Philobrya* and *Adacnarca* are not accepted herein.

Philobrya brattstromi Soot-Ryen, 1957

Philobrya brattstrømi n. sp.: Soot-Ryen, 1957: 2.
Philobrya brattströmi n. sp. (1957, p. 2): Soot-Ryen, 1959: 22, pl. 1, fig. 6.
Philobrya brattstromi Soot-Ryen, 1957: Ramorino, 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 4.1×5.5×2.1 mm (length x height x width) versus 4.4×5.8×2.3 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-

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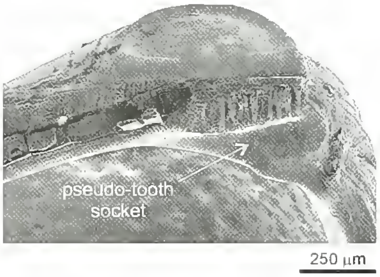

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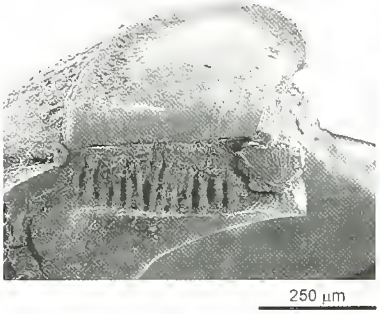

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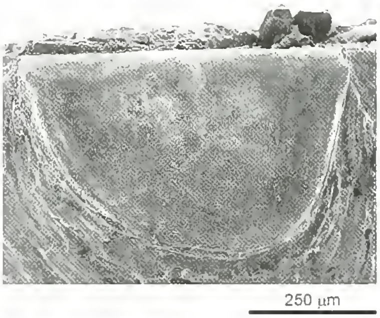

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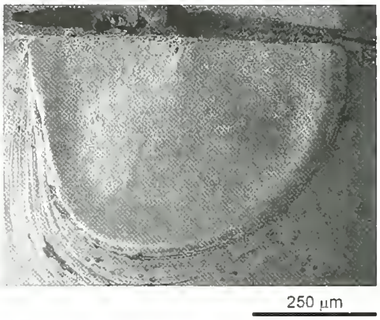

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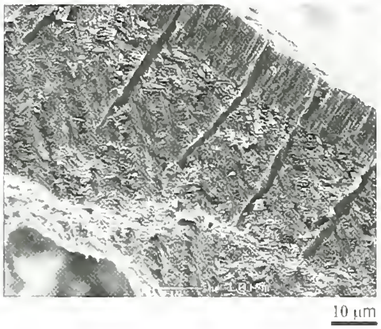

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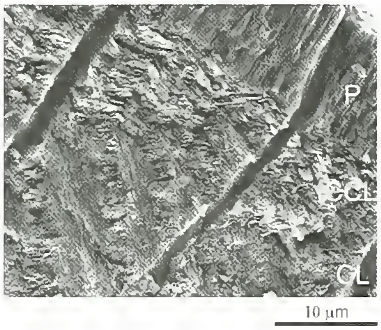

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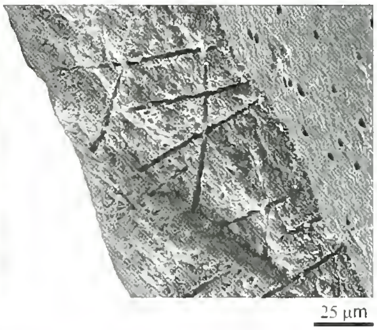

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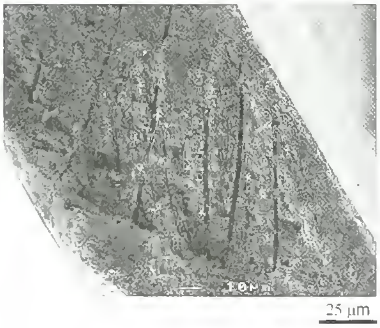

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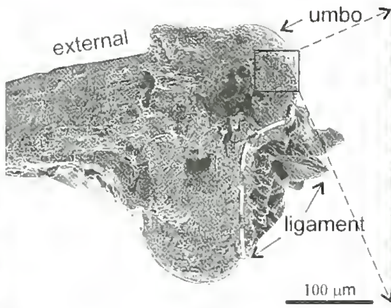

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Figures 12–23. Prodissoconch, central hinge, and microstructure of postlarval shell. **12.** Central hinge of left valve (SMNH 74831; see Figures 7, 10). **13.** Central hinge of left valve of paratype (SMNH 3894; see Figure 9). **14–15.** Central 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. Prodissoconch 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 prodissoconch a rather broad, cross-lined part extends backwards below the resilium, which starts below the middle of the prodissoconch 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 posteroventral part. Mantle margin with brownish pigment, but lacks eyes. Length 15 mm." (Should read 5.8 mm, see above).

Amended Shell Description: The prodissoconch 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 prodissoconch 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 prodissoconch. 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).

Distribution: Golfo de Ancud (41°44' S) to Bahía de Valparaiso (33° S) along the Chilean coast (Soot-Ryen, 1959; Ramorino, 1968).

Discussion: *Philobrya brattstromi* is an easily recognized species given the combination of (1) a smooth prodissoconch 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 periostracum.

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?) *Adacnarca* 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 philobryid genera *Cratis* and *Cosa* (e.g. Hayami and Kase, 1993). The distribution of these characters is consistent with the generally assumed ancestor-descendent relation 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.

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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 kiheiziebisu* (Otuka, 1939), *O. eltanini* Dell, 1990, and *Calliostoma jacquelinae* 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 margaritine species, such as *M. shinkai* Okutani, Tsuchida and Fujikura, 1992, *M. salmonea* (Carpenter, 1864), and *Solariella tavernia* Dall, 1919, and with calliostomatid species such as *Calliostoma nudiusculum* (von Martens, 1881), *C. magaldii* Caldini and Guimarães-Prado, 1998 and *C. keenae* 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 malacofauna 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 Bouchet et al., 2005), two of them belonging to the genus *Otukaia* (*O. chilena* (Rehder, 1971) and *O. delli* (McLean and Andrade, 1982) and two to the genus *Bathybembix* (*B. macdonaldi* (Dall, 1890) and *B. humboldti* Rehder, 1971).

The diversity of the Trochoidea from the coast of northern Chile (18 to 31°S) was subsequently studied by Véliz 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 alphonsi* from 800 m depth from off Chiloé, 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 consimilis* (E. A.Smith, 1881)).

In relation to the shallow-water malacofauna 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 from the Arauco Peninsula (~38°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 a 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 Olu, 1998).

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 *Bathybembix macdonaldi*, *Otukaia chilena*, *Zetela alphonsi*, and the two unnamed species proposed herein. In this paper we describe a species of *Otukaia* and a species of *Margarites* 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 Gormáz 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 Natural History Museum of Chile, Santiago (MNHNCL) and Institut 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* Ikebe, 1942

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

Otukaia crustulum 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 coeloconoidal 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.

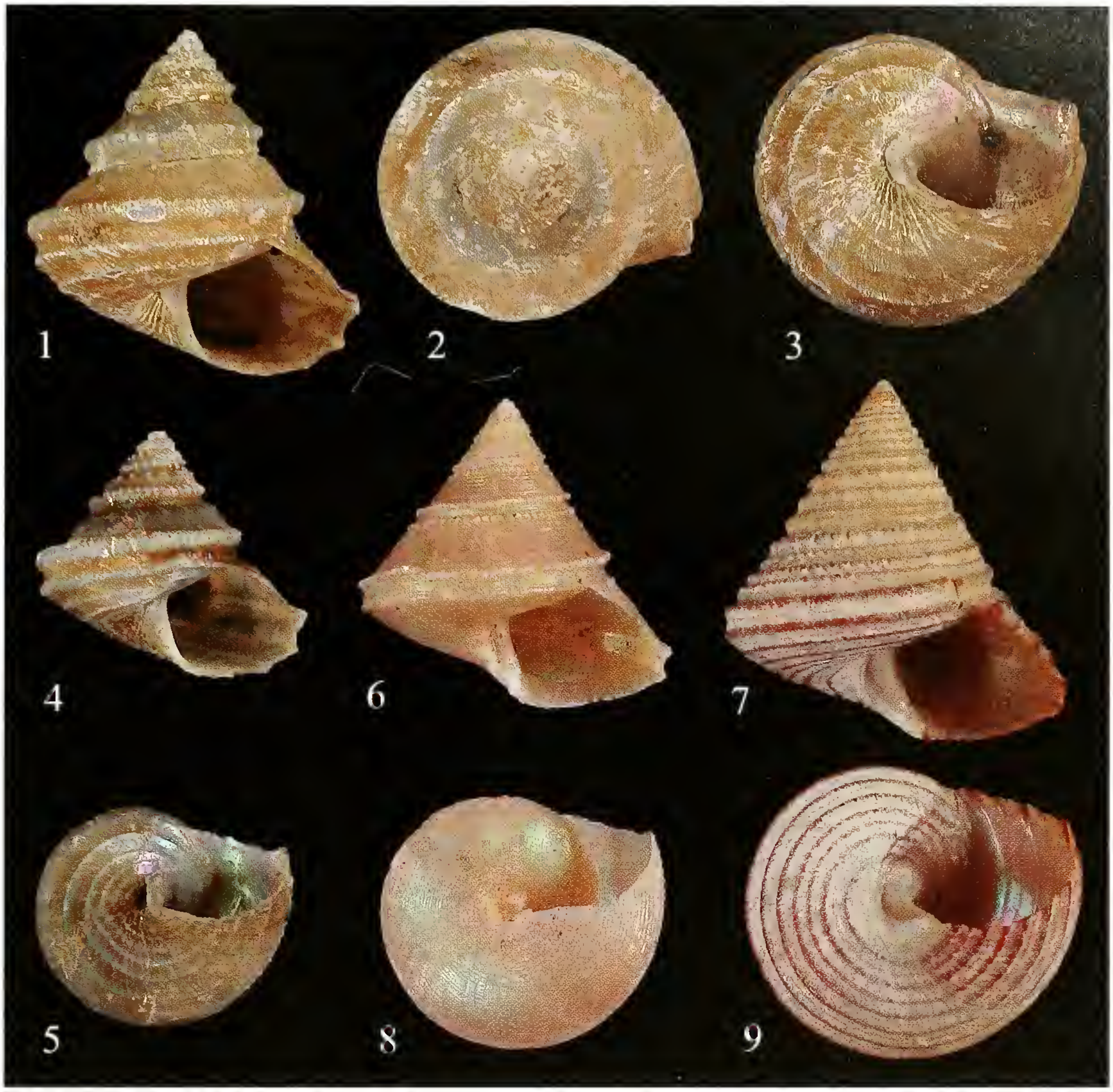
Teleoconch of up to 6 moderately convex whorls, bearing 3 spiral granular cords, adapical one the weakest, only poorly visible on last whorls; prosocline ribs on first 3 whorls connecting beads on spiral cords and very thin, axial lamellate threads between cords of the base. Suture visible, impressed, 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; prosocline 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 abapical third of whorl, 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 lirae corresponding to external cords, producing strong angle at the rim; inner lip curved, projecting over umbilical area. Columella 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, 843–728 m, South Pacific Ocean.

Type Material: Holotype MNHNCL (201649) (lv), AGOR Vidal Gormáz, stn AGT 13, from type locality, 15.6 × 14.4 mm; Paratype IRSNB 30514 568 (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 Ikebe 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

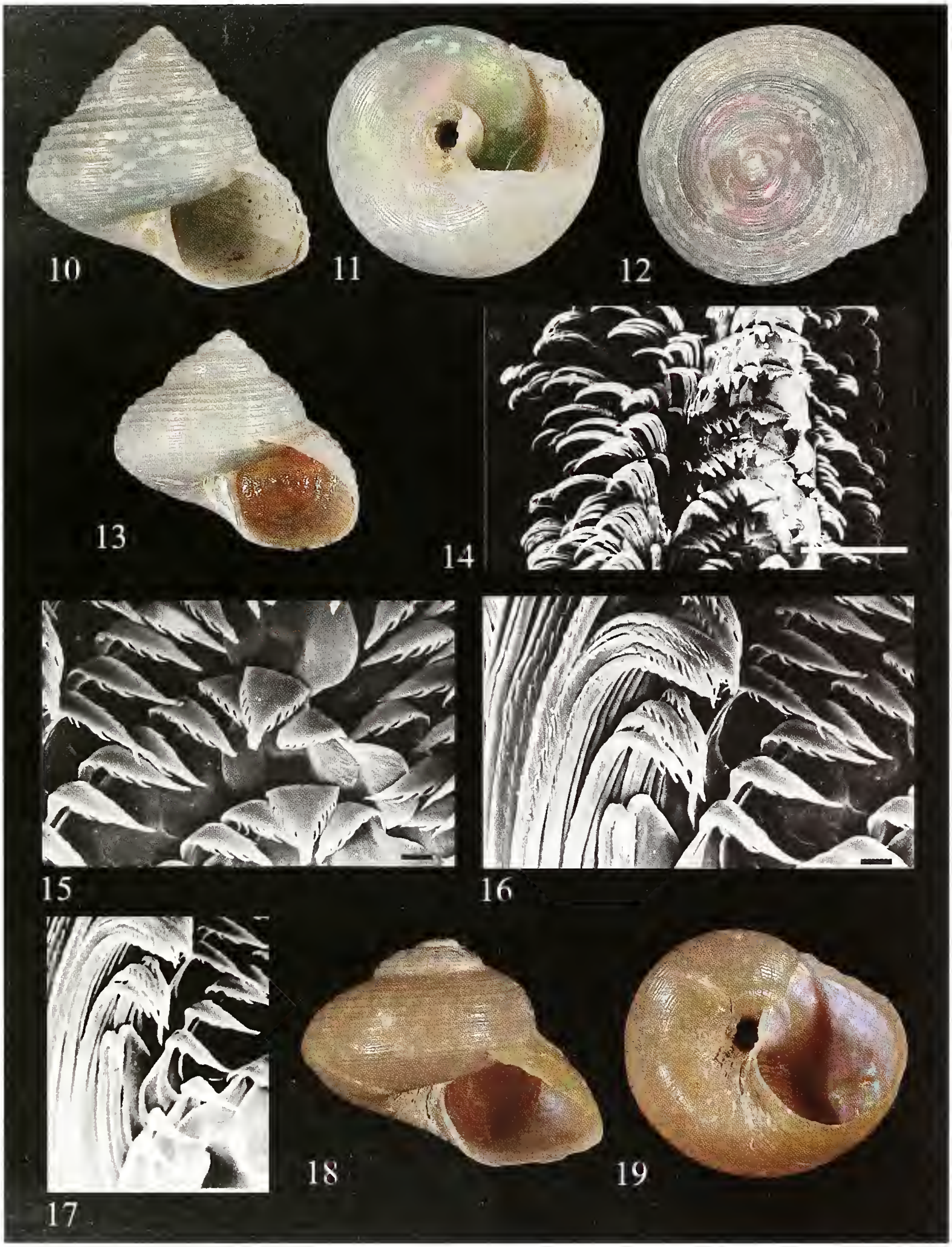


Figures 1–9. *Otukaia* and *Calliostoma* species. **1–5.** *Otukaia crustulum* new species, Central Chile. **1–3.** Holotype MNHNCL 201649, 15.6 × 14.4 mm. **4–5.** Paratype IRSNB 30514, 10.4 × 11.0 mm. **6, 8.** *Calliostoma jacquelinae* McLean, 1970, C.Vilvens coll., Galapagos Islands, 12.0 × 13.0 mm. **7, 9.** *Calliostoma fonkii* (Philippi, 1860), C.Vilvens coll., northern Chile, 16.0 × 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* Ikebe, 1942, seems to be the most adequate to include the new species. *Otukaia crustulum* new species weakly resembles *O. kiheiziebisu* (Otuka, 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



Figures 10–19. *Margarites* species. **10–17.** *Margarites huloti* new species, Central Chile; **10–12.** Holotype MNHNCL 201650, 12.5 × 13.4 mm. **13.** Paratype MNHNCL 201651, 9.8 × 11.5 mm; **14–17.** Paratype MNHNCL 201651, features of the radula. **14.** General view. Scale bar = 100 µm. **15.** Rachidian and lateral teeth. Scale bar = 10 µm; **16.** Marginal teeth, lateromarginal plate and lateral teeth. Scale bar = 10 µm; **17.** Details of lateromarginal plate. **18–19.** *Margarites shinkai* Okutani, Tsuchida and Fujikura, 1992, holotype NSMT Mo 69635, Japan, 11.0 × 15.1 mm.

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.

Character	TW	H	W	HA	H/W	H/HA
Range	4.00–5.00	9.80–12.50	11.50–13.40	4.60–5.30	0.85–0.94	2.04–2.43
Mean	4.55	11.45	12.50	4.95	0.91	2.31
Standard deviation	0.38	1.10	0.82	0.27	0.04	0.16

Type species: *Turbo helicinus* 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), cyrtoconoidal 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; P1 appearing under suture, smooth; interval between cords of about half of 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; P8 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 lirae 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 (lv), AGOR Vidal Gormáz, stn AGT 13, from type locality, 12.5 × 13.4 mm; paratypes: MNHNCL 201651 (5 lv), IRSNB 30514 569 (1 lv), all from type locality.

Etymology: Named after Andre 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. shinkai* Okutani, Tsuchida 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 whorls, radula with 8 lateral teeth (in contrast to only 6 in the new species); in addition, the rachidian and lateral teeth in the Japanese species have a more slender base (Okutani, Tsuchida and Fujikura, 1992: figs. 15–16).

The new species seems rather similar to *Margarites salmonea* (Carpenter, 1864) from southern California, but the latter is much smaller for a similar number of whorls, has less spiral cords on the base, and a broader umbilicus. *Margarites huloti* new species may also be compared to *Solariella tavernia* Dall, 1919, from the Galapagos Islands. This latter species, however, has a smaller size for about the same number of whorls and bears more convex whorls with thinner spiral cords. The new species also resembles *Calliostoma nudiusculum* (von Martens, 1881) from the southwestern Atlantic, but the latter species differs from the new species by having a more depressed spire, less numerous spiral cords on whorls, and lacks an open umbilicus. The new species weakly resembles *Calliostoma magaldii* Caldini and Guimarães-Prado, 1998, from the southwestern Atlantic, but shells of this latter species have no umbilicus, are pinkish white, and have whorls and base bearing less numerous and thicker spiral cords. *Margarites huloti* new species may also be compared to *Calliostoma keenae* 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 whorls.

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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, Helicoidea, 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.

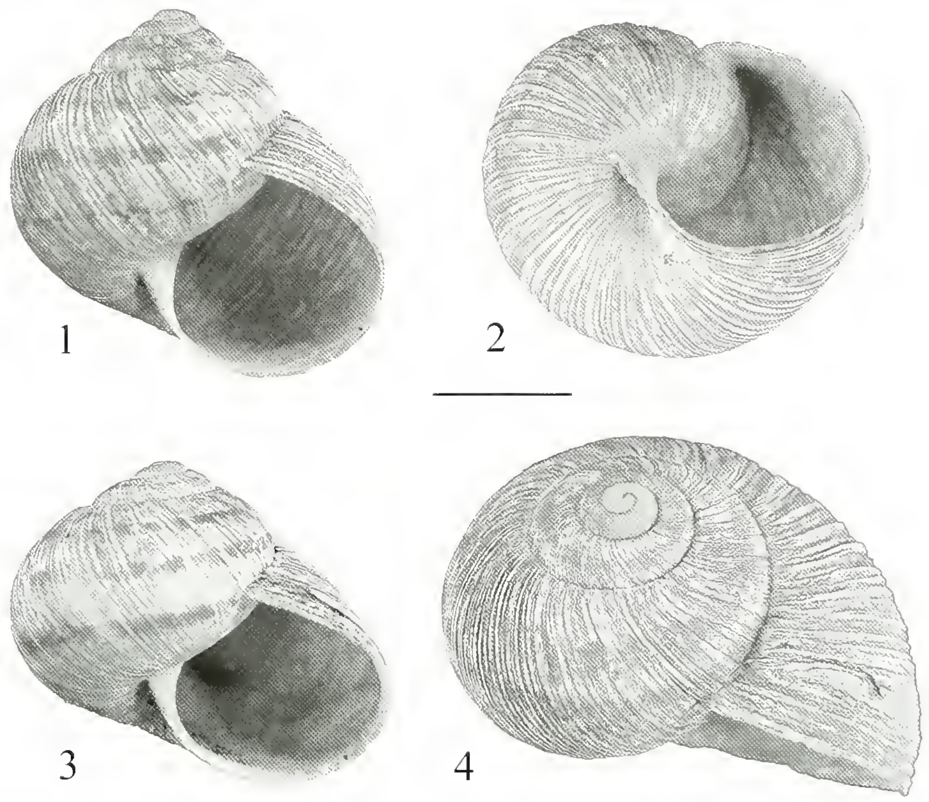
SYSTEMATICS

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 0.85–1.00 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 frontal 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



Figures 1–4. *Humboldtiana iversoni* new species. Shells. **1–2.** Holotype, UF 103588. **3–4.** Paratypes, UF 367594. **3.** Paratype A. **4.** Paratype B. Scale bar for Figures 1–3 = 10 mm. Figure 4 is enlarged 25% in relation to Figures 1–3.

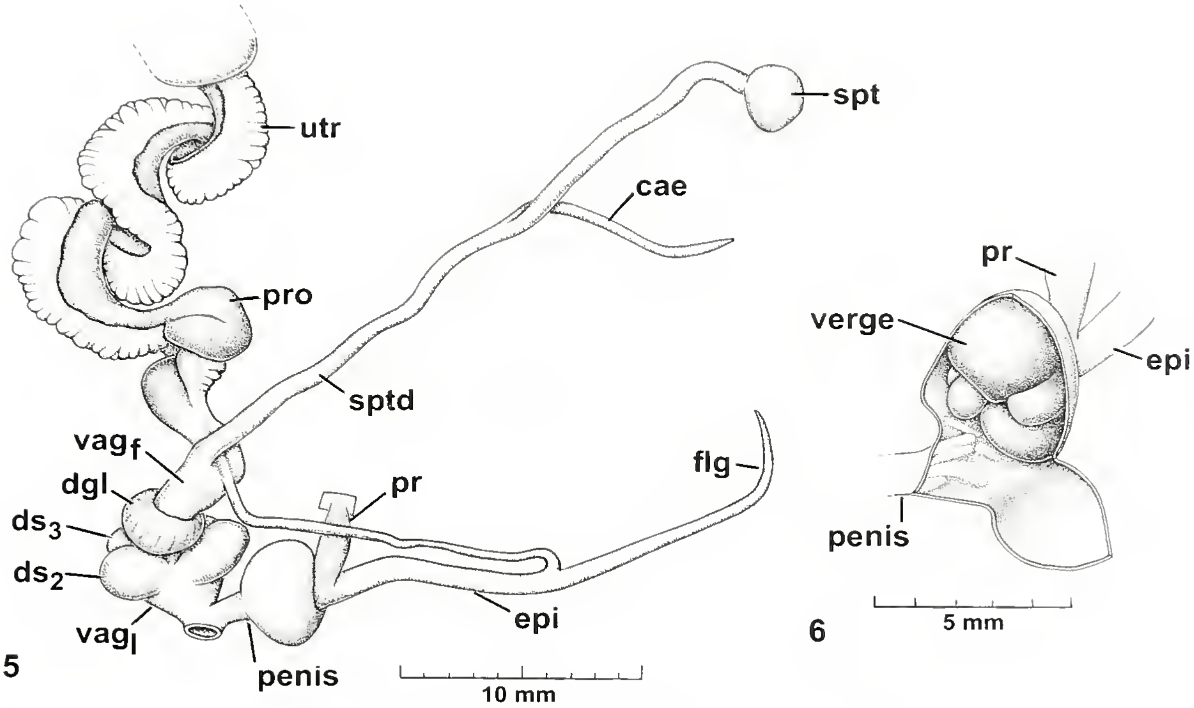
lobes (Figure 6). The penis retractor muscle **(pr)** is short and stout; length 3.5 mm. It originates on the center of the mantle cavity about 1/8 of a whorl behind the mantle collar and inserts on the base of the epiphallus **(epi)** juxtaposed to the penis. It does not form a sheath around the epiphallus. 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$_l$)** 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 (sptd) is 27 mm long. It bears a caecum **(cae)** 16 mm above it base. The caecum 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 Anteojitos; 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.

Table 1. *Humboldtiana iversoni* new species. Shell measurements in mm of the holotype and three paratypes. H: shell height; W: shell width; AW: aperture width; AH: aperture height; AA: angle of aperture to shell axis.

	H	W	AW	AH	Whorls	H/W	AW/W	AH/H	AW/AH	AA
Holotype	28.6	28.5	16.0	20.6	4.4	1.00	0.56	0.72	0.78	37°
UF	27.3	29.2	16.4	21.7	4.3	0.93	0.56	0.79	0.76	39°
UF	24.4	28.8	15.1	18.5	4.0	0.85	0.52	0.76	0.82	43°
ITCV	30.6	35.6	17.8	22.7	4.6	0.91	0.50	0.75	0.78	40°



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

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 (Pilsbry, 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 Pilsbry (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* Pilsbry, 1940, and *H. inferior* Pilsbry, 1948 (formerly *Humboldtiana montezuma inferior* Pilsbry, 1948). The group is found in southeastern Nuevo León. *Humboldtiana montezuma* is found at 3080 m altitude at the summit of El Infiernillo, a mountain near Pablillo, south of Galeana; and *H. inferior* is found lower at about 1850 m altitude, near Pablillo. The species have in common coarse postembryonic

Figure 7. Type locality of *Humboldtiana iversoni* new species at Las Lorias, Nuevo León, Mexico.

sculpture of close thread-riblets and minute beaded granules that are aligned on or between the riblets. The color pattern consists of light-colored ribs on a light brown or yellowish background. Spiral bands are absent in adult shell, or when present they are weakly defined. The female reproductive system has four dart sacs on the vagina, and the dart glands form a ring around the vagina just above the dart sacs.

Humboldtiana iversoni 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 iversoni* 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 iversoni* is like *H. montezuma* by having four equal-sized dart sacs on the vagina. In *H. inferior* dart sacs ds_2 and ds_3 are reduced in size compared to ds_4. *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. iversoni*.

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 ds_2 and ds_3 are conspicuously smaller than is $\mathbf{ds}_4$. The reduced size of dart sacs $\mathbf{ds}_2$ and $\mathbf{ds}_3$ 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.

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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 sylvania* 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 insular distribution patterns. Uniform distributions over areas larger 1 km^2 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

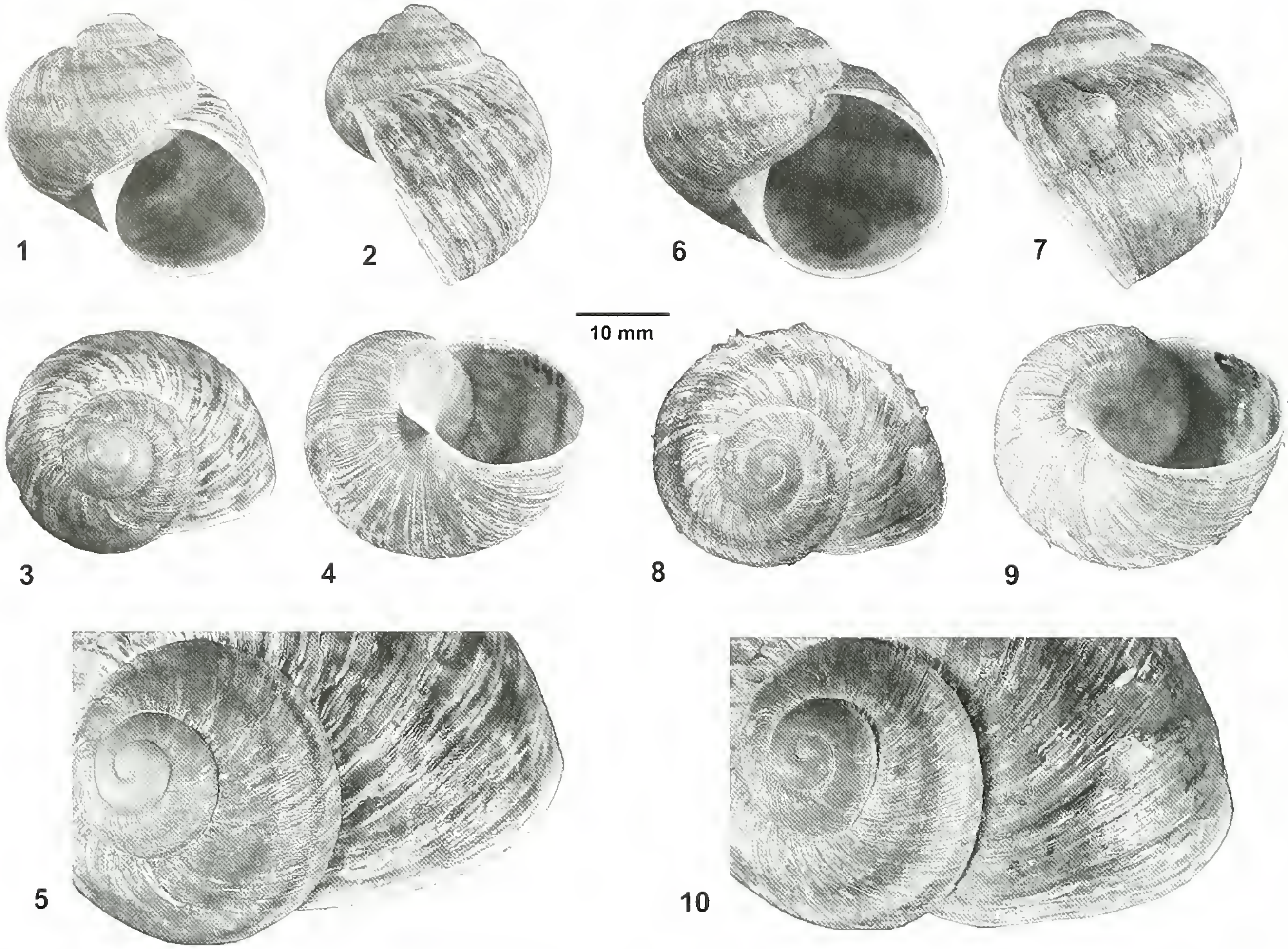
Humboldtiana corruga new species

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 4.0 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



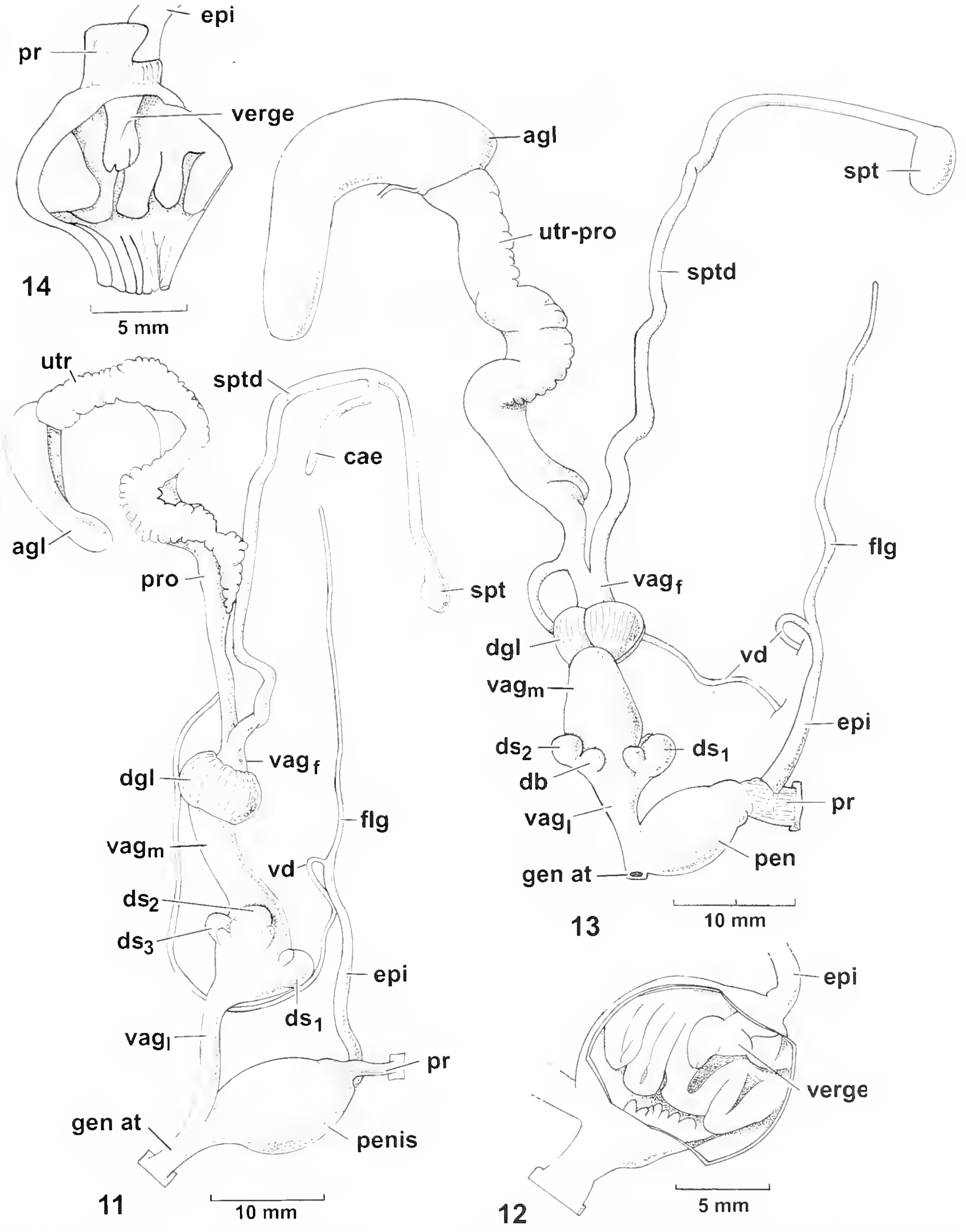
Figures 1–10. New species of *Humboldtiana*. Shells. **1–5.** *Humboldtiana corruga* new species. Holotype, UF 358872. **6–10.** *Humboldtiana sylvania* new species. Holotype, UF 353714.

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$_l$)** has a long slender neck, and bears four dart sacs of equal size **(ds$_1$, ds$_2$, 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 **(vag$_m$)** is about as long as the lower vagina, and is considerably stouter. The free vagina **(vag$_f$)** 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.

	H	W	AW	AH	Whorls
Holotype	31.5	31.0	17.6	23.0	3.8
Paratype	—	32.5	18.5	—	4.0



Figures 11–14. New species of *Humboldtiana*. Reproductive anatomy. **11–12.** *Humboldtiana corruga* new species. **11.** Reproductive system. **12.** Interior of penis. Abbreviations: **agl:** albumen gland; **cae:** caecum; **db:** dart bulb; **dgl:** dart gland; **ds:** dart sac; **epi:** epiphallus; **flg:** flagellum; **gen at:** genital atrium; **pr:** penis retractor; **pro:** prostate; **spt:** spermatheca; **sptd:** spermathecal duct; **utr:** uterus; **vag:** vagina; **vd:** vas deferens. **13–14.** *Humboldtiana sylvania* new species. **13.** Reproductive system. **14.** Interior of penis.

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

Type Locality: Chihuahua, 0.8 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 *corruga* 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 corruga* differs from other known species by its distinct anatomical features. *Humboldtiana corruga* 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 corruga 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. corruga* 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 *Humboldiana corruga*, 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. corruga*, and its shell has similar sculpture.

Humboldtiana sylvania new species

Diagnosis: This species is distinguished by its large size, globose shape, and rotund whorls with a distinct shoulder. The color is straw yellow with three well-defined black bands. The embryonic whorls 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 columellar margin of the peristome (Figure 9). The shell has 4.0 rotund whorls 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 whorls are smooth (Figures 8, 10). The first embryonic whorl is 5.1 mm wide transverse to the initial suture. The postembryonic whorls are sculptured with relatively strong incremental striations and wrinkle which extend undiminished from the suture to the umbilicus. Granular sculpture is absent on all parts of the shell. The rotund 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 **(flg)** 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_l)** is short and tapers below to a narrow neck. It bears four dart sacs of equal size **(ds_1, ds_2, 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 **(vag_m)**, which is slightly longer than the lower vagina. The free vagina **(vag_f)** 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 uterus-prostate **(utr-pro)** is 43 mm.

Holotype: UF 353714, collected by Omar Mejía, 31 August, 2003. Height: 32.0 mm; width: 36.2 mm; aperture 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°30.93' 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 *sylvania* derives from the Latin word for woods or forest.

Remarks: Shell and anatomical features in *Humboldtiana sylvania* are similar to those of an unnamed species from near Rancho Blanco, NNE 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 bulbous penis has a moderately slender verge that is surrounded 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 spermatheeal 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 sylvania*, 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.

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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 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 285 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 cm^3. 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 79 cm interval of the core dating to ~8000–4000 calibrated ^{14}C years before present (cal yr BP) (Figure 1). The fauna for this interval included *Pisidium liljeborgi*, *Pisidium nitidum*, *Pisidium rotundatum*, *Sphaerium nitidum*, *Lymnaea atkaensis*, and *Valvata sincera helicoidea* (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. liljeborgi* was the most abundant bivalve species, occurring in 46 samples between 8300 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 helicoidea* 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

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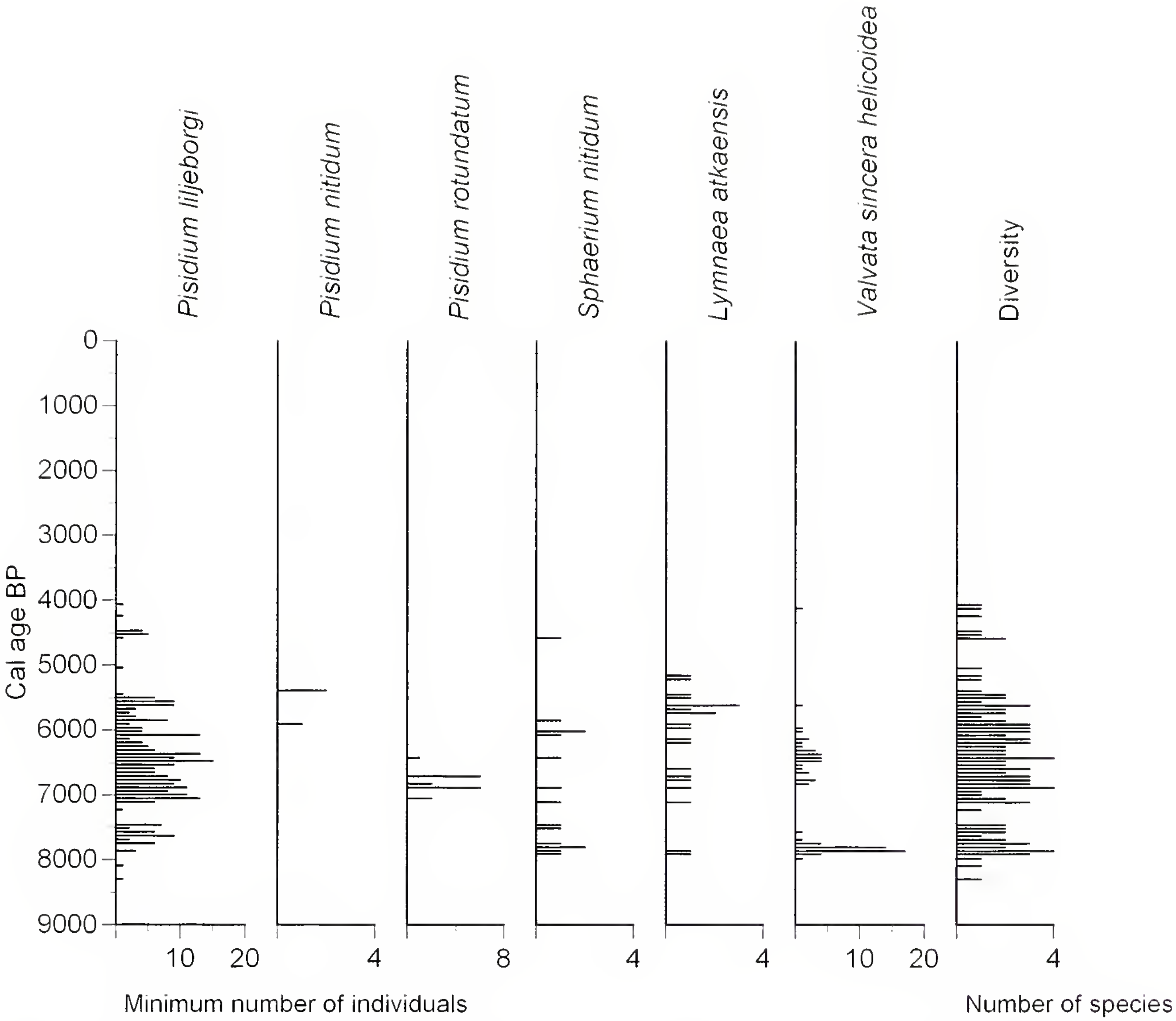

Figure 1. Changes over time in the abundance of mollusk species in a sediment core from Red Green Lake, northern Alaska. Y axis is calibrated ^{14}C years before present (cal age BP). Abundance value (x axis) of the mollusks is the minimum number of individuals per 20 cm^3.

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. liljeborgi*, and *L. atkaensis* 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 helicoidea* 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).

Table 1. Mollusk species found in the Red Green Lake sediment core.

Pisidium (Cyclocalyx) liljeborgi (Clessin, 1886)
Pisidium (Cyclocalyx) nitidum Jenyns, 1832
Pisidium (Cyclocalyx) rotundatum Prime, 1852
Sphaerium (Sphaerium) nitidum Westerlund, 1876
Lymnaea atkaensis Dall, 1884
Valvata sincera helicoidea Dall, 1905

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 paleoecological and paleolimnological approaches are needed to understand past changes in the linkages between terrestrial and aquatic ecosystems in the Arctic.

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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 Gellar, 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 billions of dollars to control, 3) have altered biodiversity, primarily by outcompeting 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 pro-active 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; Szefer et al., 1998; Boehs 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 (Szefer 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‰ range (Ruelas-Inzuna and Paez-Osuna, 2000; Boehs 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 northernmost 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.

Figure 1. *Mytella charruana* from Mosquito Lagoon, Florida, left (top) and right (bottom) valves. BMSM 34067, length 2.4 cm. Scale bar = 1 cm.

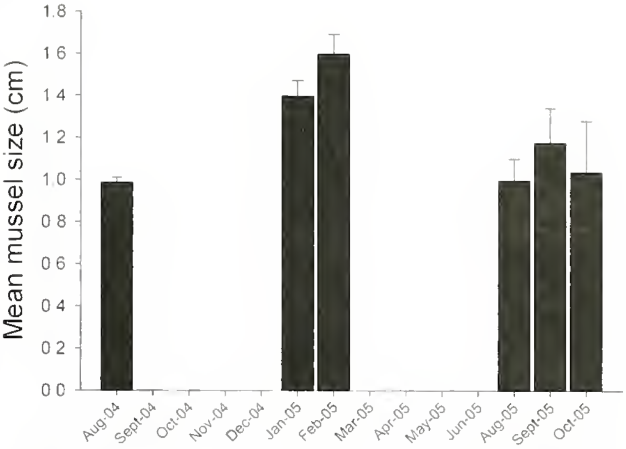

Figure 2. Mean length±standard error (cm) of *Mytella charruana* collected in Mosquito Lagoon, Florida.

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* (Loiseleur, 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. charruana* 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 charruana* 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 demissa* (Dillwyn, 1817). In Mosquito Lagoon, water temperature on dates when *M. charruana* 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 charruana* 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. charruana* 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: $F = 32.61$; $p \leq 0.0001$) (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. charruana*, 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).

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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 1580
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:

(239) 395-2233; fax (239) 395-6706

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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 8½ × 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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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.

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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.

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FLORIDA Arts

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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 (*Keratoisis ornata* 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 meters. 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. yucatecanum* 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 pleurotomariid *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 trochoideans. 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 Bouchet 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: 59–60, plate 40; Abbott, 1972: 46; Quinn, 1992: 79, figs. 80, 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 peripheral keel and suture, iridescence of aragonitic nacre visible through thin calcitic outer layer. Protoconch (Figures 14–15) paucispiral, smooth, glassy, transluscent, increasing from 150 to 500 μm in diameter in about ¾ whorl (270° rotation). Transition to teleoconch marked by flared terminal varix. Teleoconch of 7 1/8 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. Adapical cord (Figures 14, 15, P1) begins as spiral thread in first teleoconch whorl, ¾ 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 columella forming an angle of 87° with the base of previous whorl and 17° with the coiling axis of the shell. Columella rounded, nacreous inductura nearly seals very narrow umbilicus.

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

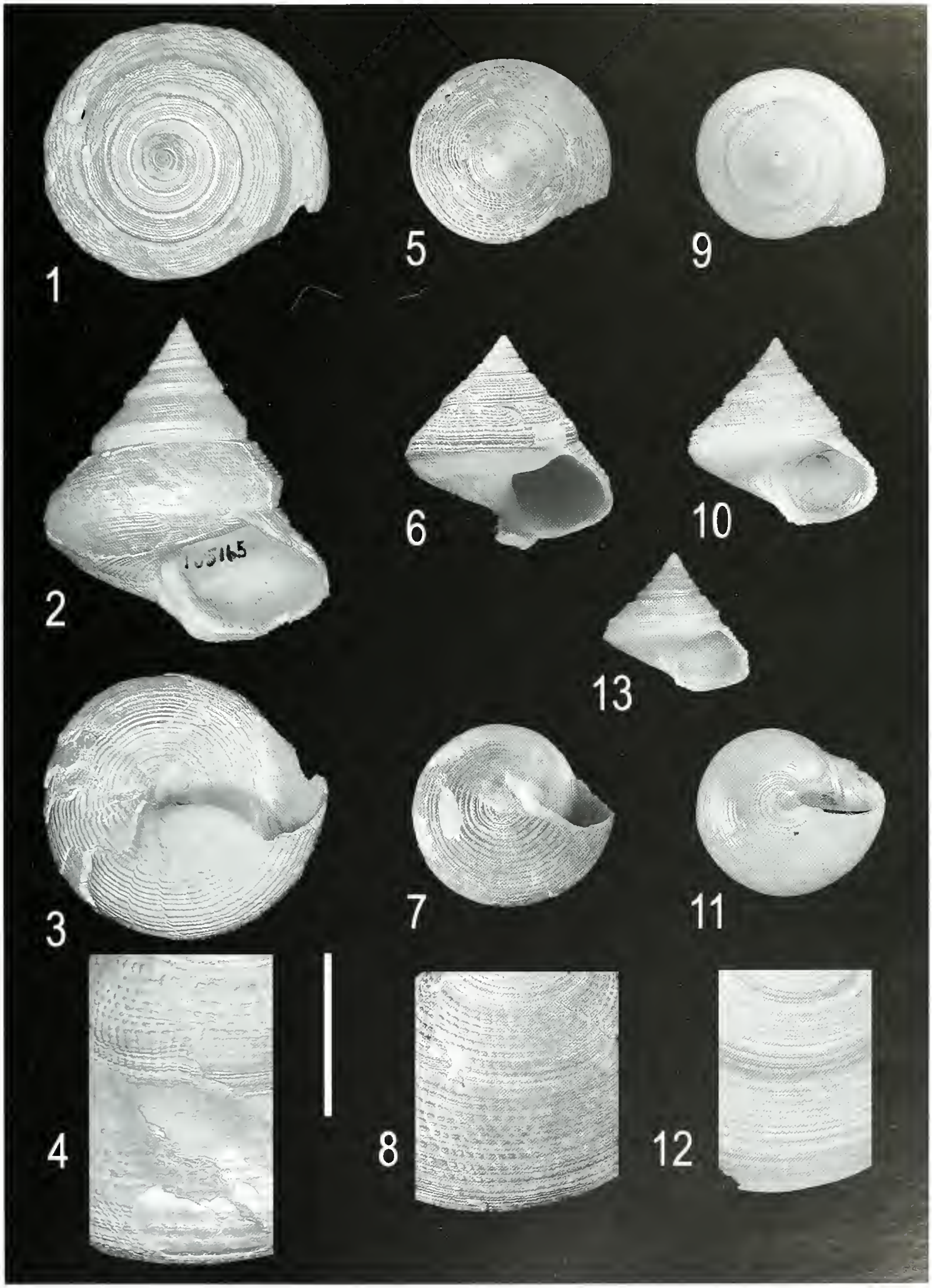
Gross Anatomy: Exposed portions of animal yellowish tan. Foot long, narrow, posteriorly tapering; epipodium broad, with broad, scalloped, inhalant and narrow, tapering, enrolled, exhalant neck lobes; 4 epipodial tentacles per side. Cephalic lappets small, simple, cephalic tentacles long, eye stalks short, 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, **imm**) 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 Matanzas, 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 T10041060), larger specimen (Figures 9–12) USNM 1069300, smaller specimen (Figure 13) SERTC/SCDNR collection S1005.

Figures 1–13. *Calliostoma torrei* Clench and Aguayo, 1940. **1–4.** Holotype, MCZ 153165, off Matanzas, Cuba, 23°13′ N, 81°22′ W, in 385 fms. [704 m], Harvard-Havana Expedition, ATLANTIS Station 3485. **1.** Apical, **2.** apertural, and **3.** basal views. **4.** Detail of sculpture on last two whorls. **5–8.** *Calliostoma rugosum* Quinn, 1992, holotype, USNM 860262, Straits of Florida, JAMES M. GILLIS Cruise 7307, Station 13, depth and exact location unknown. **5.** Apical, **6.** apertural, **7.** basal views. **8.** Detail of sculpture on last two whorls. **9–12.** *Calliostoma torrei*, larger of two specimens of collected at Cutthroat Cliff, about 135 miles E of Jacksonville, Florida, 30°17.0547′ N, 79°20.2514′ W, in 870 m, JOHNSON–SEA–LINK II Dive 3470. **9.** Apical, **10.** apertural, **11.** basal views. **12.** Detail of sculpture on last two whorls. **Figure 13.** Apertural view of smaller specimen from the same locality. Scale bars = 2 cm for entire shells, 3 cm for images of sculptural details.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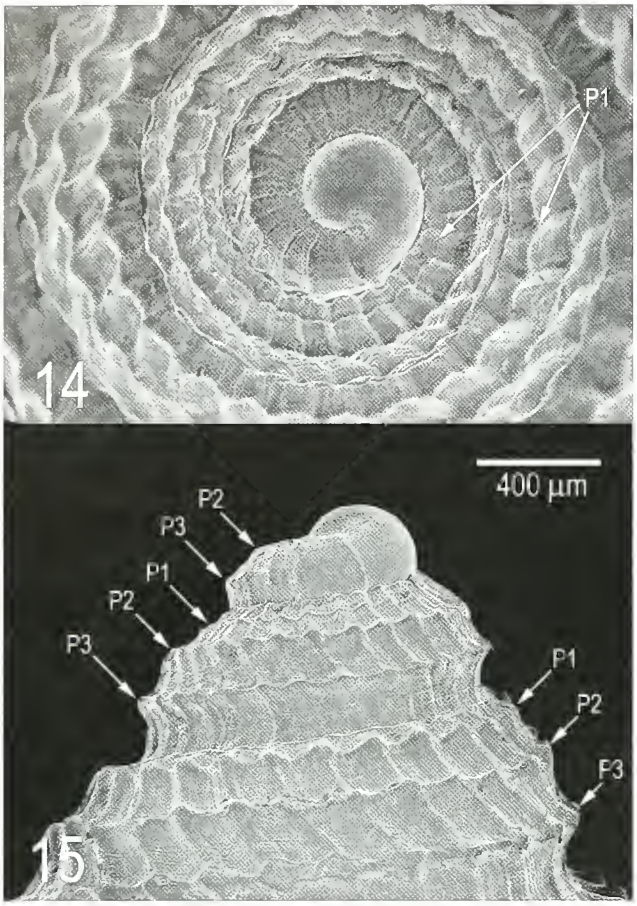


Figures 14–15. *Calliostoma torrei.* **14.** Apical, and **15.** lateral views of protoconch of specimen in Figures 9–12.

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 crinoids, small globular and encrusting sponges, and small erect hard corals (*Lophelia* spp.) were common on the dark rocks. A few cutthroat eels (*Synaphobranchus* 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 (CO I) (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 zizyphinum* Linnaeus, 1758.

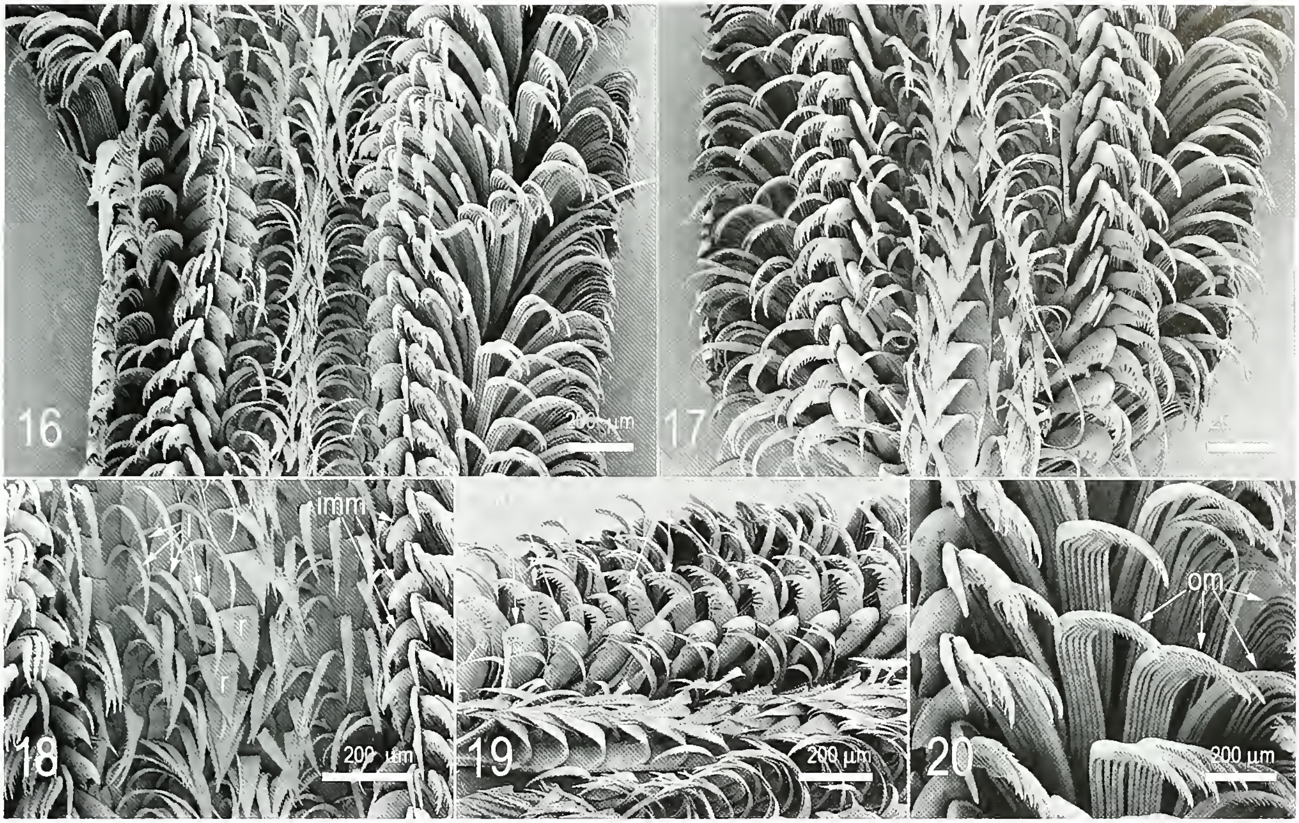
Remarks: *Calliostoma torrei* was described on the basis of a single, very large (41 mm) but dead-collected specimen, that has deteriorated over time, primarily through delamination of the outer, calcareous shell layers from the inner nacreous layers (compare Clench and Turner, 1960: pl. 40; Quinn, 1992: 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 35 mm), shallow water (30–65 m), South American species *Calliostoma militare* Ihering, 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 radular morphology has been published, the radula of *C. torrei* appears most similar to that of *C. yucatecanum* Dall, 1881 (see Clench and Turner, 1950: pl. 4, fig. 4), especially in having rachidian 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. caribbeanum* 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,



Figures 16–20. *Calliostoma torrei*. Radula of specimen in Figures 9–12. **16.** Radular ribbon near mid-length. **17.** Radular ribbon anterior to section in Figure 16. Marginal teeth reflected to better reveal rachidian, lateral, and inner marginal teeth. **18.** Detail of rachidian and finely serrated lateral teeth. **19.** Lateral view of radular ribbon, showing details of innermost lateral and inner lateral teeth. **20.** Scythe-like outer lateral teeth. **im,** inner marginal teeth; **imm,** innermost marginal teeth; **l,** lateral teeth; **om,** outer marginal teeth; **r,** rachidian teeth.

off Mariel, Cuba and Great Inagua), *C. torrei* (including *C. rugosum* synonymized herein) (704–870 m, NE Florida to Cuba), *C. dnopherum* (Watson, 1879) (640 m, Recife, Brazil), *C. atlantoides* Quinn, 1992 (417–589 m, St. Lucia), *C. rota* Quinn, 1992 (20–30 m, Brazil), and *C. coronatum* Quinn, 1992 (768–805 m, Brazil) form a distinctive species group. In this group, he also provisionally included *C. cubanum* 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. leptophyma* 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.

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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*, *Thieleella*) 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 calyptraeiform *Depressizona* Geiger, 2003, and even the new slit-less forms such as *Trogloconcha* 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*, *Sinezona*, *Satondella*, *Incisura*) and Anatomidae (*Anatoma*, *Thieleella*) do not form a clade, whereas other lineages (Sutilizoninae, Temnocinclinae, Depressizoninae) 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 Muséum 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
? Anatomidae McLean, 1989.
Sasakiconcha new genus

Type species: *Sasakiconcha 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–*: honoring Takenori Sasaki of the University Museum of the University of Tokyo for his significant contributions to the systematics of basal gastropods. *–concha*: Latin for shell. Sasaki's shell. Gender feminine.

Remarks: *Sasakiconcha* is tentatively placed in Anatomidae 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 *Sasakiconcha* represents yet another independent lineage of slit-bearing, small vetigastropods.

Many species of *Anatoma* show converging margins of the slit, but in no species do they fuse and enclose a foramen. *Sasakiconcha* is not based on senile 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.

Sasakiconcha must form its foramen by a different process compared to most *Sinezona* or *Sukashitrochus*. *Sasakiconcha* 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 *Sinezona* and *Sukashitrochus* have an open slit, which only closes once the animal is fully grown. Only *Sinezona globosa* Geiger, 2006, known from the two type specimens and USNM 500687 (Caribbean locality data most likely wrong), also closes the foramen in not fully grown specimens (Geiger, 2006). Comparison to other foramen-bearing small vetigastropod genera of the scissurellid grade (*Sutilizona*, *Temnocinclis*, *Temnozaga*, *Depressizona*) 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., 1960): e.g., *Agniesella* Cossmann, 1909 (Portlockiellidae), *Umbotropis* Perner, 1903 (Gosseletinidae), and *Catachisma* Branson, 1909 (Gosseletinidae). The overall shell morphology is most similar to the caenogastropod genus *Cochliolepis* Stimpson, 1858 (Vitrinellidae), though this latter misses the selenizone indicative of a vetigastropod placement for *Sasakiconcha*. 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, 1828) 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.

Sasakiconcha elegantissima new species
(Figures 1–2)

Differential Diagnosis: The cited generic characters will readily identify *S. elegantissima*. The most similar species is *Anatoma paucispiralia* (Bandel, 1998) described from Satonda, Indonesia. Shared characters include the overall biconical depressed shell shape, the protoconch lacking an apertural varix, and the short teleoconch I. The protoconch is half the size in *A. paucispiralia* (150 μm vs. 325 μm), teleoconch I is longer in *A. paucispiralia* (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, 1998: pl. 14, figs. 2–4) is slightly chipped.

Description: Shell biconical-depressed, *Sinum*-shaped, to 8.5 mm (holotype); thin, fragile. Protoconch 285–325 μm (mean = 311 μm, n = 4, 325 μm in holotype), 0.75 whorls, flocculant 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 II with axial cordlets only, interstices irregular with tiny pits; after 0.5 whorls, axial cordlets with approximately one dozen nodules, nodules becoming spirally 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

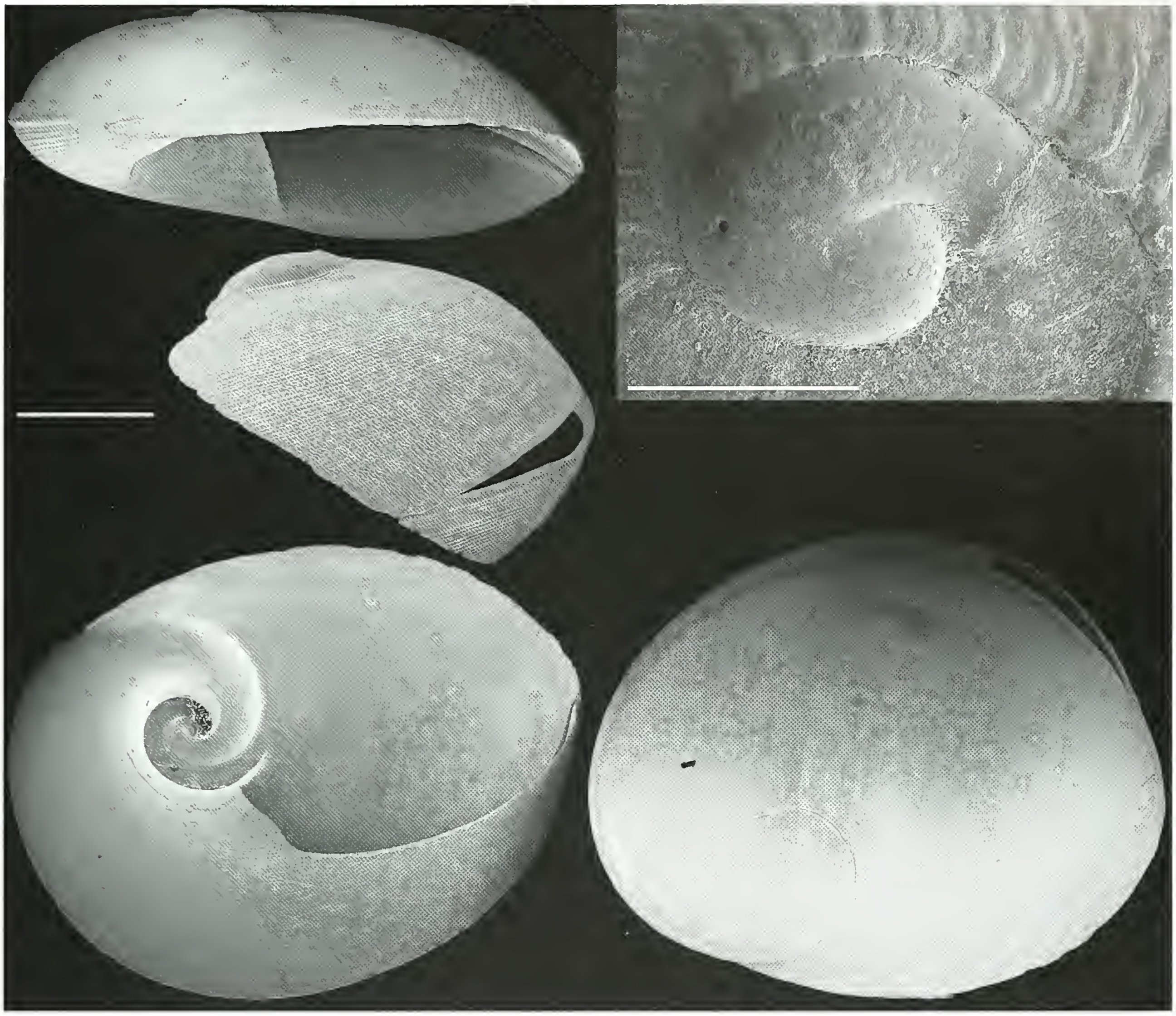

Figure 1. Holotype of *Sasakiconcha elegantissima* new genus and new species, MNHN type collection. Scale bar shell = 2 mm; scale bar protoconch = 200 μm.

subsequent whorl; slit closed anteriorly to form foramen, foramen formed in specimens ≥4 mm. In fully mature specimens (holotype), last 0.125 whorls 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, 21.683° S, 175.317° W; UMUT RM29213, 1; NMNZ 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, DW1509, Tongatapu, 21.083° S, 175.367° W; MNHN, 2, 578 m, BORDAU2, DW1585, Vava'u group, 18.550° S, 173.950° W; French Polynesia: MNHN, 1, 600–620 m, BENTHAUS, DW1889, east of Rap, 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

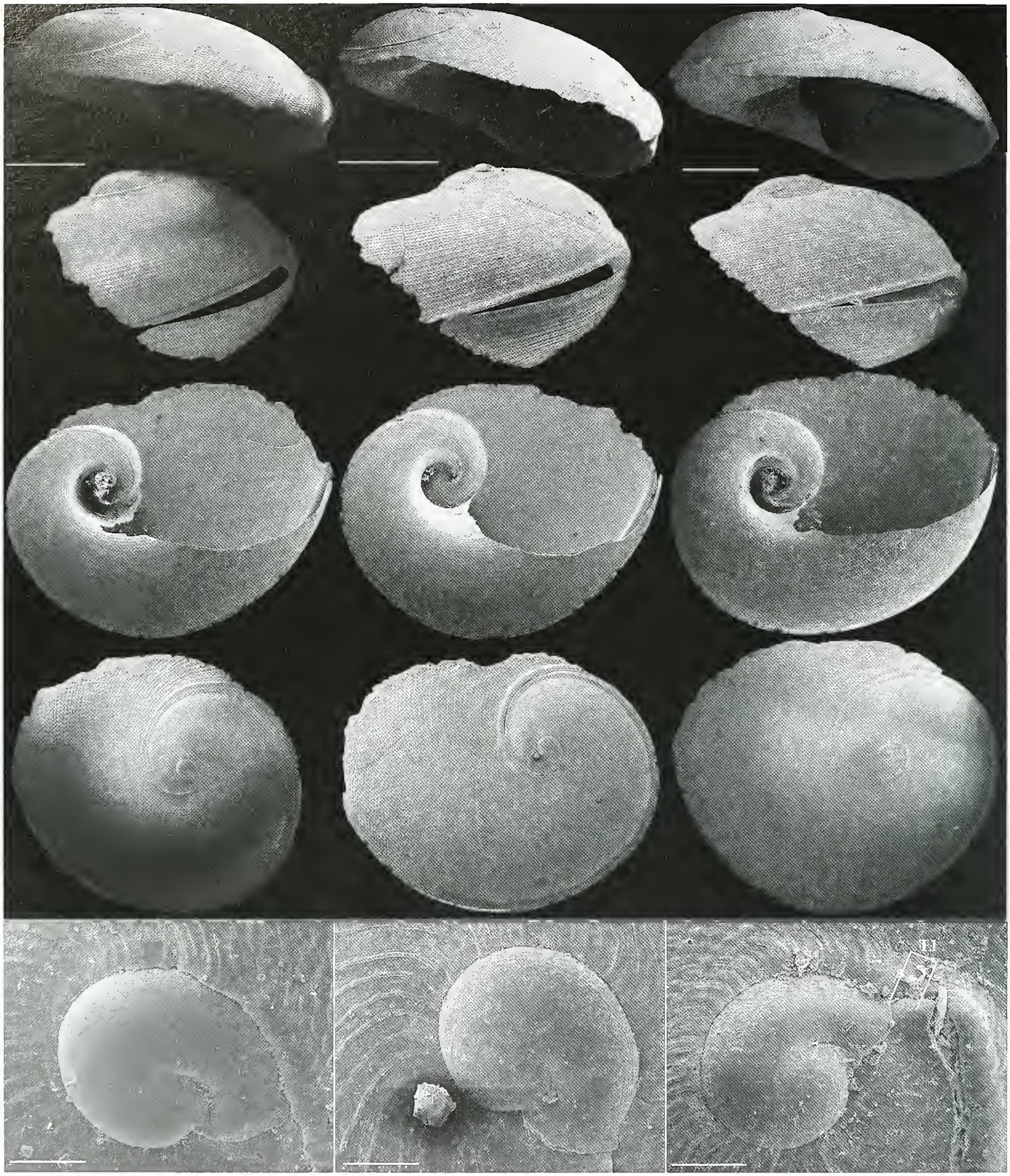

Figure 2. Paratypes of *Sasakiconcha elegantissima* new genus and new species. First row: apertural view; second row: lateral view showing closure of slit to foramen; third row: umbilical view; fourth row: apical view; fifth row: protoconchs. Left: MNHN, 1, 477–493 m, off Fiji, 17.333° S, 178.733° W; middle: MNHN, 1, 300–302 m, Eua, 21.300° S, 175.000° W; right: MNHN, 2, 391–421 m, haut-fond, 21.683°S, 175.317° 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; T1: extent of teleoconch 1.

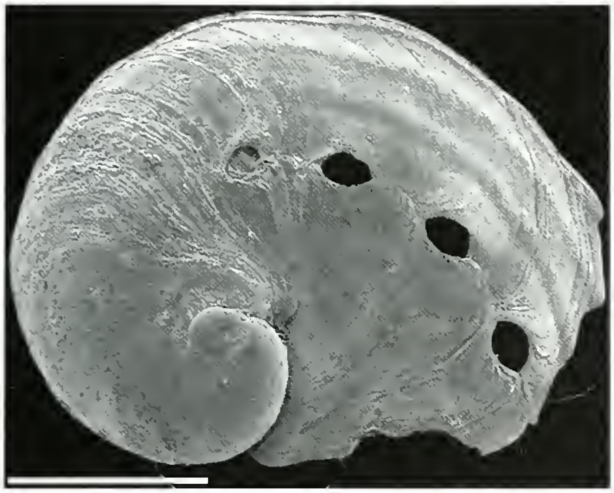

Figure 3. Juvenile *Haliotis rubra* Leach, 1814, from a hatchery. A short slit-less teleoconch I follows the protoconch. Teleoconch II immediately forms a series of foramina. Scale bar = 1 mm.

Thielcella species from the Indo-Pacific awaiting detailed study through electron microscopy. None of these even remotely approaches *Sasakiconcha*.

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).

Sasakiconcha 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 *Anatoma euglypta* (Pelseneer, 1903) from Antarctica is 10.5 mm in diameter (Zelaya and Geiger, unpubl. data).

The protoconch of *Sasakiconcha 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); *Anatoma euglypta*: 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, 1988). 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 Scissurellidae 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 *Seguenzia* in Scissurellidae, whereas this latter genus is placed today in its own group besides 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., 1960; Harasewych, 2002), as well as in juveniles of *Sinezona* and *Sukashitrochus*, 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 (Delhaes, 1909). 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 skirt can be observed (McLean and Geiger, 1998).

Intermediate forms are not widely known. Delhaes (1909) discussed the keyhole-shaped double foramen of the fossil pleurotomarioideans in the genera *Ditremaria* and *Phragmostoma*. Ontogenetically, Haliotidae immediately form a series of holes after a short slit-less teleoconch 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 Montouchet (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, NMNZ, USNM; many smaller collections not listed). Despite other abnormalities observed such as senile 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

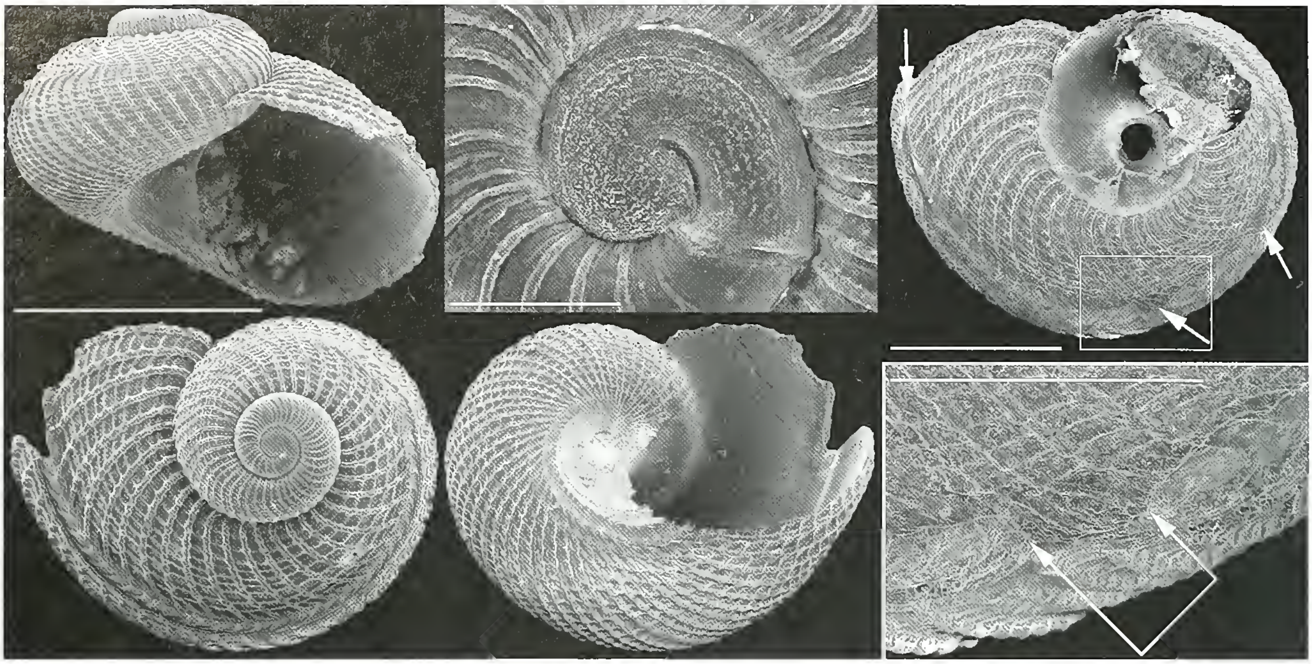

Figure 4. *Scissurella morretesi* Montouchet, 1972. Left: four views of normal specimen. Scale bar shell = 1 mm; scale bar protoconch = 100 μm. Right: apical view of aberrant specimen with evidence of three-fold successive closure of slit to foramen (bold arrows). Square shows portion of shell shown enlarged below; inset: Enlarged view of second closure; connected arrows show onset and end of closure; MNHN, 295 m, SE, Brazil, 18.983° S, 37.833° W. Scale bar shell = 1 mm; scale bar inset = 500 μm.

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.

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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 siphoniferus* Lesson, 1844, and *Typhis martyria* Dall, 1902. 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 protoconchs of the four species are illustrated for the first time. Lectotypes are designated for *Murex siphoniferus* 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, 1989a, 1989b, 1996; Houart, 1991, 1994, 2002; Absalão and Santos, 2003). DNA work currently under way elsewhere (Oliverio and Houart, in prep.) for *Typhinellus 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 Zoologia, San José, Costa Rica; SBMNH: 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 Zandali 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

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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)
(Figures 1–15, 16, 44–46, 56–57, 61–62, 67)

Typhis coronatus Broderip, 1833: 178; Sowerby, 1841, pl. 200, figs 3,4.
Typhis quadratus Hinds, 1843: 18; Hinds, 1844: 10, pl.3, figs 3, 4.
Murex siphoniferus Lesson, 1844: 168.
Typhis martyria Dall, 1902: 550; Dall, 1908, pl.15, fig.11.
Typhis (*Typhisopsis*) *coronatus*.—Keen, 1944: fig. 17; Keen, 1971: 540, fig. 1051 right [type figure of *T. quadratus*] Abbott, 1974: 192 (2017).
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, 1987: 34–35, figs 7–11; D'Attilio and Hertz, 1988: 21, fig. 109.
Typhis coronatus.—Kaicher, 1978: card 1595.
Typhis (*Typhisopsis*) *grandis*.—Keen, 1971, 540, fig. 1052 [not *Typhisala grandis* (A. Adams, 1855)].
Not *Typhis* (*Typhisopsis*) *coronatus*.— Keen, 1971: 540, fig. 1051 (left) not Broderip, 1833 [= *Typhisala 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; intritacalx covering penultimate and final whorl with microsculpture consisting of regular gouge-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

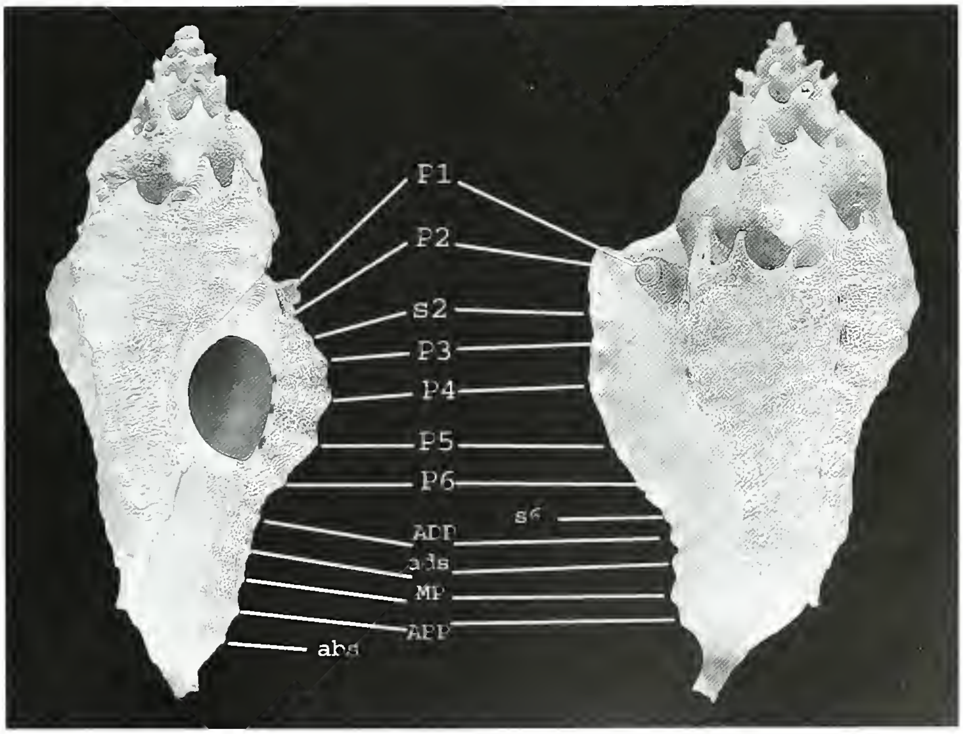


Figure 1. Morphology of the spiral cords in *Typhisopsis coronatus* (Broderip, 1833).

Table 1. Terminology used to describe the spiral cords (based on Merle 1999, 2001)

P	Primary cord
s	Secondary cord
P1	Shoulder cord
P2–P6	Primary cords on the convex part of the teleoconch whorl
s1–s6	Secondary cords on the convex part ot the teleoconch whorl
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
ABP	abapertural primary cord on the siphonal canal
ads	adapertural secondary cord on the siphonal canal
ms	median secondary cord on the siphonal canal
abs	abapertural secondary cord on the siphonal canal

sealed along its length with 5 cords (probably ADP, ads, MP, ABP, abs), tapering with long, backwards facing, sealed tube at distal end. Sutural line strongly shifted to the right. Aperture white, moderately large, smooth, subcircular, entire, forming an erect peristome appressed posteriorly. Intritacalx chalky, off-white, deeply and irregularly pitted. Shell color white to cream with brown suffusions on varices, tips of shoulder spines, and tip of siphonal canal; two to five brown spots on edge of apertural lip, sometimes none, on occasional specimens these spots also on leading side of varices. Operculum corneus, light brown with 13–15 concentric lamellae and terminal nucleus. Radula (Figure 67) with rachidian tooth bearing a long central cusp, and on each side 3 or 4 slightly shorter, narrower lateral denticles of varied strength and length or erratically fused, and a broad lateral cusp, slightly shorter than central cusp. Lateral teeth sickle shaped, broad.

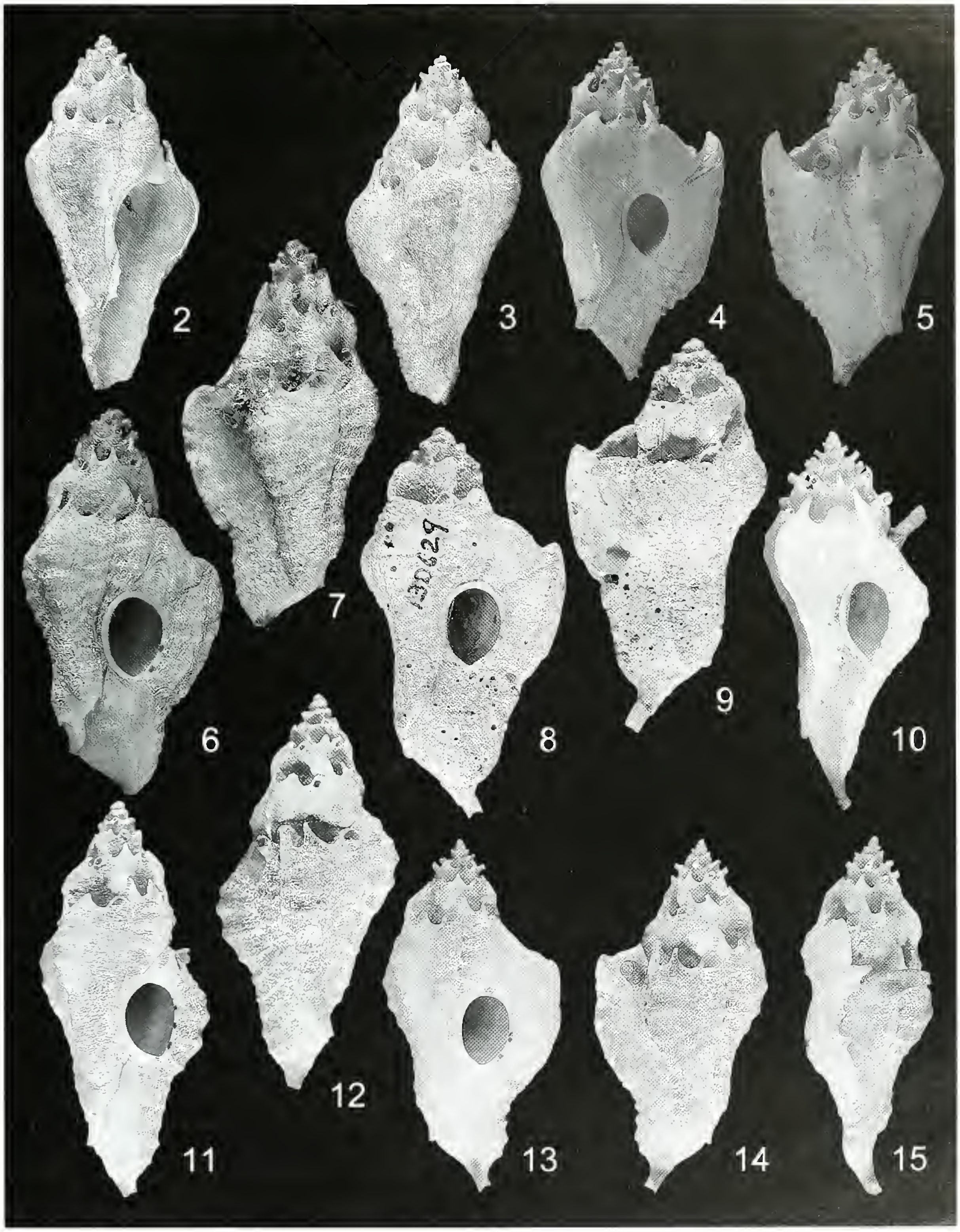
Type Material: *Typhis coronatus:* Ecuador, Salango, holotype BM(NH) 1966447; *Typhis quadratus*: Costa Rica, Golfo de Nicoya, and Ecuador, Bahía de Guayaquil, dredged from a muddy bottom 7 to 18 fms (13–33 m) (Golfo de Nicoya is here designated as type locality), holotype BM(NH) 1844.6.7.35; *Murex siphoniferus*: Mexico, Acapulco, Guerrero, 1 lectotype MNHN (here selected); *Typhis martyria*: Golfo de California, off San Pedro Martír, 26 m, sand, holotype USNM 130629.

Other Material Examined: Mexico, Bahía Magdalena, Baja California Sur, 1 spec. (SBMNH); San Felipe, Baja California, 1 spec. (SBMNH); Bahía de los Angeles, Baja California, dredged 27 m, 1 spec. (SDNHM 23216 [figured in Radwin 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 dd spec. (SDNHM); Isla Danzante, Baja California Sur, dredged 35–40 m, 3 spec. (CS); dredged 30–45 m, 3 spec. (CJH); Bahía Concepción, Baja California, 1 spec. (SDNHM); Cabo Tepoca, Sonora, dredged 20–30 m, sand bottom with rocks, 5 spec. (CS); Guaymas, Sonora, dredged, 24 m, 1spec., (RH); 1 spec. dredged (SDNHM 43812); 55 m 1 dd spec. (MNHN); Bahía Bacochibampo, 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_Bahía San Carlos, Sonora, 19–38 m, 1spec. (IRSNB IG 26.158); dredged 18–22 m, 98 spec. (CJH); dredged 15–30 m , 14 spec. (CS); 4 spec., 31 m (SDNHM 90837); dredged 100 m, 3 spec. (SDNHM 71920); off Tetas de Cabras, dredged 60–100 m, 7 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, Playas 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 dd spec. (SDNHM 91506); 1 spec. (SBMNH); 16 spec. (SBMNH); Panama, 21 spec. (SBMNH); Isla Santa Catalina, dredged 5–8 m, 5 spec. (RH); Boca de la Honda, 7°27′N, 80°51′W, in white sand, 2 spec. (RH); SE Isla Rancheria, Golfo de Chiriquí, 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); Bahía Montijo, Veraguas, 19 m, 1 spec. (RH); Arenas de Quebro, dredged 19–38 m, 1 spec. (RH); Isla Venado, 1 dd 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. coronatus* (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. coronatus* 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 sutural line.

Of the two syntypes of *Murex siphoniferus* (MNHN), one is *Typhisala grandis*, the other is conspecific with *Typhisopsis 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 *Typhisala grandis* (A. Adams, 1855) are specimens of *Typhisopsis 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.



Figures 2–15. *Typhisopsis coronatus* (Broderip, 1833). **2–3.** Ecuador, Salango, holotype BM(NH) 1966447, 26 mm (photo P. Crab, BMNH). **4–5.** *Typhis quadratus* Hinds, 1843, Costa Rica, Golfo de Nicoya (herein designated as type locality), holotype BM(NH) 1844.6.7.35. 17.5 mm (photo P. Crab, BMNH). **6–7.** *Murex siphoniferus* Lesson, 1844, Mexico, Acapulco, Guerrero, lectotype MNHN (here designated), 27.9 mm (photo D. Brabant, MNHN). **8–9.** *Typhis martyria* Dall, 1902, holotype USNM 130629. Golfo de California, off San Pedro Martir, 27.6 mm. **10.** *Typhisopsis coronatus.* Tetas de Cabra, Guaymas, Sonora, Mexico, 19.4 mm, CJH (photo P. Sadeghian) (protoconch illustrated Figures 43–45). **11–12.** Panama, Santa Catalina, 5–8 m, RH, 26 mm. **13–15.** West Panama, Boca de la Honda, 7°27′ N, 80°51′ W, in white sand, RH, 23.56 mm.

Typhisopsis carolskoglundae new species
(Figures 17–25, 47–49, 59, 63)

Typhisala grandis.—D'Attilio, 1987: 32, figs. 1–6; D'Attilio and Hertz, 1988: 72–73, figs. 108 a–e [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 protoconch 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 appressed to previous partition. Varices broader and swollen at shoulder periphery. Apertural varix with a moderately broad, recurved, sinuous 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 roundly 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 squamose. 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. Intervarical sculpture faint or absent under magnification (20×). Sealed rounded anal tube appressed to partition on preceding varix, forming an angle of approximately 80–90° 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 intritacalx showing occasional axial striae. 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 93558); 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 1084298); 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 (RH); off Isla Gobernadora, intertidal, 1 paratype (RH); off Isla Venado, Bahía Panama in muddy sand at low tide, 1 paratype (IRSNB IG 26.817/566); Bahía Chiriquí, 74 m, 1 paratype (IRSNB IG 28.466/567); Contadora, Perlas Archipelago, Bahia de Panama, 4 paratypes, 15–30 m (SBMNH 359432); 1 paratype (SBMNH 359429); Ecuador, Isla Santiago, Islas Galápagos, 1 paratype (SBMNH 359433).

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

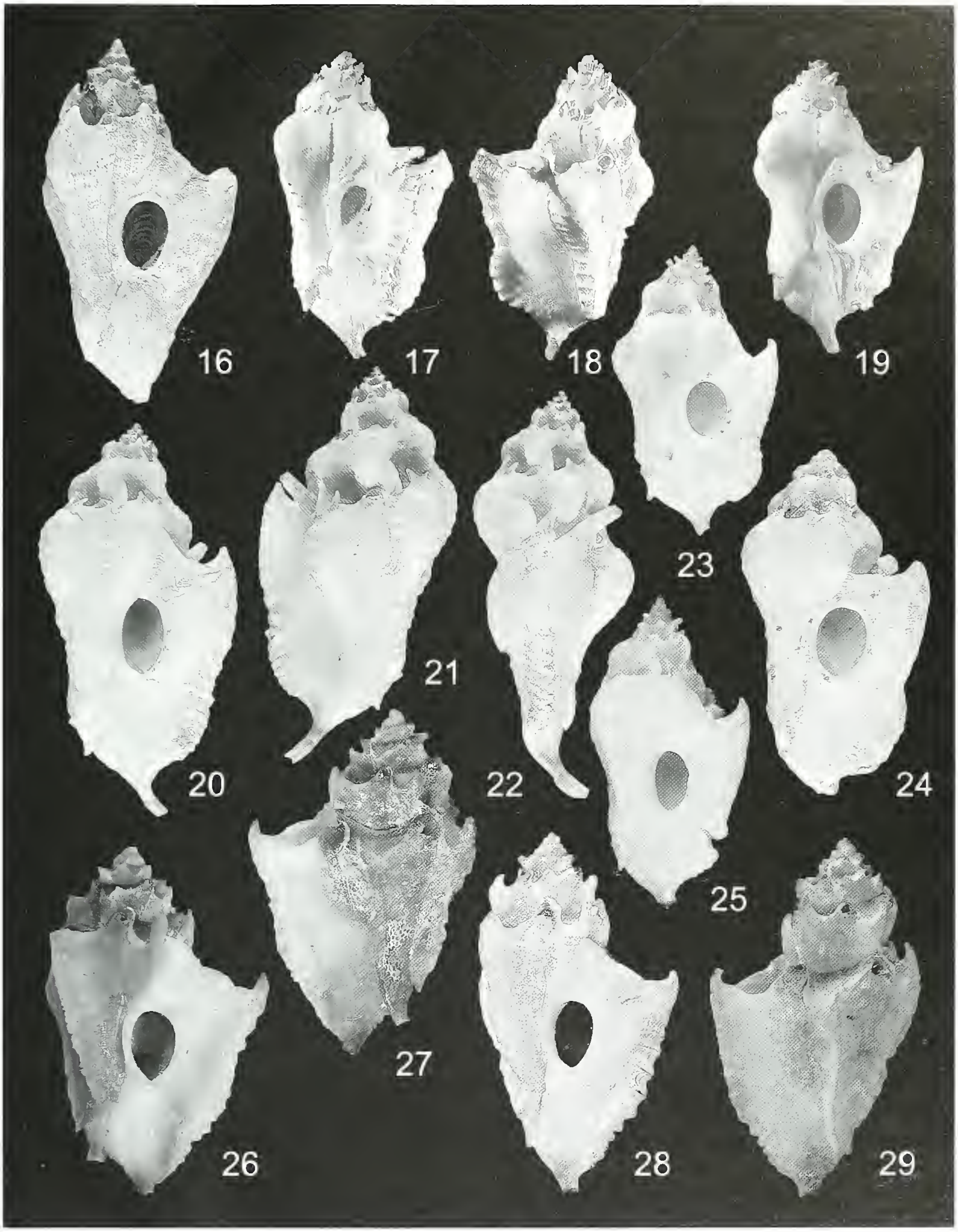
Type Locality: Costa Rica, Guanacaste, Playas del Coco, on mud bottom, 24–37 m.

Distribution: Sonora, Mexico to Isla Venado Bahía de Panama, 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 carolskoglundae* 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, roundly 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 intritacalx, compared to the squamose, pitted intritacalx 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 carolskoglundae* was il-



Figures 16–29. Species of *Typhisopsis* and *Typhisala*. **16.** *Typhisopsis coronatus* (Broderip, 1833), Mexico, Colima, Manzanillo, near harbor entrance, 15–22 m. coll. RH, 24.38 mm. **17–25.** *Typhisopsis carolskoglundae* new species **17–18.** Costa Rica, Playa del Coco. Guanacaste. on mud bottom, 24–37 m, holotype SDNHM 90773, 17.8 mm (photo K. Barwick) **19.** Paratype SDNHM 93558 17.1 mm (photo K. Barwick). **20–22.** Western Panama. Boca de la Honda, 7°27′ N, 80°51′ W. in white sand. paratype RH 30.1 mm. **23.** Western Panama, Boca de la Honda. 7°27′ N, 80°51′ W, in white sand, paratype MNHN Moll 6991. 18.9 mm. **24.** Mexico. Sonora. Bahía San Carlos, 31 m, RH. 26 mm. **25.** Paratype SBMNH 359436, type locality, 16.6 mm (photo P. Sadeghian) (protoconch illustrated Figures 46–48). **26–29.** *Typhisala clarki* (Keen and Campbell. 1964). **26–27.** Bahía Panamá. Isla Venado, holotype CASIZ 064667 [ex-SUPTC 9724], 22.8 mm (photo G. Metz) **28–29.** Paratype BMNH), 22 mm (photo P. Crab, BMNH)

lustrated 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 varical 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 siphonal canal 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 flange and a smooth shell under a simple chalky intritacalx.

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 flange 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)

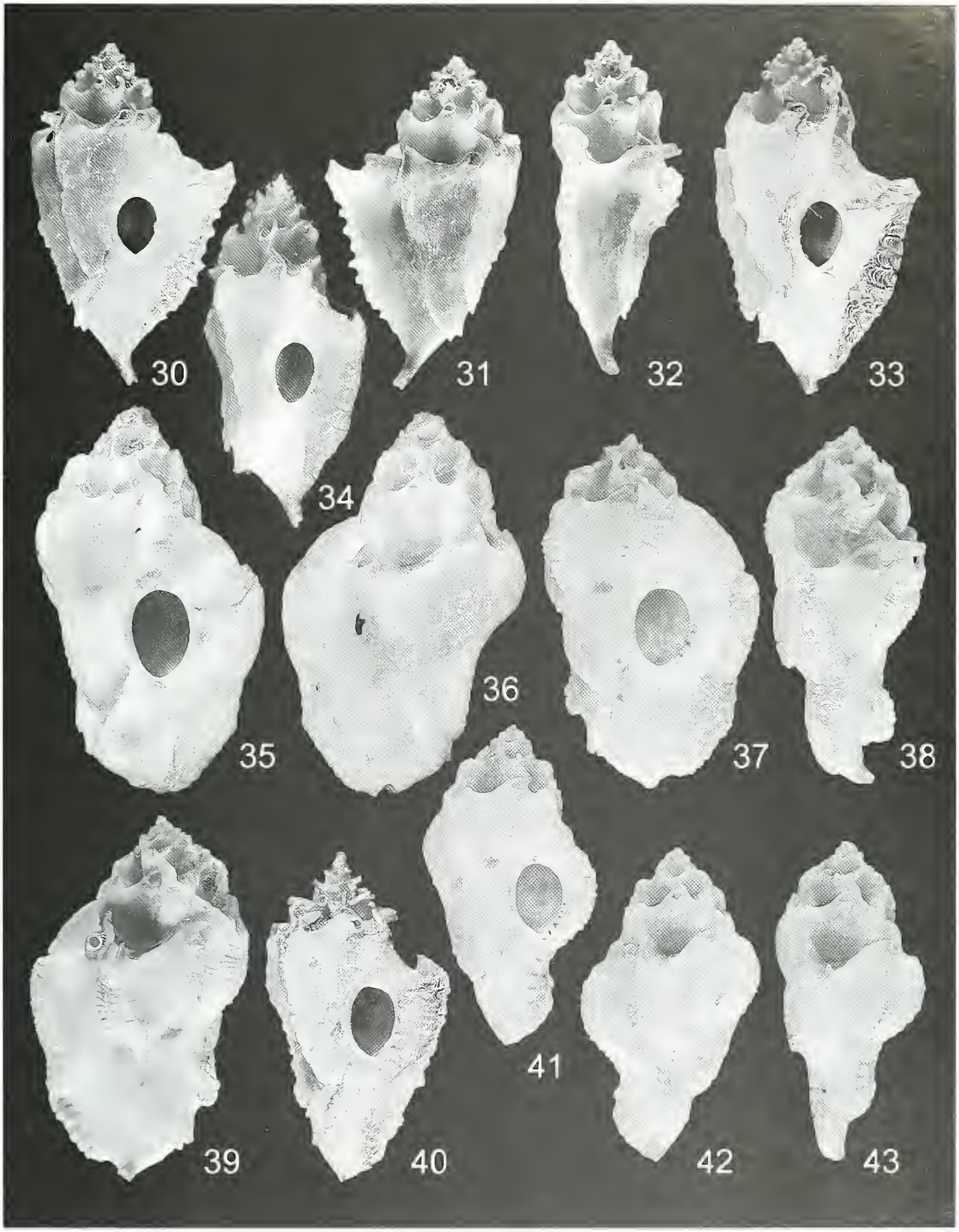
Typhis (Typhisopsis) clarki Keen and Campbell, 1964: 48, pl. 9, figs. 15, 19, 23.
Typhis (Typhisopsis) clark.—Keen, 1971: 540, fig. 1050; Abbott, 1974: 192 (2016).
Typhis clarki.—Gemmell, 1974: 100–103, 5 figs.; Kaicher, 1980: card 2508.
Typhisala clarki.—D'Attilio, 1975: 58, text fig.; Radwin and D'Attilio, 1976: 211, pl. 31, fig. 5; Gemmell and D'Attilio, 1979: 88–93, figs. 1–8; D'Attilio and Hertz, 1988: 20, fig. 107.

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 pustulose, 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 appressed laminae, one on the receding edge extending further than the one on leading edge, the two forming the slightly open spine at shoulder. Anal siphon (tube) forming an angle of approximately 85–90° with axis of shell, placed approximately midway between varices and appressed 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. Spiral sculpture faint, where present, 12–14 intervarical lines visible on some specimens under magnification (10×) corresponding to open spinelets at outer apertural edge. On fresh specimens, not over-cleaned, intritacalx sculpture of simple axial striae present. P1 with sealed, tapering, anal tube. P2 ornamented with long, upwards curved spine at intersection with varix.

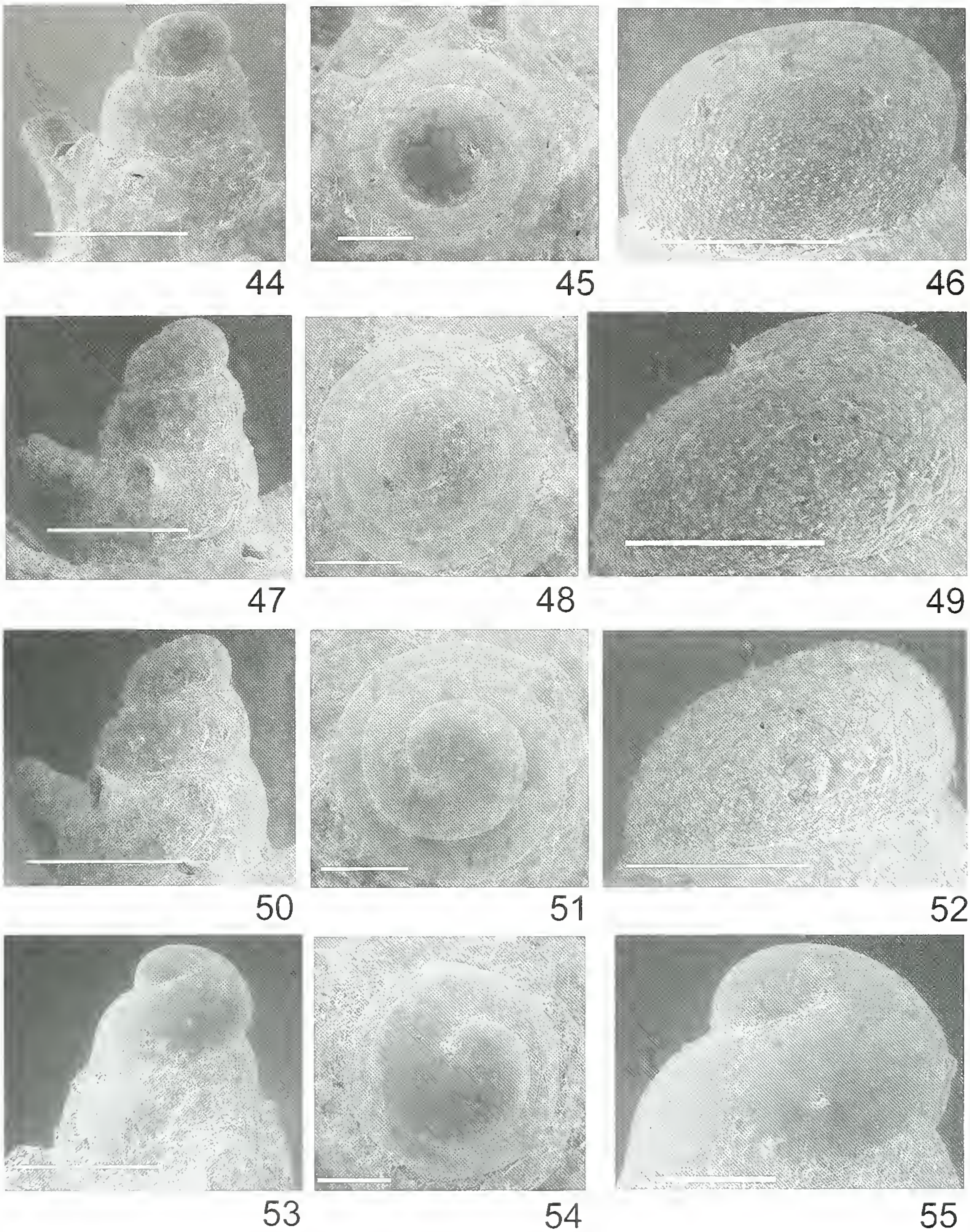
Aperture small, ovate, forming a continuous peristome, erect at outer lip and anterior portion of columellar lip. Siphonal canal long, broad, ventrally sealed, tapering to a slender, dorsally curved tube at distal end. Sutural line weakly shifted to right, left side of canal weakly overlapping right side. Color of protoconch off-white with white pustules on first whorl; teleoconch brown, cream 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, intritacalx sculpture of simple axial striae present. Operculum corneus, light brown with 12 or 13 concentric lamellae and terminal nucleus. Radula (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, intertidally, in mud and rocks, 28 spec. (CJH); 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 53452, figured in Radwin and D'Attilio, 1976); intertidal, 9 spec. (SDNHM 82868); 31 spec., intertidal (SBMNH); Bahía la Cholla, Sonora, intertidal in sand over rocks, 7 spec. (CS); intertidal, −1.5 m tide, 2 spec. (SDNHM 90835);

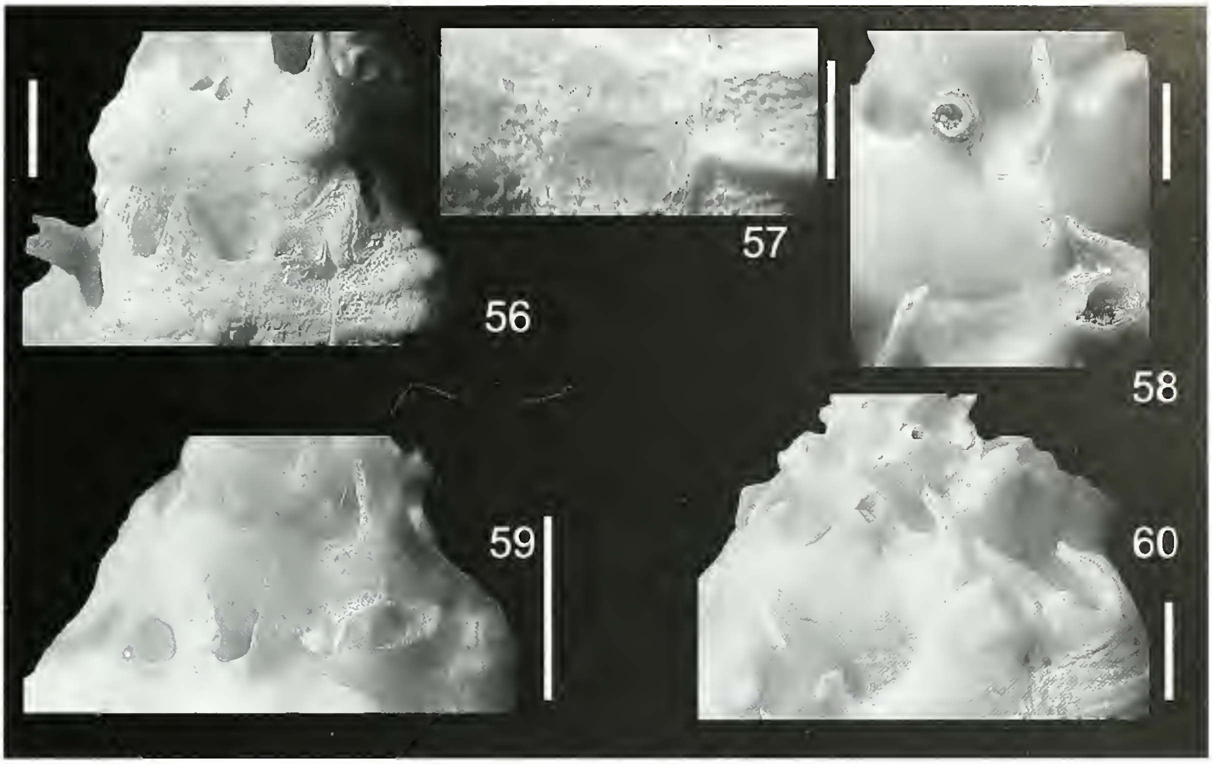


Figures 30–43. Species of *Typhisala*. **30–34.** *Typhisala clarki* (Keen and Campbell, 1964) **30–32.** Panama, off Isla Cébaco, dredged in 6–9 m, silty sand and rubble, RH, 22.8 mm. **33.** Bahía Panama, Isla Venado, under stones at low tide, RH, 22.3 mm. **34.** Mexico, San Felipe, Baja California, (CS), 25.0 mm (photo P. Sadeghian). **35–43.** *Typhisala grandis* (A. Adams, 1855). **35–36.** California. **lectotype BM(NH) 1974470 (here selected),** 37.9 mm (photo P. Crab, BMNH). **37–39.** Mexico, Sonora, San Carlos, Punta Doble, 20–22 m, in rubble, RH, 33.7 mm. **40** *T. grandis*, SBMNH, Mexico, Sonora, Guaymas, Bahía San Carlos, 15 m, 18.0 mm (photo P. Sadeghian). **41–43.** Costa Rica, Province of Puntarena, Isla Ballena, Canton de Osa, offshore, between 12–25 m, RH, 24.0 mm.



Figures 44–55. Protoconchs. **44–46.** *Typhisopsis coronatus* (Broderip, 1833). **47–49.** *Typhisopsis carolskoglundae* new species **50–52.** *Typhisala clarki* (Keen and Campbell, 1964). **53–55.** *Typhisala grandis* (A. Adams, 1855). Scale bars: figures 44, 47, 50, 53 = 0.5 mm; other figures = 200 µm. All photos by D. Geiger.

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 IG 26.817); intertidal, 9 spec. (CS); Isla Gobernadora, intertidal, 1 spec. (SDNHM 93342); Bahía de Panama intertidal (SDNHM 62897); Isla Pedro Gonzales, Islas Perlas, 2 spec. (SBMNH).



Figures 56–60. Detail of spines and intritacalx. **56–57.** *Typhisopsis coronatus* (Broderip, 1833). **58.** *Typhisala clarki* (Keen and Campbell, 1964). **59.** *Typhisopsis carolskoglundae* new species **60.** *Typhisala grandis* (A. Adams, 1855). All RH. Scale bars = 2 mm.

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

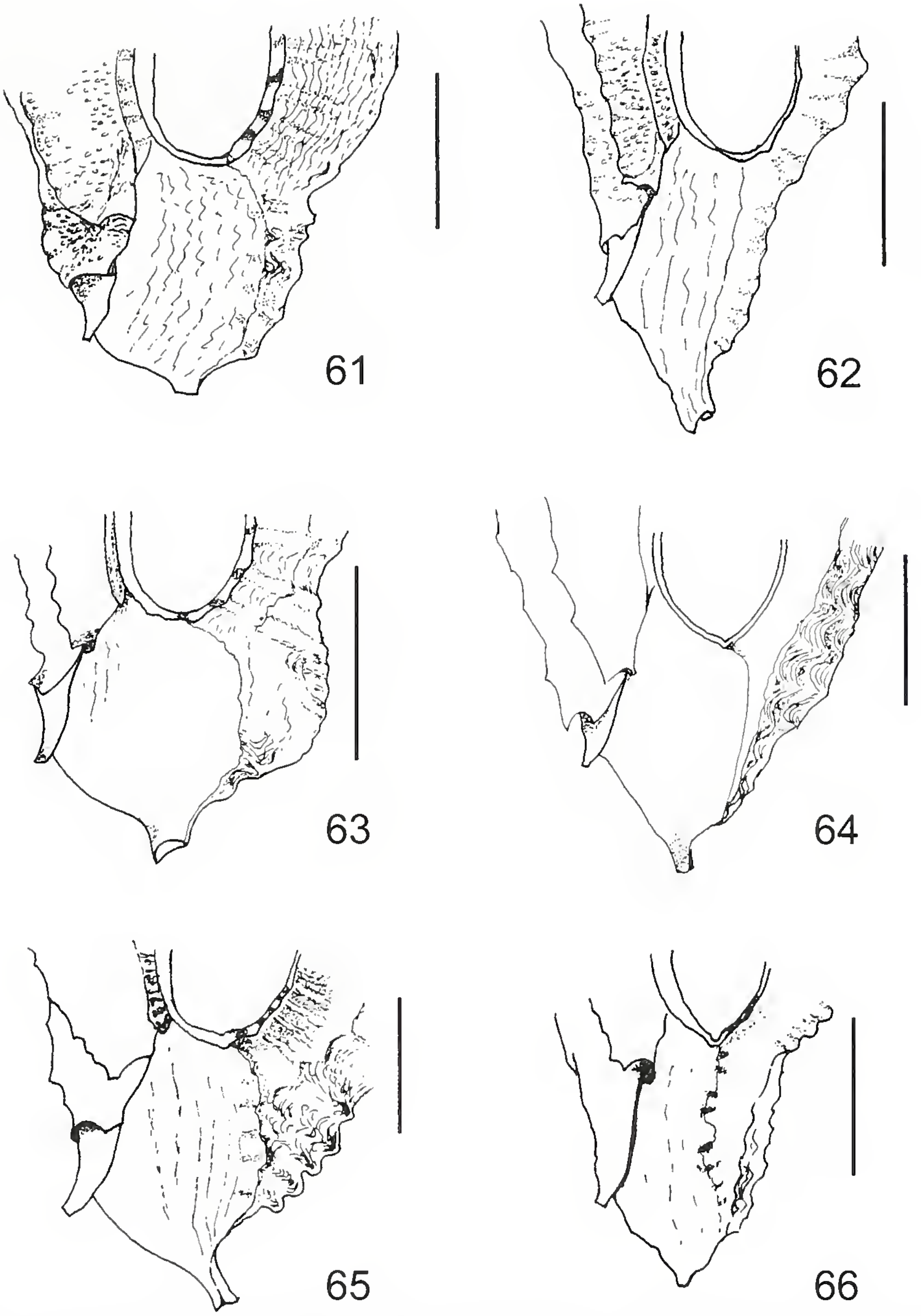
Typhisala grandis (A. Adams, 1855)
(Figures 35–43, 53–55, 60, 65-66, 69)

Murex siphoniferus Lesson, 1844: 168 (paralectotype MNHN) (see under *Typhisopsis coronatus*).
Typhis grandis A. Adams, 1855: 42, pl. 27, fig. 4.
Typhis (*Typhisopsis*) *grandis*.—Keen, 1944: 54, fig. 18; Abbott, 1974: 192 (2018).
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 (*Typhisopsis*) *coronatus*.—Keen, 1971: fig. 1051 (left) (not *T. coronatus* Broderip, 1833).
Not *Typhis* (*Typhisopsis*) *grandis*.—Keen, 1971: 540, fig. 1052 (= *Typhisopsis coronatus*).
Not *Typhisala grandis*.—D'Attilio, 1987: figs. 1–6; D'Attilio and Hertz, 1988: fig. 108, a–e (= *Typhisopsis carolskoglundae* new species).

Description: Shell up to 37.9 mm in length, broad, heavy. Spire low or moderately high, angulate; protoconch 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 succeeding 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 anal siphon (tube) rests against the former partition. Final 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. Apertural spine short, sharply dorsally curved.

Spiral sculpture of sharp, raised primary cords, secondary 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 magnitude, 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 peristome; outer lip with 3–5 brown spots often appearing as well on leading edge of varices, brown spot also appearing on each intervarical area; Siphonal canal long,

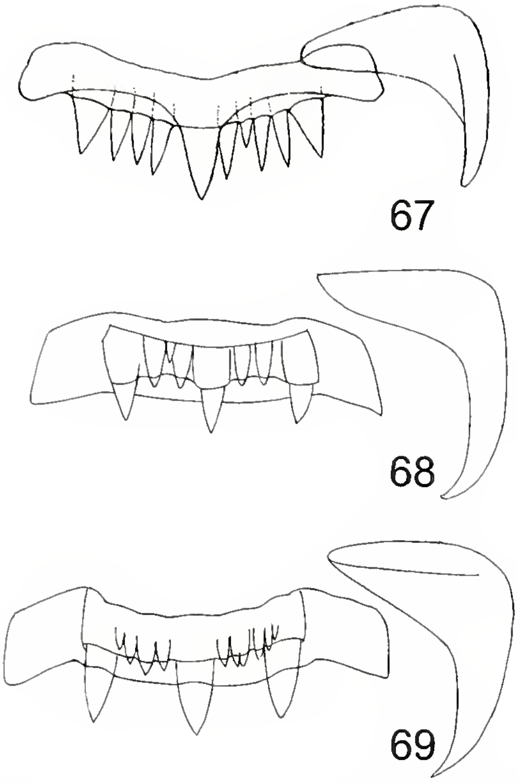


Figures 61–66. Siphonal canal. **61–62.** *Typhisopsis coronatus* (Broderip, 1833). **61.** Adult specimen. **62.** Juvenile. **63.** *Typhisopsis carolskoglundae* new species **64.** *Typhisala clarki* (Keen and Campbell, 1964). **65–66.** *Typhisala grandis* (A. Adams, 1855). **65.** Adult specimen. **66.** Juvenile. All RH. Scale bars = 0.5 mm.

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. Intritacalx 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



Figures 67–69. Radulae (from D'Attilio and Hertz, 1988). **67.** *Typhisopsis coronatus* (Broderip, 1833), Islas Galápagos, Isla Jervis. **68.** *Typhisala clarki* (Keen and Campbell, 1964), Mexico, Baja California , San Felipe. **69.** *Typhisala grandis* (A. Adams, 1855), 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) 197470, 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, 1spec. (RH); 2 dd spec. 20–21 m diving, (SDNHM 90834); 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 mi SE San Antonio, Guaymas, Sonora, dredged 100 m, 2 dd spec. (SDNHM 80764); Manzanillo, 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); Isla 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 IG 26.817); 37–52 m, 1 spec. (IRSNB IG 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 Bahia James, 30–35 m, coll. D.R. Shasky, 1 spec. (SBMNH 366003).

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

Remarks: Of the three syntypes of *Typhis grandis* housed in BM(NH), two are *Typhisopsis coronatus*, 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 varical flange, a narrower, more acute, siphonal canal, with the ventral sutural 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 martyria* Dall, 1902; to Kathie Way and Phil Crabb (BMNH) for digital images; to Virginie 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 carolskoglundae*; to George Metz , Novato, California, for digital images of the holotype of *Talityphis clarki* at CAS; to Kelvin Barwick (City of San Diego EMTS Lab) for digital images of the holotype and paratype of *Typhisopsis carolskoglundae*; to Daniel Geiger (SBMNH) for SEM photographs of the protoconchs of the four species; to Patricia Sadeghian (SBMNH) for digital images of the complete speci-

Table 2. Characters of Eastern Pacific Species of *Typhisopsis* and *Typhisala*.

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

° Characters of adult shells only

mens with protoconchs; to Jacky Van Goethem, Claudine Claes and Diana Hoortman (IRSNB) for help in searching literature and access to the collection of IRSNB; to Ricky Zandali, 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.

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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 fasciolarine fasciolarid? *Saxituberosa* new genus is comprised of the lineage *Saxituberosa fons* 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 fusinine fasciolarid? *Perrilliata 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 *Perrilliata califia* are similar in morphology and geologic age to Gulf Coast *Ornopsis* (*Ornopsis*) *glenni* Wade, 1916, and *Fasciolaria? plummeri* Gardner, 1933, respectively; whereas probable congeners 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 Nacimiento area, San Luis Obispo County, west-central California, illustrated a specimen of *Ornopsis?* n. sp. from the uppermost Cretaceous part of the El Piojo 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 Taliaferro (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 fons* new species, of early Paleocene age.

The fourth species described in this report, *Perrilliata 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 superfamily Buccinoidea 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

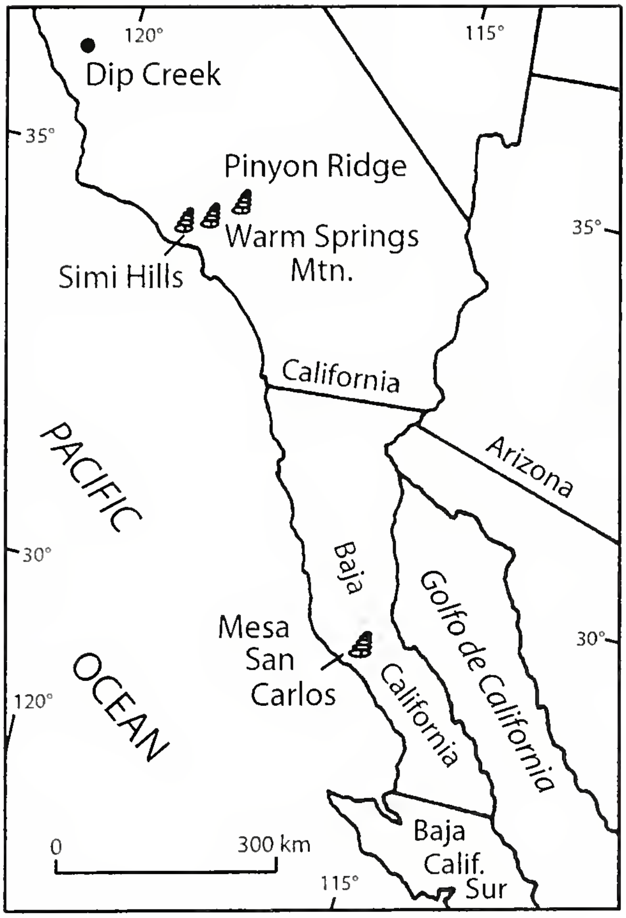

Figure 1. Location of formations bearing the new taxa.

Museo del Paleontologia del Instituto de Geología; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; PU, Purdue University; UCLA, University of California, Los Angeles (collections now housed at LACMIP); LSJU, Leland Stanford Junior University (collections now housed at CAS).

STRATIGRAPHY

The ages and depositional environments of all of the formations bearing the new taxa discussed in this paper can be found in the following papers: El Piojo Formation (Saul, 1986a; Seiders, 1986, 1989; Squires and Saul, 1993); lower San Francisquito Formation (Squires, 1997); lower Santa Susana Formation (Squires, 1997); and Sepultura Formation (Squires, 1997).

PALEOBIOGEOGRAPHIC IMPLICATIONS

A thorough but not exhaustive search of the literature revealed that *Ornopsis*? *dysis* and *Perilliata califia* are most similar to New World gastropods from the Gulf Coast of the United States, whereas *Saxituberosa* is apparently 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*) *glenni* 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 Kaunhowen (1897: 88–89, pl. 13, fig. 13) and idenfied by him as *Fusus* (*Hemifusus*) *nereidiformis* Kaunhowen, 1897. It has the fine-spiral sculpture and strong collabral structure like that of *Ornopsis glenni*, 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, 1986b; Squires, 1987), were part of a circumglobal-tropical current that contributed to a widespread dispersal of marine biota (Haq, 1981).

The Paleocene *Perrilliata califia* is most similar to *Fasciolaria*? *plummeri* Gardner, 1933, and to *Fasciolaria* 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

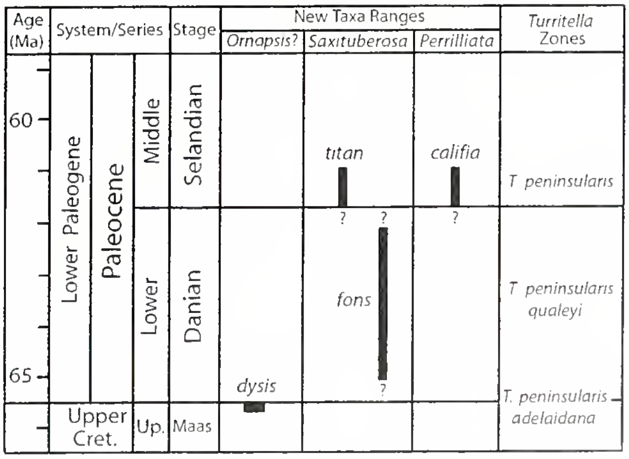

Figure 2. Chronostratigraphic positions of the new taxa. Ages of stage boundaries from Gradstein et al. (2004). *Turritella* zones from Saul (1983).


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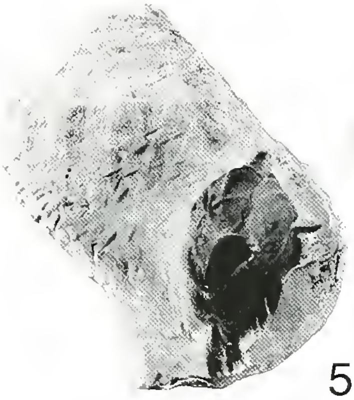
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Figures 3–13. New fasciolariid? gastropods. Specimens coated with ammonium chloride. **3–7.** *Ornopsis? dysis* new genus and species. **3–4.** Paratype LACMIP 13352, LACMIP loc. 26527, height 31.1 mm, diameter 20.9 mm. **3.** Apertural view. **4.** Abapertural view. **5–7.** Holotype LACMIP 7564 LACMIP loc. 26525, height 37.6 mm, diameter 32 mm. **5.** Apertural view. **6.** Apertural view turned slightly to right. **7.** Abapertural view. **8–11.** *Saxituberosa fons* new genus and species. **8–9.** Holotype LACMIP 13354, LACMIP loc. 21581, height 55.6 mm, diameter 40.4 mm. **8.** Apertural view. **9.** Abapertural view. **10.** Paratype LACMIP 13355, LACMIP loc. 21580A, apertural/right-lateral view (specimen crushed), height 48.4 mm, diameter 35 mm. **11.** Paratype LACMIP 13356, LACMIP loc. 1588, abapertural view, height 52.5 mm, diameter 42 mm. **12–13.** *Saxituberosa titan* (Waring, 1917) new combination, hypotype LACMIP 10983, LACMIP loc. 22688, height 60.4 mm, diameter 36.2 mm. **12.** Apertural view. **13.** Right-lateral view.


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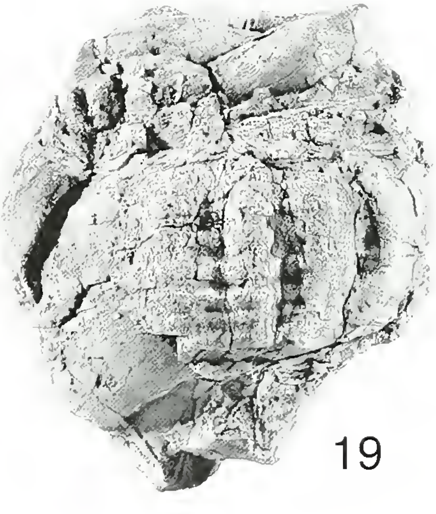
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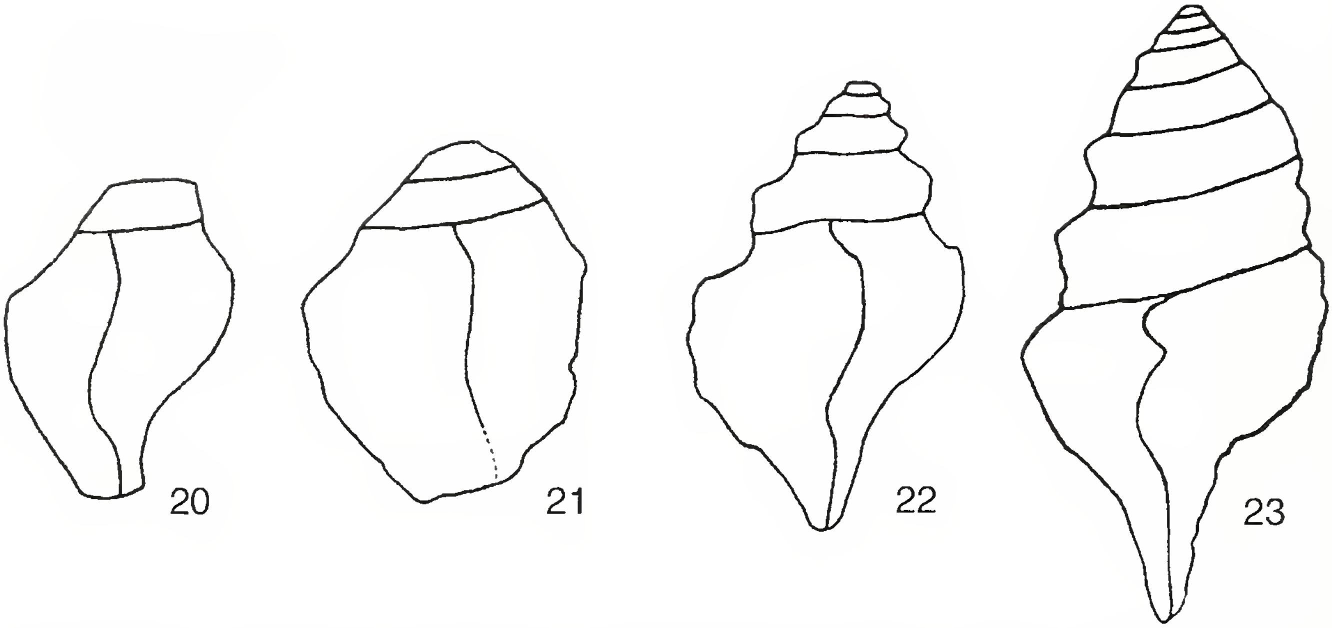
Figures 14–19. New fasciolariid? gastropods. Specimens coated with ammonium chloride. **14–15.** *Saxituberosa titan* (Waring, 1917) new combination. **14.** Abapertural view of same specimen shown in Figures 12–13. **15.** Hypotype LACMIP 10982, LACMIP loc. 22701, slightly oblique right-lateral view, height 53.1 mm, diameter 28.8 mm. **16–19.** *Perrilliata califia* new genus and species. **16–18.** Plasto-holotype IGM 4432, PU loc. 1334, height 101.3 mm, diameter 51.5 mm. **16.** Apertural view. **17.** Apertural view, closeup of growth lines on inflated peripheral part of last whorl. **18.** Abapertural view. **19.** Paratype LACMIP 13357, LACMIP loc. 22330, abapertural view, height 74.8 mm, diameter 66.2 mm.



Figures 20–23. Growth-line trends of the new taxa, abapertural view. **20.** *Ornopsis? dysis* new genus and species, see Figure 4. **21.** *Saxituberosa fons* new genus and species, see Figure 11. **22.** *Saxituberosa titan* (Waring, 1917) new combination, see Figure 14. **23.** *Perrilliata califia* new genus and species.

Gulf Coast into California, via the same circumglobal-tropical current system 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 lirate. 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 prosocline on the ramp but opisthocline 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, 1853. 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 Fraussen 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: sarganids (e.g., *Sargana* 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* Röding, 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, *Ripleyella* Harbison, 1945, and *Pornosis* 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 buccinid? *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? n. sp. Saul, 1986a: 30, figs. 57–58.

Diagnosis: Large *Ornopsis*? with weak collar, wide pleural angle, and strong columellar 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 diameter 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 posteriorly on ramp. Ramp broad, slightly concave, usually smoothish, and bearing weak subsutural 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 intersecting spiral ribs on inflated medial part of whorls; intersections demarked by weak nodes. Nodes most prominent 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 toward outer lip. Collabral ribs usually extending very weakly across ramp and obsolete 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 periphery, 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 (latest 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 specimens. 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 (Campanian 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 closely spaced and more spiral ribs, and stronger collabral 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 Maastrichtian) strata in Tennessee (Sohl, 1964), but the new species differs by having rounded rather than tabulate shoulders, 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 crassa* (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 Maastrichtian) 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, wheras spiral ribs dominant 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 lirate. 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 tubercles, 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 shouldered with tubercles, and well developed collabral and spiral ribs make it likely that *Saxituberosa* is a fasciolarine.

Genus *Saxituberosa* new genus

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

Description: Shell moderately large (up to approximately 70 mm height). Fusiform-tabulate. 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 subsutural 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 opisthocline to orthocline on periphery, sinuous on anterior part of most inflated part of body whorl, and nearly orthocline on neck.

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

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

Discussion: *Saxituberosa* resembles genus *Lupira* Stephenson, 1941, which Sohl (1964) placed in the family Xancidae Pilsbry, 1922. As far as it known, this genus is restricted to Upper Cretaceous (upper Campanian to Maastrichtian) 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 *Taioma* Finlay and Marwick, 1937, but *Taoima* lacks folds on its columella and has a growth line that trends opposite to the direction of *Saxituberosa*. The familial affinities of *Taioma* are not well understood. Stilwell et al. (2004) reviewed the history of the contentious placement of this genus, and they concluded, with some reservation, that it a fusinine fasciolariid. *Taioma* is apparently confined to the Cretaceous and Tertiary of South America, Antarctica, New Zealand, and Greenland (Griffin and Hünicken, 1994; Stilwell et al., 2004). Bouchet et al. (2005) classified *Taioma* as a neogastropod in its own family: family Taiomidae 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 *Fasioplex* Marwick, 1934, known from the Eocene of New Zealand. The new genus differs considerably from *Fasioplex* by having a much higher spire, a fusiform rather than a vasid-like shell, and a narrower aperture.

Saxituberosa fons 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-tabulate. 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 subsutural 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 tubercles. 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 unnoded 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, opisthocline on periphery, prosocline near neck area, and almost orthocline 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 qualeyi* Zone of Saul, 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 tubercules, and occasionally broader ramp bordered by indistinct sutures.

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

Trachytriton titan Waring, 1917: 87, pl. 14, fig. 18.
Penion titon [sic] (Waring).—Zinsmeister, 1983a: table 1, pl. 3, figs. 22, 23.
Penion titan (Waring). Zinsmeister, 1974: 141–142, pl. 15, figs. 1, 2; 1983b: 1294, figs. 3 H, 3 I.
not *Penion* cf. *P. titan* (Waring).—Paredes-Mejia, 1989: 256–257, pl. 8, figs. 3, 4.

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. Subfusiform with turreted spire. Spire approximately 48% 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 subsutural collar. Suture moderately impressed, somewhat wavy. Sculpture consisting of spiral ribs intersecting with collabral 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, unnoded. Aperture moderately wide and elliptical. Columella straight to slightly concave (on adults), with wide callused area, and bearing two strongly raised folds immediately posterior to slightly twisted?, narrow siphonal canal. Growth lines sinuous, prosocline on ramp, opisthocline over periphery, sigmoidal 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 59253].

Type Locality: CAS loc. 61901.

Geologic Age: Middle Paleocene (Selandian) [= *Turritella peninsularis* Zone of Saul, 1983].

Distribution: San Francisquito Formation, Pinyon Ridge near Big Rock Creek, Valymero 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 vinculum* Hall and Meek, 1854, and this type species was reported by Wenz (1941) as being in the ranellid genus *Argobuccinum* Bruguière, 1792. *Trachytriton* does not have the tabulate whorls, subsutural collar, strongly noded sculpture, nor the folds on the columellar that characterize the shells studied herein.

Waring (1917) reported that *titan* is very similar to *Trachytriton tejonensis* Gabb (1869: 154, pl. 26, fig. 34) 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 ranellid *Olequahia hornii* (Gabb, 1864).

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

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

Saxituberosa titan is most similar to *S. fons* new species, and *S. titan* differs by having a narrower pleural angle, higher spire, much more tabulate whorls, and a more distinct suture.

Saxituberosa titan strongly resembles the shell shape of the fossil "*Surcula*" *mayi* Hanna and Israelsky (1925: 45, pl. 7, fig. 12), known from beds transitional with the Heath Formation near Quebrada Mancora, in the extreme northwestern coastal region of Peru. The locality description for this species is very imprecise, but it is likely that the species occurs in the transitional beds between the Heath and Mancora formations, both of which are early Miocene in age, according to Dunbar et al. (1990). *Saxituberosa titan* differs from "*Surcula*" *mayi* by having spiral ribs and two columellar folds. It is likely that "*S.*" *mayi* belongs to genus *Taioma* Finlay and Marwick, 1937, which was discussed earlier.

Saxituberosa titan resembles the cassid *Galeodea* (*Taieria*) *klingeri* Kiel and Bandel (2003: figs. 6.6–6.8) from the Upper Cretaceous (middle Santonian-lower Campanian) Umzamba Formation in South Africa. The new species differs by having folds on the columella, stronger collabral sculpture, straighter columella, less twisted posterior portion of the siphonal canal, and an absence of a small pseudo-umbilicus. In addition, *S. titan* apparently lacks a posterior canal.

?Subfamily Fusininae Wrigley, 1927

Discussion: On fusinines, the shoulder is rounded, the columella lacks folds, and shells can be large with high spires and long siphonal canals. The subfamilial placement of *Perrilliata* new genus is uncertain, mainly because the columella and aperture are not complete. In addition, the growth lines on the ramp area are not preserved. *Perrilliata* might be a fusinine based on its fusiform shape, large size, high spire, and absence of any columellar 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.

Perrilliata new genus

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

Description: Shell large, up to 101 mm height. Fusiform with very spire high. Tabulate whorls. Ramp moderately broad and concave. Nodes strong on shoulder. Spiral ribs very prominent and closely spaced on periphery and base. Neck smoothish. Columella long, straight, and callused.

Geologic Age: Middle Paleocene (Selandian).

Etymology: 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 *Hercorhyncus* Conrad, 1868, 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 spire, a narrower pleural angle, growth lines prosocyrt rather than opisthocline 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 *Hercorhyncus* is a variable feature. The new genus might have a constriction at posterior end of neck, like that present on *Hercorhyncus*.

Sohl (1964) and Snyder (2003) placed *Hercorhyncus* in the fusinine fasciolariids, but Bandel (1993: 40) considered the genus probably to be a buccinid, based on its protoconch, which is similar to that of the buccinid *Ornopsis*. Cossmann (1901: 73) considered *Hercorhyncus* to be a subgenus of *Streptosiphon* Gill, 1867, and Wenz (1943: 1306) considered *Streptosiphon* to be a synonym of *Afer* Conrad, 1858, hence making *Hercorhyncus* a subgenus of *Afer*, which, as mentioned earlier, was placed in family Buccinidae by Fraussen and Hadorn (1999). Sohl (1964: 220), however, cited that the apertural features, the higher spire, and the lack of any columellar folds negates that *Hercorhyncus* belongs to either *Streptosiphon* or *Afer*.

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

Perrillata califia new species
(Figures 16–19, 23)

?"*Penion*" n. 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 diameter ratio approximately 2.0. Fusiform. Spire very high, approximately 52% of shell height. Pleural angle approximately 73°. Protoconch unknown. Teleoconch up to at least eight whorls. Whorls tabulate. Ramp broad, concave, and usually smoothish with occasional spiral ribs. Suture moderately impressed and wavy; usually indistinct. Sculpture consisting of collabral ribs and intersecting spiral ribs. Intersections of ribs on shoulder demarked by tubercles; intersections of ribs on periphery of juvenile specimens forming cancellated sculpture pattern. Collabral ribs weak and moderately widely spaced, most prominent on shoulder, somewhat less prominent on base of whorls and becoming obsolete anteriorly toward base of last whorl; approximately 12 nodes (tubercles on adults) on shoulder of last whorl. Collabral ribs can extend across ramp but, if so, are usually poorly developed. Collabral ribs obsolete on neck. Spiral sculpture consisting of numerous strong and moderately closely spaced ribs. Upper spire whorls with one spiral rib anterior to shoulder; middle spire whorls with two spiral ribs anterior to shoulder; lower spire whorls with three spiral ribs anterior to shoulder. Spiral ribs most prominent on last whorl in area from shoulder to neck. Posterior end of neck possibly delineated by constriction. Neck smooth. Aperture probably small and narrow. Columella straight and callused, with slightly raised, smooth area along left margin. Growth line sigmoidal around nodes on shoulder area with antispiral sinus on shoulder, prosocyrt on periphery, and nearly orthocline on neck.

Holotype: IGM 4432, 101.3 mm height, 51.5 mm diameter.

Paratype: LACMIP 13357.

Type locality: PU loc. 1334.

Geologic Age: Middle Paleocene (Selandian).

Distribution: Lower Santa Susana Formation ("Martinez marine member" of Nelson, 1925), Meier Canyon, Simi Hills, eastern Ventura County, southern California; and Sepultura Formation, Mesa San Carlos, northern Baja California, Mexico.

Etymology: Named for California.

Discussion: The new species is based on two specimens. The holotype, which is from float material derived from the Sepultura Formation at Mesa San Carlos, has been crushed dorso-ventrally. It is a large specimen (101.1 mm height, 47.6 mm diameter), whose height to diameter ratio is 2.1, and it shows very good preservation of the sculpture. The sculpture on the spire is very similar to that found on specimens of *Saxituberosa titan* less than approximately 45 mm in height. On the remaining whorls of this large specimen, spiral sculpture is very strong on the anterior portion of the penultimate whorl and on the base of the last whorl.

The paratype, which is from the Simi Hills, consists of just the very large peripheral part (42 mm diameter) of the last whorl of an adult specimen.

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 specimen 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 (1986: 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* (*Haplovoluta*) *triliratus* 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 *Saxituberosa 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.

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APPENDIX

LOCALITIES CITED

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

CAS 6190. [= LSJU 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 1910.

21579. Limey 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 Francisquito Formation (lower part). Coll.: R. W. Webb and E. H. Quayle, June 5, 1941.

21580. 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 Francisquito Formation (lower part). Coll.: R. W. Webb and E. H. Quayle, June 5, 1941.

21588. Concretions in shale along elongate 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 Francisquito 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

Hills, Ventura County, southern California. Middle Paleocene (Selandian). Santa Susana Formation (lower part). Coll.: W. P. Popenoe, April 3, 1946.

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 1967), Ventura County, southern California. Santa Susana Formation (lower part). Middle Paleocene (Selandian). Coll.: J. H. Fantozzi, circa June, 1951.

26525. Approximately 232 m elevation, poorly sorted conglomeratic sandstone exposed on east side of Dip Creek, south side of Lake Nacimiento, 427 m south and 61 m west of northeast corner of section 30, T. 25 S, R. 10 E, Lime Mountain Quadrangle (7.5 minute, 1948), San Luis Obispo County, west-central California. Upper Cretaceous (uppermost Maastrichtian). El Piojo Formation. Coll.: R. B. Saul and L. R. Saul, December 31, 1977.

26527. Approximately 225 m elevation, south side of Lake Nacimiento, poorly sorted conglomeratic sandstone on east side of narrows of Dip Creek, 777 m south and 304 m west of northeast corner of section 30, T. 25 S, R. 10 E, Lime Mountain Quadrangle (7.5 minute, 1948), San Luis Obispo County, west-central California. Upper Cretaceous (uppermost Maastrichtian). El Piojo Formation. Coll.: R. B. Saul and L. R. Saul, December 31, 1977.

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 Gasteropoda [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, Cypraea, 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 Conchyliorum,' afforded a greater amount of novelty. Mr. Sowerby, junr., 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 *Amphiperas* or *Volva*, the spelling of *Ovula bullata* being corrupted to *Amphiperas 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 (1932) *The living species of Amphiperatinae*, 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 Cypraeid 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 chresonymies of any of the SAMARANG species. It must be mentioned that a Sowerby entry does appear under "*Phenacovolva acuminata* (A. Adams and Reeve, 1848)." That reference is:

> 1859 *Ovula acuminata*; Sowerby ^{2nd}, Index Brit. Shells: 21, plt. 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 *Rhizorus* 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*, Reeve 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 bulla 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 concinnum G. B. Sowerby II in Adams and Reeve, 1848
Ovulum dentatum G. B. Sowerby II in Adams and Reeve, 1848 [Preoccupied; invalid; renamed *Prosimnia renovata* Iredale, 1930].
Ovulum formosum G. B. Sowerby II in Adams and Reeve, 1848
Ovulum gracile G. B. Sowerby II in Adams and Reeve, 1848
Ovulum nubeculatum G. B. Sowerby II in Adams and Reeve, 1848
Ovulum recurvum G. B. Sowerby II in Adams and Reeve, 1848
Ovulum subreflexum 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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CONTENTS

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

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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 thence giving rise in the Neogene to *Scaphella*. In the Old World the record of *Scaphella* is uninterrupted from the Paleocene to the middle Pliocene, 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 carlae* 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* Röding, 1798, *Scaphella* Swainson, 1832, and *Volutifusus* Conrad, 1863 (Darragh, 1988). In the Recent fauna they occur in the western Atlantic Ocean, including the southeastern United States, Gulf of Mexico and Caribbean (*Scaphella*, *Volutifusus*), 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 (Dockery, 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 du Pont, 1970), the Caribbean, up to Colombia (Clench, 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, 1866). 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 (Lamothe and Dautzenberg, 1907).

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* Röding, 1791. *Ampulla priamus* (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 Brébion (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 Lamothe and Dautzenberg (1907) 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 Carnide 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 molluscan shells. At Vale de Freixo, the basal fossiliferous beds of the Carnide 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. Velerín, Estepona region, southern Spain. Mediterranean. Estepona Basin. These deposits consist of a variety of different lithologies, from fine clayey sands (Velerín carretera outcrop), deposited at relatively greater depths, to coarse conglomerates (Velerín conglomerates outcrop). These conglomerates, which must have been deposited relatively rapidly or in storm conditions (Sanz de Galdeano 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 Galdeano and Lopez Garrido (1991) and Guerra-Merchán et al. (2002), for the Estepona Basin.

The Pliocene malacofauna 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 (MPMU1) of Monegatti and Raffi (2001).

The material herein discussed is housed in the following collections: IRScNB: 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 R. 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-V coll.: Manuel Molin/Daniela 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 columellar 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 radular 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 papilliform protoconch, usually with a spur-like calcarella present, the teleoconch ". . . is sculptured with spiral[sic] lirae and incised lines . . . ", the columella has three or more anterior plaits, 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 columellar plaits 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 radular morphology. The nominal subgenus is characterized by uniserial Y-shaped radular 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 radular structure. They stressed that these subgenera were based mainly on radular characters, with conchologically similar species having quite different radular 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, 1887), 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, 1835, 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 (Atraktus) pycnopecta* Gardner, 1937 from the Shoal 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.

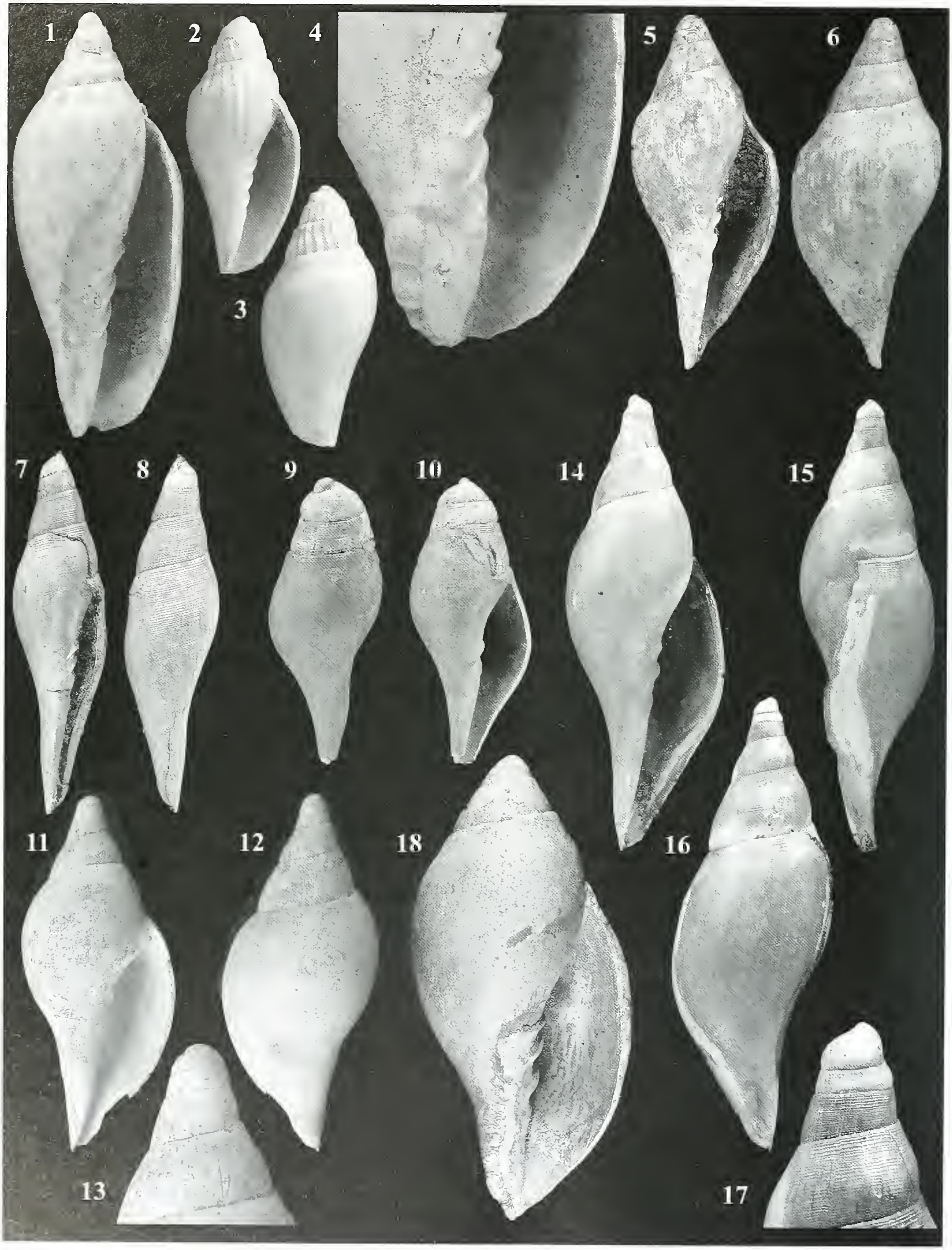
Two species present in the Paleocene of the eastern United States (Porters Creek Formation, Matthews Landing Marl Member, Alabama) are much more similar in their tall, elongated shape to the *Scaphella* representatives in the Old World. We refer to the former two species as the Paleocene New World *Scaphella* 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 leana* Dall, 1890, (Figures 7–8) 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 crenistria* (Von Koenen, 1885) and *Scaphella faxensis* (Ravn, 1902) from the Paleocene of Denmark (Ravn, 1933). The shells of these Paleocene species have the typical fusiform shape, but only three columellar folds (Ravn, 1933) rather than the four or five ones present in the shells of Neogene and Recent species. *Scaphella wetherellii* 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* Glibert, 1938 from the upper Eocene, Bartonian (Wemmelian) of Belgium is somewhat unusual, with a carina on the last whorl bearing large sub-obsolete tubercles (Glibert, 1938, 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, Lattorfian, of Germany, by *S. siemssenii* (Boll, 1851), which has an elongate shell with a tall spire, no axial sculpture at all, and no siphonal fasciole (Beets, 1950), to the Kruisschans Sands (Marquet, 1997), Piacenzian, middle Pliocene (Van Vliet-Lanoë 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. miocaenica* (Fischer and Tournouër, 1879) in the middle Miocene, Serravalian, of the Loire Basin and *S. tarbelliana* (Grateloup, 1840) in the lower Miocene, Burdigalian of the Aquitaine Basin (Peyrot, 1928). The southernmost Miocene record is that of *Voluta lamberti* Sowerby, 1816 in the upper Miocene, Tortonian, of southern Portugal, Algarve Basin (Pereira da Costa, 1866).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In the Pliocene, *Scaphella lamberti* (Sowerby, 1816) (Figures 19–22) flourished in the North Sea Basin and was abundant in the Oorderen 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 Alboran Sea, Estepona Basin (BLP coll.). Lamothe and Dautzenberg (1907) 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 columellar 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 Aldingan, 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 Volutidae with the description of a Cretaceous volutid 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 (Misrimelo) klitzschi* Bandel, 2003.

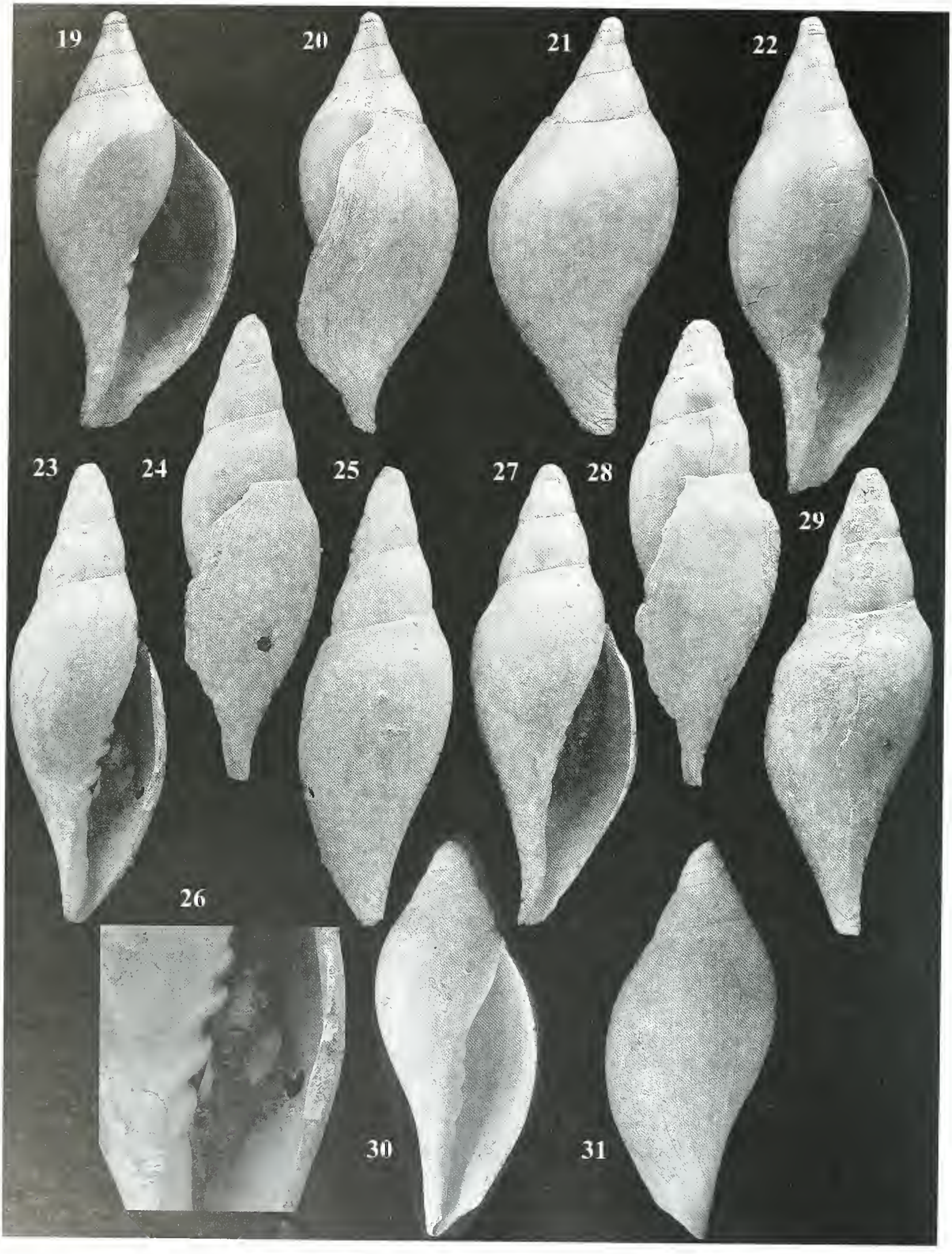
The origin of *Scaphella* is therefore even less clear. Any hypothesis on dispersal of the Scaphellinae must encompass: the first appearance of *Caricella* in the Tethyan Realm; the presence of *Caricella* and *Scaphella* in the New World Paleocene, *Caricella* only in the New World Eocene to Oligocene, *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-Caribbean 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 Volutidae produce planktonic larvae that could favor this westward transatlantic dispersal (Bouchet and Poppe, 1988; Darragh and Ponder, 1998). Some Cenozoic *Athleta* species produced planktonic larvae (Hansen, 1978); possibly some *Lyria* species (Bouchet and Poppe, 1988); some *Calliotectum* species (Bouchet and Poppe, 1995); and *Provocator*, which appeared in New Zealand late in Pliocene time (Maxwell, 2003). However, we must note that the Ath-

Figures 1–18. *Scaphella* species. **1.** *Scaphella (Scaphella) junonia* (Shaw, 1808) (BLP coll.). North New River Canal, South Bay, Palm Beach County, Florida, USA, Bermont Formation, Pleistocene, height 79.6 mm. **2–3.** *Scaphella* sp., juvenile (BLP coll.). APAC Pit, Sarasota, Sarasota County, Florida, USA, lower Pliocene, Pinecrest Beds, height 32.1 mm. **4.** *Scaphella (Scaphella) martinshugari* Petuch, 1994 (BLP coll.). Early Pliocene, Pinecrest Beds Unit 10, Quality Aggregates Phase 6, Sarasota, Sarasota County, Florida. Detail to show ratchet-shaped columellar folds. **5–6.** *Scaphella showalteri* (Aldrich, 1886), (CG coll.). Dixon's Creek, Alabama River, Wilcox County, Alabama , Porters Creek Formation, Matthews Landing Marl Member, Paleocene, height 22.8 mm. **7–8.** *Scaphella leana* (Dall, 1890), (CG coll.). Dixon's Creek, Alabama River, Wilcox County, Alabama, Porters Creek Formation, Matthews Landing Marl Member, Paleocene, height 26.9 mm. **9–10.** *Scaphella siemssenii* (Boll, 1851), juvenile (BLP coll.). Krefeld, Germany, Chattian, upper Oligocene, height 19.3 mm. **11–13.** *Scaphella* sp. (AC coll.), Estoti, St.-Paul-lès-Dax, Landes, Chattian, upper Oligocene, height 67.0 mm (photo A. Cluzaud). **14–17.** *Scaphella bolli* (Koch, 1862), (BLP coll.). Borgerhout Ring Highway, Antwerp, Belgium, Beechem Formation, Antwerp Sands, middle Miocene, height 80.4 mm. **18.** *Scaphella miocaenica* (Fischer and Tournouër, 1879) (RM coll.). Mathelin, Loire Basin, France, Serravallian, middle Miocene. Height 102 mm (photo Robert Marquet).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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 "Volutes 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 Alboran 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 *Alcithoe* 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 protoconch-type 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 showalteri* 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

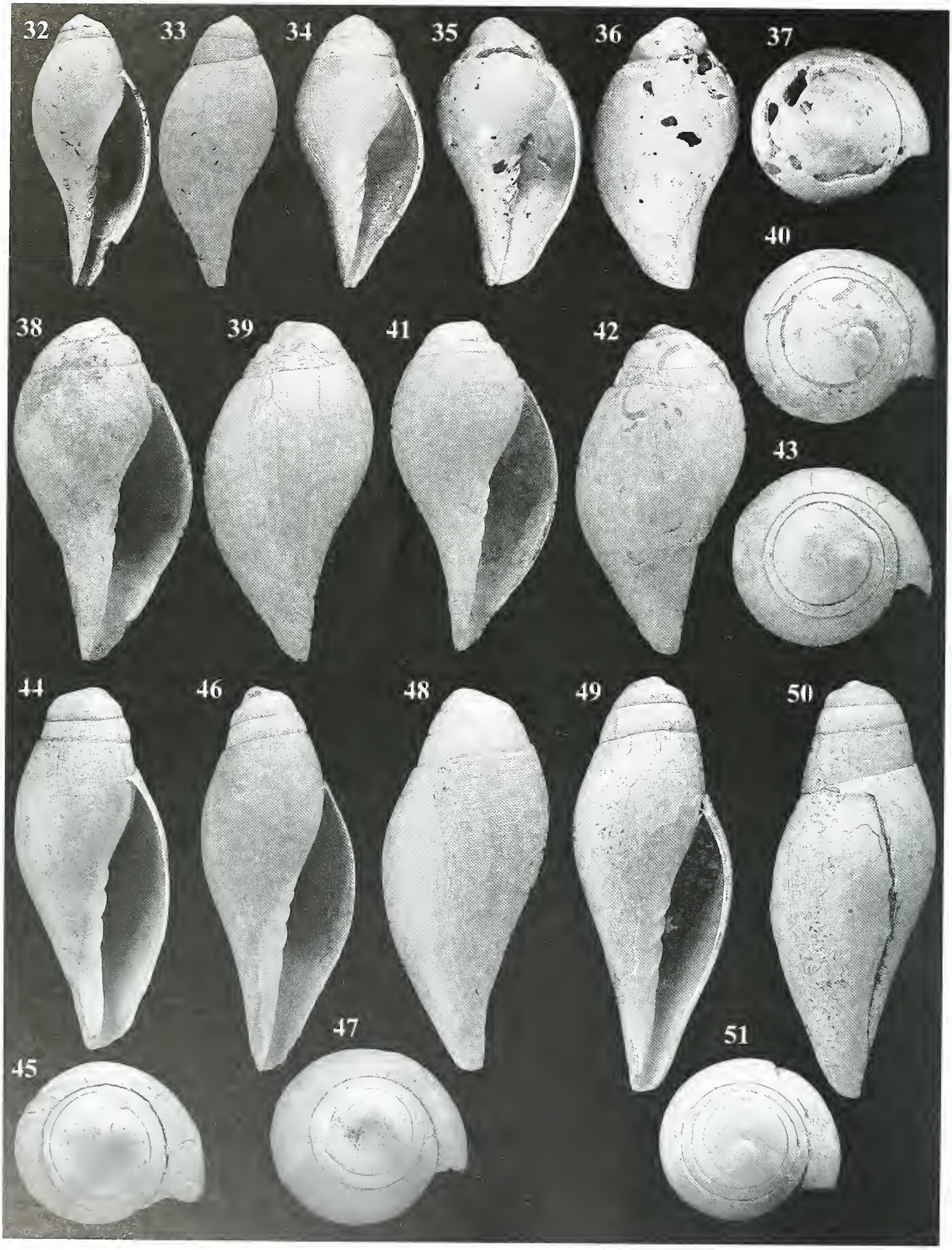
Type species: *Voluta junonia* Shaw, 1808, by subsequent designation, Gray, 1847 (Clench, 1946). Recent, western Atlantic Ocean.

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 *Clenchina* in not having axial sculpture on the early teleoconch whorls, and in having no siphonal fasciole 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 abapically, 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 folds 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 *Amalda* (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 Kruisschans 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

Figures 19–31. *Scaphella* species. **19–21.** *Scaphella lamberti* (Sowerby, 1816), (BLP coll.). 'Broad form', Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 133.0 mm. **22.** *Scaphella lamberti* (Sowerby, 1816), (BLP coll.). 'Narrow form', Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 176.0 mm. **23–26.** *Scaphella carlae* new species, holotype, IRScNB IST 6994, Velerín Conglomerates, Velerín, Estepona, Spain, lower Piacenzian, middle Pliocene, height 147.0 mm. **26.** Detail showing rounded columellar folds. **27–29.** *Scaphella carlae* new species. Paratype (BLP coll.), Velerín Conglomerates, Velerín, Estepona, Spain, lower Piacenzian, middle Pliocene. Height 138.0 mm. **30–31.** *Scaphella tarbelliana* (Grateloup, 1840) (AC coll.). Moulin Debat, Salles, Serravallian, middle Miocene, height 85.0 mm (photo A Cluzaud).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result of the late Neogene cooling events (Monegatti and Raffi, 2001; Silva and Landau, in press), and does not survive off West Africa.

Scaphella carlae 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 sutural 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 callus very thin and worn in most specimens. Siphonal canal long and slightly recurved abapically. Siphonal fasciole absent.

Type Material: Holotype; IRScNB IST 6994, height, 147.0 mm; paratype; IRScNB IST 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 carlae* new species differs from the North Sea Basin Pliocene species *S. lamberti* in having a more elongate shell, with a higher spire, the spire whorls are relatively taller and the last whorl less inflated, the outer lip is convex in profile and not sinuous as in *S. lamberti*, and the aperture is relatively smaller and much narrower. The protoconch of *S. carlae* consists of 1.5 flattened whorls, with a small blunt calcarella at the apex. The protoconch of *S. lamberti* comprises about two whorls, 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 58) 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. carlae*, 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. carlae* 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. carlae*. 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. carlae*.

The middle Miocene Atlantic species *Scaphella miocaenica* (Figure 18) from the Loire Basin has a broader, squatter, more solid shell, with more shouldered whorls. The protoconch is rather similar in shape to that of *S. carlae*, with 1.5 flattened whorls 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. carlae* 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. carlae*. The outer lip is convex in profile and not sinuous 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 miocaenica* (Fischer and Tournouër, 1879), juvenile (BLP coll.). Ferrière-Larçon, Loire Basin, France, Serravallian, middle Miocene, height 19.5 mm. **38–40.** *Scaphella* sp., juvenile (M/V coll.). Bonares, Guadalquivir Basin, Spain, Zanclean, lower Pliocene, height 34.1 mm. **41–43.** *Scaphella* sp., juvenile (M/V 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, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 38.8 mm. **46–47.** *Scaphella lamberti* (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 35.0 mm. **48.** *Scaphella lamberti* (Sowerby, 1816), juvenile (BLP coll.). Vrasenedok, Kallo, Oost-Vlaanderen, Antwerp, Belgium, Oorderen Sands, middle Pliocene, height 32.0 mm. **49–51.** *Scaphella carlae* 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, squatter, and in having a lower spire and a more inflated, more shouldered last whorl.

Glibert (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.

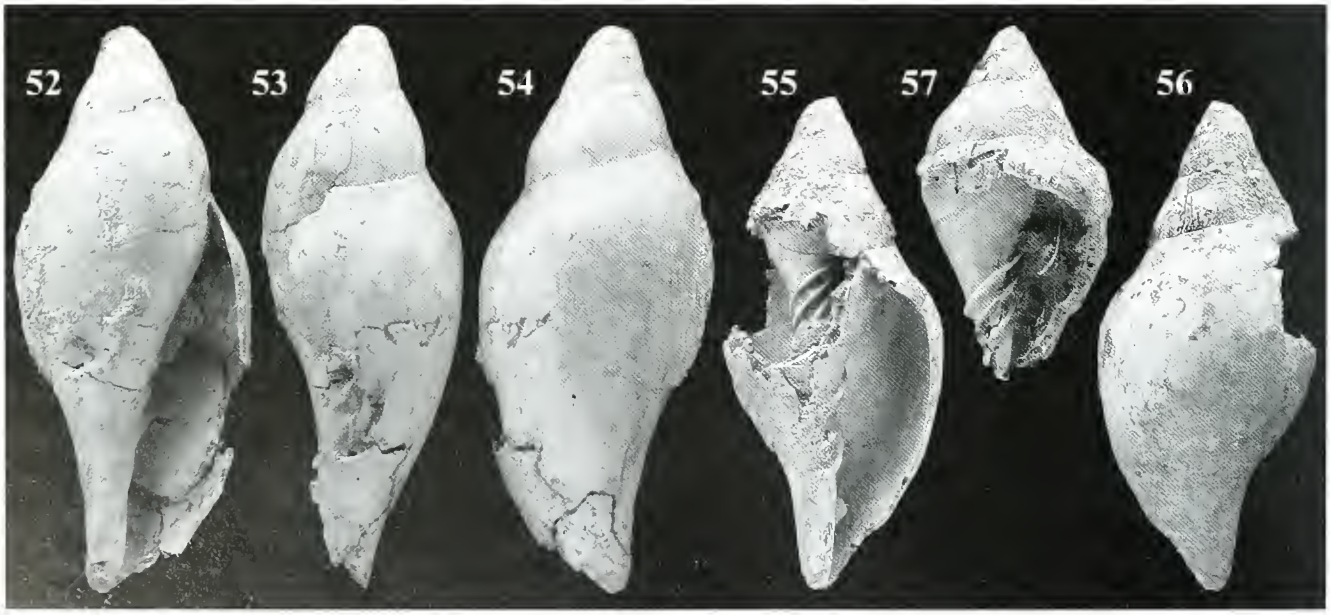
Scaphella sp.
(Figures 38–43, 52–57)

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 86% of total height, inflated, shouldered weakly a short distance below suture. Sculpture 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, abapical 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.*



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.

carlae. 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. carlae*, and they have provisionally been added to the distribution.

CONCLUSIONS

In the Recent volutid faunas, non-planktotrophic 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).

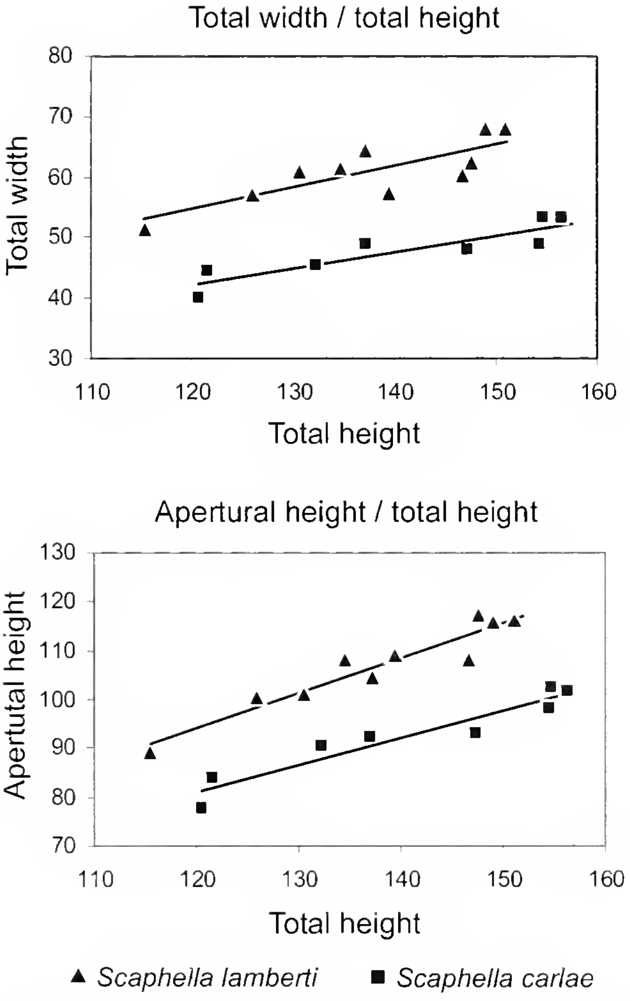


Figure 58. Morphometric comparisons between *Scaphella lamberti* and *S. carlae* new species. Measurements in mm.

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 Redonian) *Scaphella* species from the Atlantic Loire Basin, northern France are less clearly distinguished. Brébion (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 Paleocene to the middle Pliocene and form a distinct group from the Neogene to Recent New World species.

Assuming that Bondarev (1997) and Bandel (2003) are correct, and that that the Scaphellinae have a Cretaceous Tethyan origin, and that Dall (1907) is also correct, and that *Scaphella* originated from *Caricella*, it is hypothesized that the New World Paleocene *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 *Caricella*. This would explain the similarities between Old and New World Paleocene *Scaphella* and the differences with the New World Neogene stock. The European Paleocene to Pliocene 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.

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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 (Pilsbry, 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; Pilsbry, 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., 1999). Pilsbry (1902: 213) regarded *Cerion incanum* to be most closely related to the Cuban *C. maritimum* (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 viaregis* 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 Bahamian 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. viaregis* on Newfound Harbor Key and *C. casablancae* on Bahia Honda Key) have hybridized with the native *C. incanum* (see Bartsch, 1920; Woodruff and Gould, 1987).

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 Balast Point, Tampa Bay)
  - *Cerion (Eostrophia) anodonta* Dall, 1890.
  - *Cerion (Eostrophia) anodonta* 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 fasciatum* (Binney, 1859). Key Biscayne.
  - *Cerion incanum saccharimeta* 'Blanes' Pilsbry and Vanatta, 1899. Sugarloaf Key.
  - *Cerion incanum vaccinum* Pilsbry, 1902. Key Vacca.
- C. Non-native species of Cerion introduced intentionally to the Florida Keys and the Dry Tortugas by Bartsch, 1912–1924.
  - *Cerion viaregis* 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 casablancae* 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* Pilsbry and Vanatta, 1895. From Cuba introduced to: Key West; Garden Key, north side of the parapet at Fort Jefferson; Loggerhead Key.
  - *Cerion mumia* (Sowerby, 1834). From the point at Miramar, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson, Loggerhead Key.
  - *Cerion chrysalis* ("Ferussac" Beck, 1837). From near Cabanas Fort, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson, Loggerhead Key.
  - *Cerion sculptum* (Poey, 1858). From near the lighthouse at Mariel, Cuba, introduced to: Garden Key, north side of the parapet at Fort Jefferson.
  - *Cerion* "n. sp." Young. From East of 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 crassilabris* ("Shuttleworth" Sowerby, 1875). From Puerto Rico, introduced to: Loggerhead Key.
  - *Cerion uva* (Linne, 1758). From Curaçao, introduced to: Loggerhead Key.
  - *Cerion "mayori"* (not clear if this is a typographical error for *C. mayoi* 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, 1951). Source unspecified [Florida Keys], introduced to: Loggerhead Key, Man Key, Boy Key.

of Gulfstream Golf Course (26°29.247′ N, 80°03.229′ 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., Pilsbry, 1907; Mayr and Rosen, 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 Petuch (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, *Liguus 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* Pilsbry and Vanatta, 1895, and *C. bendalli* Pilsbry 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 (1935: 50) conjectured that *Cerion milleri* (Pfeiffer, 1867), described from Duck Key, Exuma

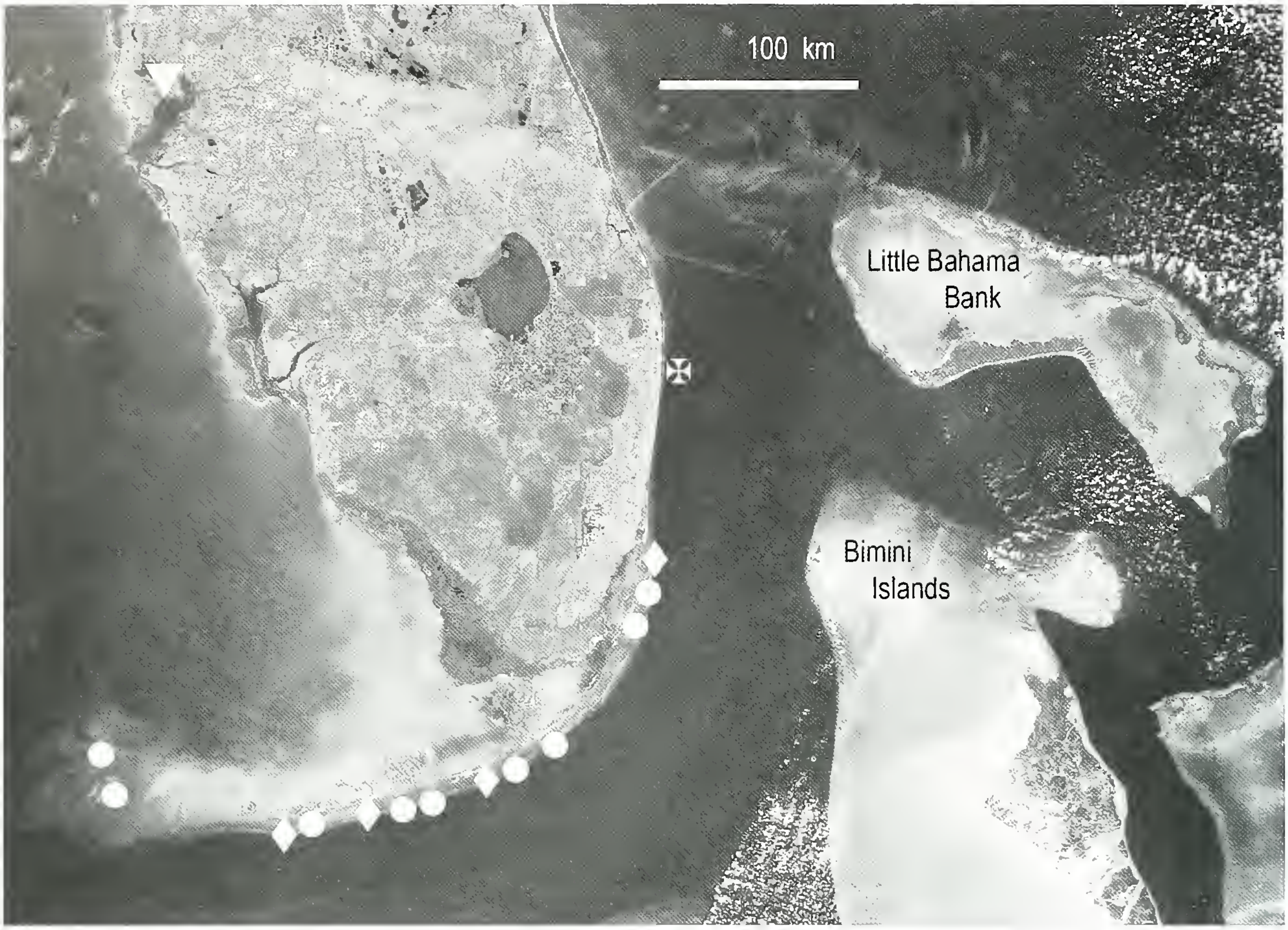


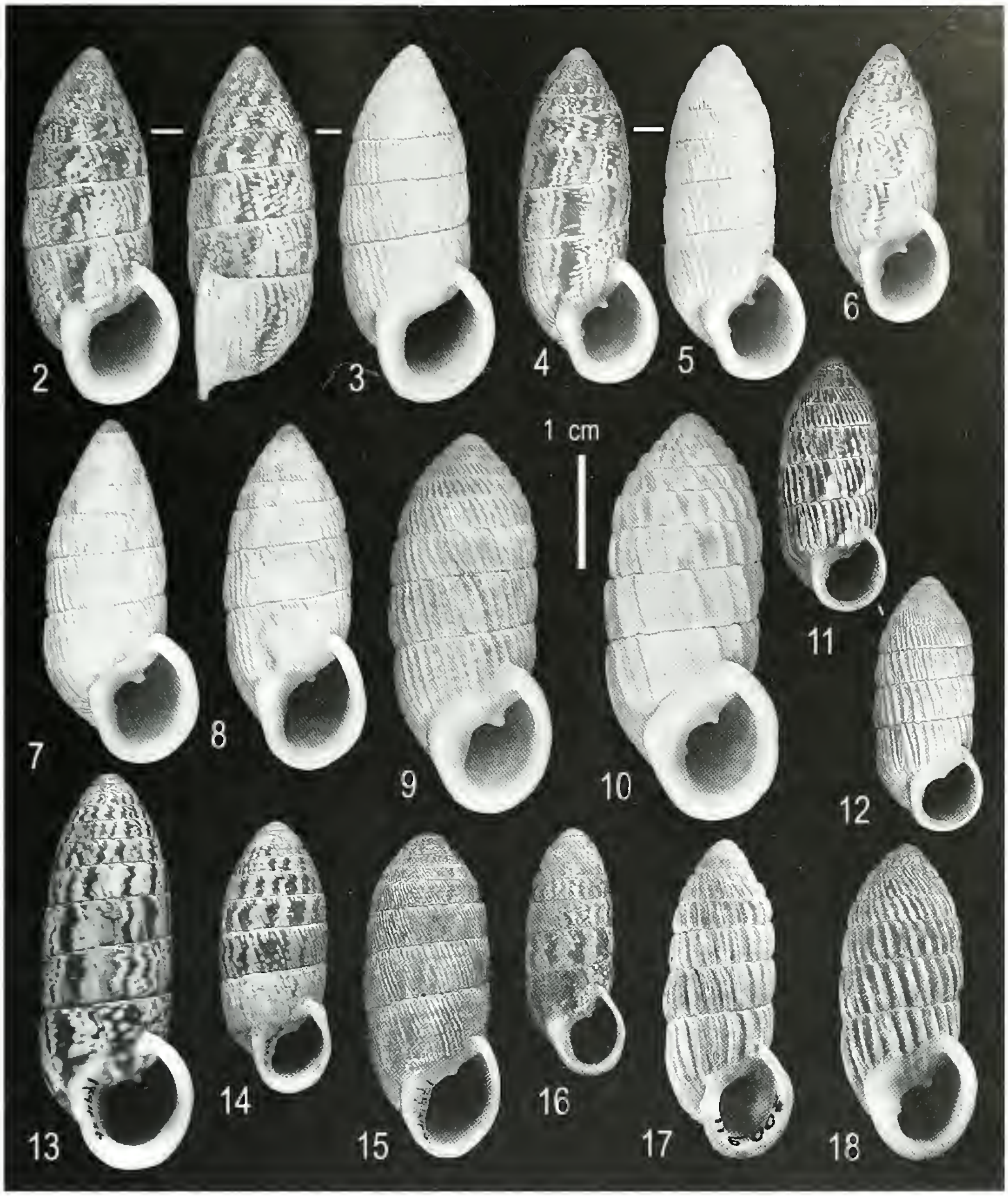
Figure 1. Distribution of the Genus *Cerion* in Florida. Late Oligocene-Early Miocene species (triangle, ▼). Recent, native species, *Cerion incanum* and subspecies (diamonds, ◆). Non-native species of *Cerion* intentionally introduced to the Florida Keys and the Dry Tortugas by Bartsch, 1912–1924 (circles, ●). New record of introduced *Cerion* (cross, ✠). Probable sources of the introduction are the Little Bahama Bank and/or the Bimini Islands. Satellite image modified from that available at http://visibleearth.nasa.gov.

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. milleri* 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 the 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, 1989). 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-



Figures 2–8. Five specimens of introduced *Cerion* from northern end of Delray Park, Delray Beach, Florida (26°28.23′ N, 80°03.39′ W), USNM 1086626. **2.** Specimen A. **3.** Specimen A coated with ammonium chloride to show sculptural details. **4.** Specimen B. **5.** Specimen B coated with ammonium chloride to show sculptural details. **6–8.** Specimens C-E, weakly pigmented or unpigmented specimens.

Figures 9–18. *Cerion* taxa from the Little Bahama Bank. **9.** *Cerion abacoensis* Pilsbry and Vanatta, 1895, lectotype, ANSP 25337, Abaco, Bahamas. **10.** *Cerion maynardi* Pilsbry and Vanatta, 1895, lectotype, ANSP 25338, Abaco, Bahamas. **11–12.** *Cerion abacoensis bendalli* Pilsbry and Vanatta, 1896, **11.** Lectotype, ANSP 25343, Great Abaco, Bahamas. **12.** Lectotype coated with ammonium chloride to show sculptural details. **13.** *Cerion oweni oweni* Dall, 1905, lectotype, USNM 179436, Little Abaco, opposite Marsh Harbor and Riding Point, Grand Bahama. **14.** *Cerion oweni reticulatum* Dall, 1905, lectotype, USNM 179443, Sugar Loaves, Abaco. **15.** *Cerion oweni incisum* Dall, 1905, lectotype, USNM 179440, Stranger Cay, NW of Little Abaco. **16.** *Cerion oweni vermiculum* Dall, 1905, lectotype, USNM 179442, Mathews Point, south side of Great Abaco Bahamas. **17.** *Cerion chrysaloides* Plate, 1907, MCZ 116008, Eight Mile Rock, Grand Bahama Island. **18.** *Cerion lucayanorum* Clench, 1938, paratype, MCZ 116018, NW portion of Mores Island, 32 miles NW of Southwest Point, Great Abaco Island, Bahama Islands. Scale bar = 1 cm for all specimens.

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 abacoensis 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 maynardi 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 abacoensis bendalli Pilsbry and Vanatta, 1896. Great Abaco, Bahamas. Lectotype, ANSP 25343a (Baker, 1963: 206), now ANSP 25343. Gould and Woodruff (1978: figs. 1–3) report that this phenotype is broadly distributed on Grand Bahama Island, Little Abaco, and northern and central 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.

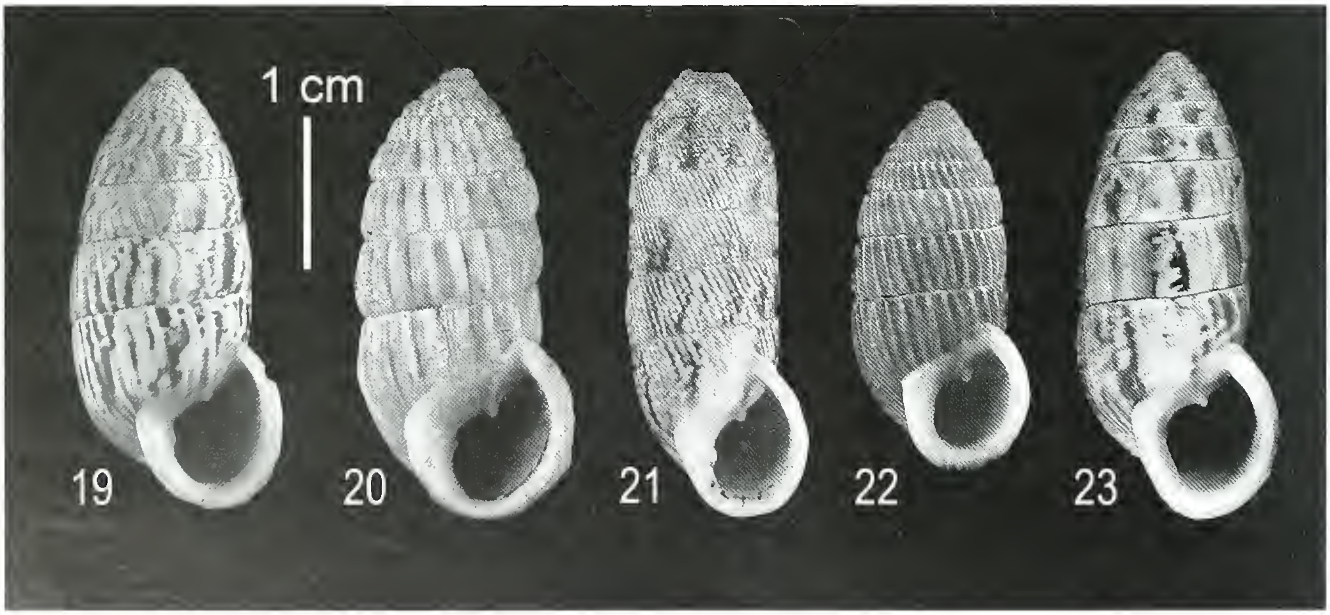
Cerion oweni incisum Dall, 1905. Stranger Cay Beach, NW of Little Abaco. Lectotype, USNM 179440 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 10) is here designated as the lectotype], 4 paralectotypes, USNM 1086733.

Cerion oweni vermiculum 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 lucayanorum Clench, 1938. NW portion of Mores Island, 32 miles NW of Southwest Point, Great Abaco Island, Bahama Islands, paratype, MCZ 116018.

tributes 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. pillsburyi* 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



Figures 19–23. *Cerion* taxa from the Bimini Islands, Bahamas. **19.** *Cerion pillsburyi* Pilsbry and Vanatta, 1897, lectotype, ANSP 72136a. Gun Cay. **20.** *Cerion canonicum* Dall, 1905, lectotype, USNM 127460. Gun Key. **21.** *Cerion northropi* Dall, 1905, lectotype, USNM 125135. One of the westernmost islets near Gun Cay. **22.** *Cerion biminiense* Henderson and Clapp, 1913, lectotype, USNM 252819. Southern end of North Bimini Cay. **23.** *Cerion eximium lerneri* Clench, 1956, holotype, MCZ 186830. East Bimini.

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 pillsburyi Pilsbry and Vanatta, 1897. Gun Cay, Bahamas. Lectotype, ANSP 72136a (Baker, 1963: 207), now ANSP 72136, 3 paralectotypes ANSP 411921.

Cerion canonicum Dall, 1905. Gun Cay, Bahamas. Lectotype, USNM 127460 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 13) is here designated as the lectotype], 4 paralectotypes, USNM 1086735.

Cerion northropi Dall, 1905. Bahamas, probably one of the westernmost islets near Gun Cay. Lectotype, USNM 124135 [originally illustrated specimen (Dall, 1905b: pl. 58, fig. 11) is here designated as the lectotype], 2 paralectotypes USNM 1086736.

Cerion biminiense 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], 158 paralectotypes, USNM 1086737.

Cerion eximium lerneri Clench, 1956. Holotype, MCZ 186830. Southern tip of East Bimini, Bimini Islands, Bahamas.

C. abacoensis and *C. oweni oweni*. 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 twentieth century. Future genetic analyses may aid in the identification of the source Bahamian population or populations for the Delray Beach colony.

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

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ABSTRACT

The cypraeid gastropod, *Muracypraea ormenoi* new species, is described from lower to middle Miocene beds of the uppermost Oligocene to middle Miocene Chilcatay Formation, Pisco Basin, southern Peru. It is the first cypraeid 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 ormenoi new species is described from the Chilcatay 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 is represented by 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. mus* (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 Chilcatay Formation and the overlying lower middle Miocene through middle upper Pliocene Pisco Formation (DeVries, 1998).

CHILCATAY FORMATION

The name Chilcatay Formation was assigned to upper Oligocene to lower Miocene strata near Pampa Chilcatay, approximately 60 km west of Ica, by Dunbar et al. (1990). The Chilcatay Formation consists of basal sandstones associated with a transgression at approximately 25 Ma (DeVries, 2001), tuffaceous 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 Chilcatay Formation at approximately 250 m.

PISCO FORMATION

Unconformably overlying the Chilcatay Formation is the Pisco Formation of Adams (1909), named for steeply dipping, white and yellowish rocks exposed at the end of the Huamaní bridge over the Río 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

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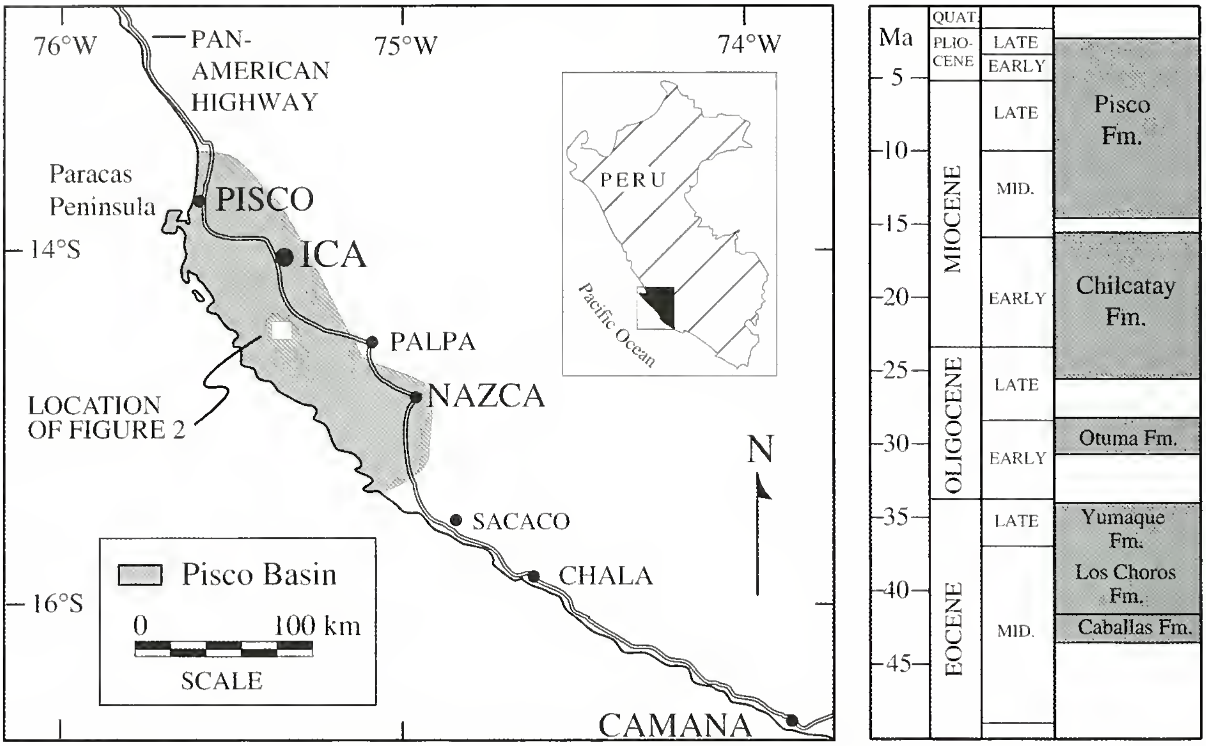

Figure 1. Index map showing location of the Pisco Basin in southern Peru and chronostratigraphy of the Pisco Basin (DeVries and Schrader, 1997).

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 Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815
Subfamily Bernayinae Schilder, 1927
Genus *Muracypraea* 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 tubercule 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 (Aquitanian) to Recent.

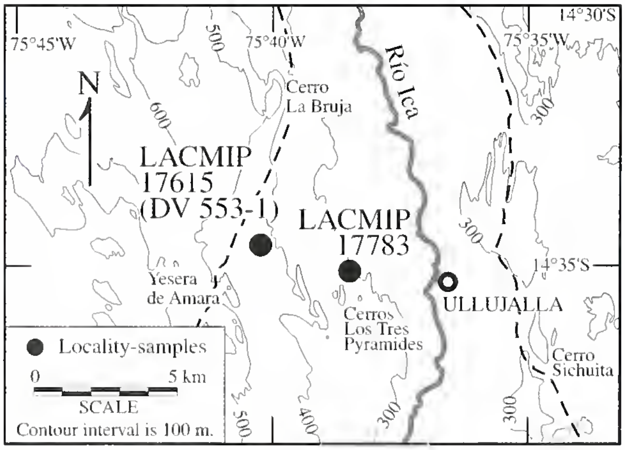

Figure 2. Index map showing the type locality of *Muracypraea ormenoi* new species at Ullujalla West (LACMIP loc. 17783), and locality DV 553-1 (LACMIP loc. 17615). Dashed lines indicate roads.

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 posteromedial 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

Figures 3–5. *Muracypraea ormenoi* new species, holotype LACMIP no. 8197, length = 64.9 mm. **3.** Dorsal view. **4.** Apertural view. **5.** Labral lateral view.

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; denticular 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 *Cypraea (Muracypraea) henekeni* [= *Muracypraea mus isthmica* (Schilder, 1927)], USNM 562603 (pl. 31, figs. 6–7) from the upper Miocene Gatun Formation of Panama. *Muracypraea ormenoi* has fewer columellar teeth, a less inflated columella, deeper terminal canals, and is not as highly arched as *M. mus isthmica*. Color pattern aside, when compared to several specimens of the Recent *M. mus bicornis* (Sowerby, 1870) [LACM 90–47.1 (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*. *Muracypraea angustirima* (Spieker, 1922), the other Peruvian muracypraeid species, from the early to middle Miocene Zorritos Formation of Tumbés Department, northern Peru, lacks the dorsal tubercules, has a straighter aperture, has more columellar teeth, and has a more inflated columella than the new species.

Discussion: *Muracypraea ormenoi* is the first cypraeid 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 (Dunbar et al., 1990) 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: *Muracypraea ormenoi* new species is represented by the moderately well-preserved holotype from the upper Oligocene to lower Miocene Chilcatay 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 *Muracypraea armenoi* new species and their occurrence in depositional basins to the north and south.

Species	Talara Basin Northern Peru	Navidad Basin Central Chile
Acanthina katzi (Fleming, 1972)		x
Eucrassatella ponderosa (Philippi, 1987)		x
Ficus distans (Sowerby, 1846)		x
Glycymeris colchaguensis (Hupé, 1954)		x
Glycymeris ibariformis (Frassinetti and Covacevich, 1984)		x
Miltha vidali (Philippi, 1887)		x
Olivancellaria claneophila (Duclos, 1835)		x
Testallium cepa (Sowerby, 1846)		x
Architectonica karsteni (Rutsch, 1934)	x	
Chionopsis sp.	x	
Conus spp.	x	x
Dosinia sp.	x	
Gonyscyon sp.	x	
Phyllonotus sp.	x	
Terebra sp.	x	x
Turritella woodsi (Lisson, 1925)	x	
Turritella infracarinata (Gryzbowski, 1899)	x	

Peru (14°34′26″S, 75°40′30″W) [DV 553–1, = LACMIP loc. 17615]

Type Material: Holotype LACMIP no. 8197, 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 Yesera de Amara and the Rio Ica, less than one km north of Cerros Las Tres Pyramides [herein designated Ullujalla West] (about 14°34′50″ S, 75°38′40″ W; Lomitas 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.

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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^2) are low. The most frequent and abundant species were *Pyganodon grandis* and *Utterbackia imbecillis*, each occurring in five lakes, and making up 50% and 15% respectively of all unionids collected. Two of the lakes have been successfully colonized by *Driessena polymorpha*, with evidence of an unsuccessful introduction in a third. In Sandy Lake, 78% of the unionids were fouled by *Dreissena*, with an average density of 271 *Dreissena*/unionid. Although none of the seven species of native unionids found in this survey are regionally endangered, the prognosis for lake populations is poor.

Additional Keywords: Unionids, zebra mussels, Pennsylvania lakes, *Corbicula*, *Dreissena*.

INTRODUCTION

With a historical richness of 292 species of Unionidae and five species of Margaritiferidae, 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; Goudreau et al., 1993; Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994; Ricciardi 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 *Epioblasma torulosa rangiana* (Lea, 1838) and *Pleurobema clava* (Lamarck, 1819) (Pennsylvania Biological Survey, 2003). Because of this relatively high richness, unionid 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-

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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 rangiana* and *Pleurobłema 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 Nalepa, 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 mollusk colonization.

STUDY AREA

Natural lakes in northwestern Pennsylvania are limited to a relatively small glaciated region (approx. 9200 km^2) 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 378 ha, and are all between 20 and 80 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 Canadohta 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 (7.6×1.5 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: 0–0.6m, 0.7–1.2m, 1.3–1.8m, 1.9–2.4m, and 2.5–3.0m. In most cases, the nearshore substrate conditions gave way to finer substrata as depth increased.

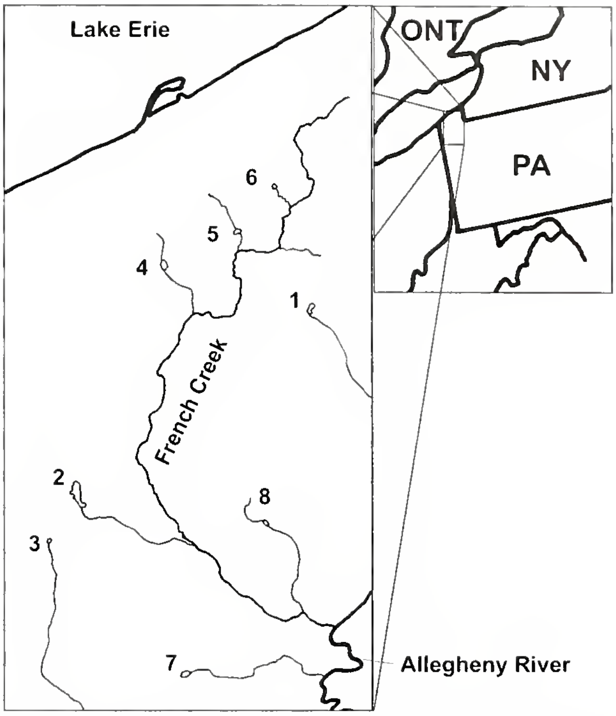

Figure 1. Study area showing the location of lakes and major streams. 1. Canadohta Lake; 2. Conneaut Lake; 3. Crystal Lake; 4. Edinboro Lake; 5. Lake LeBoeuf; 6. Lake Pleasant; 7. Sandy Lake; 8. Sugar Lake.

Quadrats were delineated with nylon rope strung 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 1.5×0.6 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/m^2. 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.)

Lake	Location	Area (ha)	Drainage basin area (km^2)	Max depth (m)	Mean depth (m)	Outflow
Canadohta	41°48.91′N 79°50.28′W	68	20.3	13.6	5.5	Oil Creek
Conneaut	41°37.5′N 80°18.3′W	378	72.3	19.8	5.6	Conneaut Outlet to French Creek
Crystal	41°33.21′N 80°22.14′W	6.1	0.28	7.1	3.3	Crooked Creek to Shenango River
Edinboro	41°52.78′N 80°08.22′W	167	65.7	9.1	3.4	Conneauttee Creek to French Creek
LeBoeuf	41°55.61′N 79°58.96′W	32.2	158.6	9.1	—	LeBoeuf Creek to French Creek
Pleasant	42°00.22′N 79°53.85′W	23.7	3.6	13.7	6.8	Lake Pleasant Outlet to French Creek
Sandy	41°20.71′N 80°06.43′W	88.5	7.2	11.4	—	Unnamed stream to Sandy Creek
Sugar	41°33.94′N 79°56.75′W	31	56.4	5.5	3.2	Lake Creek to French Creek

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 m^2 and 0.25 m^2, on fine/medium-grained and cobble substrates, respectively) and a corer (0.025 m^2, 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/m^2 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; *Lampsilis siliquoidea:* CMNH 74452; *Utterbackia imbecilis:* CMNH 74453; *Pyganodon grandis:* CMNH 74454; *Lasmigona complanata:* CMNH 74455; *Ligumia 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 cataracta*, *P. grandis*, and *P. lacustris* (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. *Lampsilis siliquoidea* (Barnes, 1823) was found in two lakes, and *Ligumia recta* (Lamarck, 1819), *Lasmigona complanata* (Barnes, 1823), *Actinonaias ligamentina* (Lamarck, 1819), and *Amblema plicata* (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/m^2 in Conneaut Lake to only 0.03 individuals/m^2 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.

Dreissenids 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.

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

Lake, the mean density of *D. polymorpha* was 52 individuals/m^2 (s.e.=48) and the mean density in Sandy Lake was 442 individuals/m^2 (s.e.=137). *Dreissena polymorpha* was densely aggregated on scattered submersed wood, rocks, and on the shells of native unionids. In Edinboro Lake, approximately 21% of the live unionids 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/unionid (s.e.=1.1). In Sandy Lake, 78% of the live unionids 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/unionid (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 Canadohta 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/m^2, respectively. In addition, the invasive snail *Cipangopaludina chinensis* (Reeve, 1863) was found in drop box samples from Canadohta 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 *Pleuroblema 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. imbecillis*, *L. siliquoidea*, *A. ligamentina* and *L. recta* all have Heritage state ranks of "secure" or "secure/vulnerable" (NatureServe, 2005) and have no status 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/m^2. In our study area, the density of all living unionids is less than 0.03/m^2 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/m^2) in oligotrophic Mirror Lake, and the size distribution of individuals there suggest regular recruitment. Frequent hermaphrodism 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 northwest Pennsylvania lakes.

	Canadohta	Conneaut	Crystal	Edinboro	LeBoeuf	Pleasant	Sandy	Sugar
Pyganodon grandis	+	+	–	+	+	–	+	–
Utterbackia imbecillis	+	–	–	–	+	+	+	+
Lampsilis siliquoidea	–	–	–	–	+	–	+	–
Lasmigona complanata	–	–	–	–	+	–	–	–
Actinonaias ligamentina	–	–	–	+	–	–	–	–
Ligumia recta	–	–	–	+	–	–	–	–
Amblema plicata	–	–	–	–	+	–	–	–
Total number of species	2	1	0	3	5	1	3	1

Table 4. Densities of live unionids and paired valves. All densities are individual per m^2. Values in parentheses are standard errors.

	Canadohta	Conneaut	Crystal	Edinboro	LeBoeuf	Pleasant	Sandy	Sugar
Live unionids	0.030	0.011	0	0.029	0.023	0	0.023	0
	(0.011)	(0.008)		(0.014)	(0.018)		(0.010)	
Paired empty valves	0.017	0	0	0.080	0.052	0.011	0.020	0.011
	(0.012)			(0.039)	(0.030)	(0.008)	(0.009)	(0.011)
Combined	0.047	0.011	0	0.109	0.075	0.011	0.040	0.011
	(0.019)	(0.008)		(0.039)	(0.028)	(0.008)	(0.014)	(0.011)

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/abundance 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 lentic systems. Predictors of lentic 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 "Conneauttee" 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 mussels/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/m^2 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 lentic 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, 1999) and the invasive snail *Cipangopaludina chinensis* in Lake Pleasant and Canadohta Lake highlights the need for continued public education as to the causes and potential impacts of the spread of invasive species.

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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, 1999) 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 (nomina 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 (nomina 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 ____." 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.

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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 recatalogued 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 nomina 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 undatoides* 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 undatoides* 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 liana* 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 liana* is here proposed for the species described by Li. Type in the California Academy of Sciences paleontology type collection, dredged off Meanguera 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. panamanensis*. (Li's species and Hertlein and Strong's replacement are both synonyms of *Tellina eburnea* Hanley, 1844 [Coan and Valentich-Scott, in 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) *Arca* (*Arca*) *fernandezensis* Hertein and Strong, nom. nov.—(1943: 154)

This name was proposed as a replacement name for *Arca angulata* King and Broderip, 1832, *non* "Meuschen, 1787" [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 nomina 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 planicostatum*, has been used earlier by Sedgwick and Murchison; therefore a new name is required for *Cardium planicostatum* 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 homonymy never existed and the correct name to use is *Americardia planicostatum* (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 lenis* 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 lenis* by Pilsbry and Lowe [1932] and the name *Pitar mexicanus*, based on a specimen off Maldanado Point, Mexico, is proposed." The CAS staff determined that their type material had no type status.

(6) *Tellina* (*Moerella*) *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* (*Angulus*) *recurva* 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*) *proclivis* 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 proclivis*." (*Tellina declivis* G. B. Sowerby I, 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 *nomen dubium*.)

Hertlein (1968) later decided that this was the case of a replacement name, and he then named the eastern Pacific taxon *Tellina ulloana* 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 unrenamed, 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. proclivis* has no type status under that name.

(8) *Latirus 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 *Leucozonia cingulifera* Lamarck. . . . It therefore becomes necessary to propose a new name for Reeve's *Turbinella castanea* and the name *Latirus mediamericana* 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 *Murex 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 *Murex 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 cultrata* Keen, n. sp.—(1958: 240)

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

(3) *Macoma* (*Psammacoma*) *elytrum* Keen, n. sp. (1958: 244)

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

(4) *Crucibulum personatum* Keen, n. sp.—(1958: 247)
Calyptraea radiata Broderip, 1834, *non* Deshayes, 1830.

For all four of the taxa listed above Keen gave a full description, type locality, discussion, and designated holotypes with repository named. However, the curatorial staff at the CAS interpreted her new type material as having no type status.

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 wordings 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 proclivis*, 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.

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Book Review

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

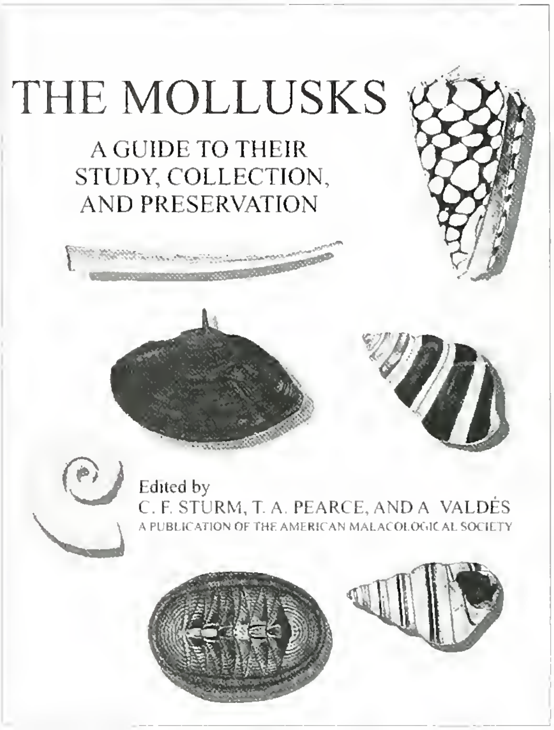
Sturm, Charles F., Timothy A. Pearce, and Ángel Valdés. 2006. The Mollusks: A Guide to Their Study, Collection, and Preservation. American Malacological Society, Pittsburgh, and Universal Publishers, Boca Raton, xii + 445 pp. ISBN 1-58112-930-0 (paperback), 1-58112-931-9 (e-book); retail price (paperback): $35.95, from http://universal-publishers.com.

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 AMS 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 *bonafide* 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".



THE MOLLUSKS

A GUIDE TO THEIR
STUDY, COLLECTION,
AND PRESERVATION

Edited by
C. F. STURM, T. A. PEARCE, AND A. VALDÉS
A PUBLICATION OF THE AMERICAN MALACOLOGICAL SOCIETY

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" (Amélie H. Scheltema), "Monoplacophora" (Clement L. Counts, III), "Polyplacophora" (Enrico Schwabe and Anreas 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 Örstan), "Rearing Terrestrial Gastropoda" (Aydin Örstan), 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. Korniushin), and "Marine Bivalvia" (Eugene V. Coan and Paul Valentich-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 "Computerizing 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 "Applield [sic] photography . . ."; I read "Monoplacpophora" 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 obsolence, 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.

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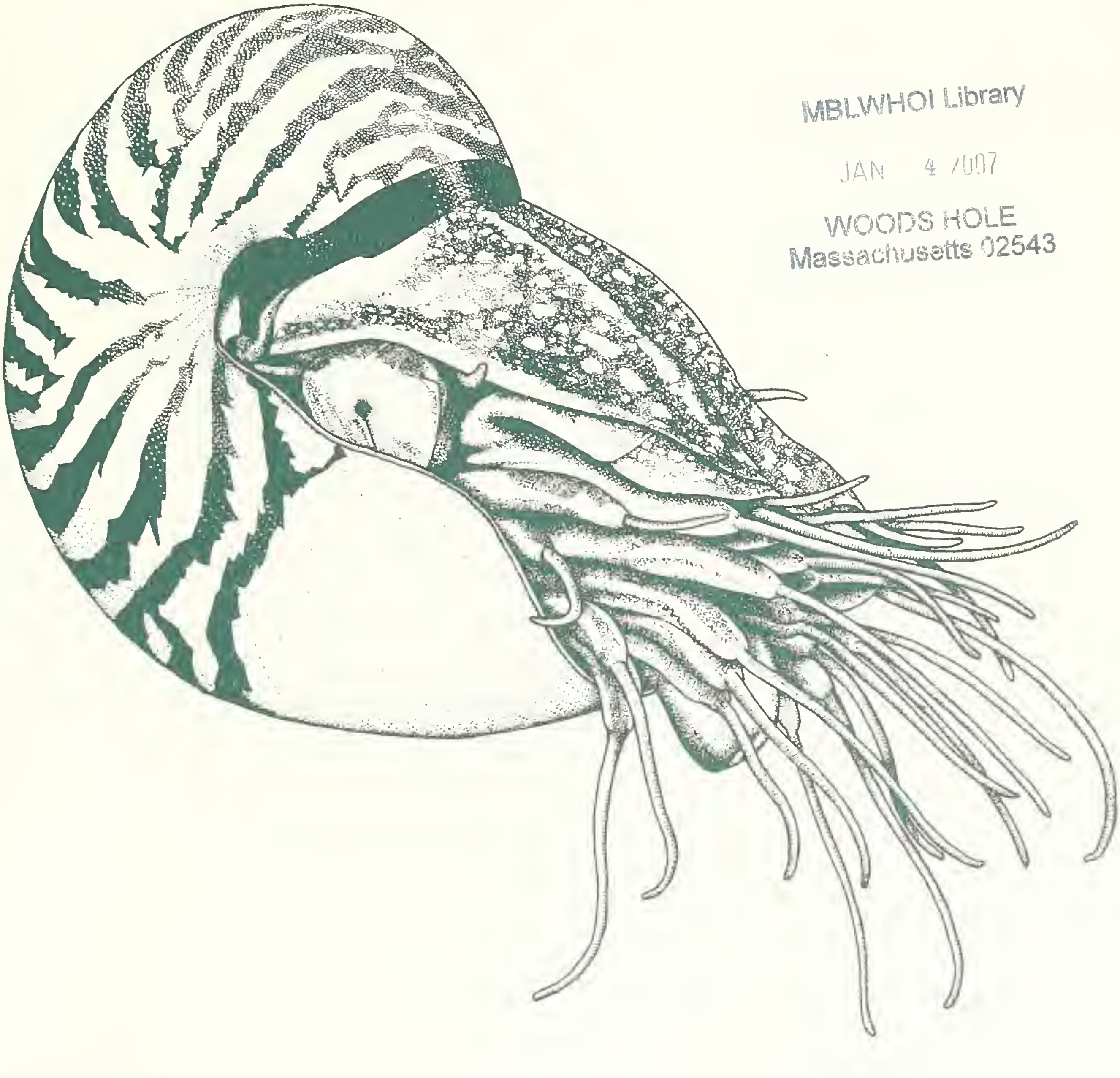

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Paryphantopsis (Gastropoda: Pulmonata: Charopidae) from the Louisiade Archipelago of New Guinea

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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 charopid 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 charopid 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 charopid 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 *Ilonesta* (Iredale, 1941), later synonymized with *Paryphantopsis* (Solem, 1958).

The Louisiade Archipelago, a group of volcanic islands and coral islets, with a total area of approximately 1600 km^2, 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 (EPCT), 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 undersampled.

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

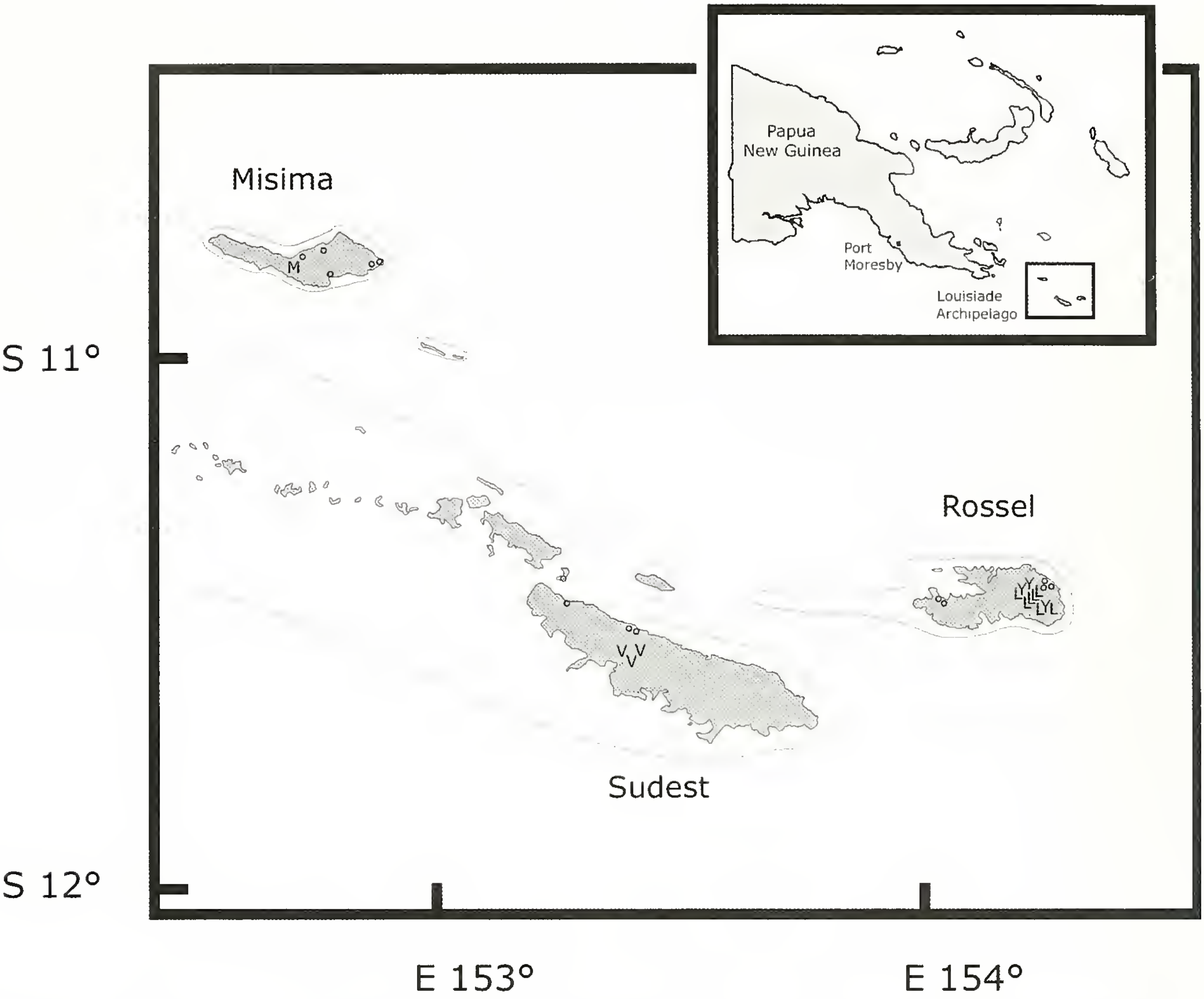


Figure 1. Distribution of *Paryphantopsis* in the Louisiade Archipelago, Papua New Guinea; L = *P. louisiadarum*, M = *P. misimensis*, V = *P. vanatinensis*, Y = *P. yelensis*, o = other sites sampled .

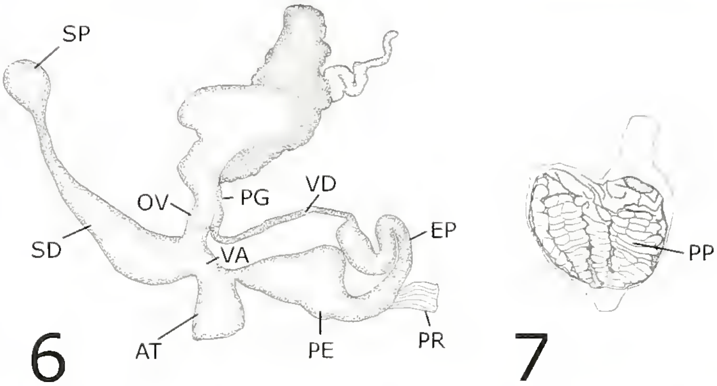
with the aid of a cardboard circle divided into ten equal parts of 36°. Spire diameter was the length of a straight line passing from the apertural edge of the suture through the middle of the apex to the opposite suture. Diameter was the greatest width of the shell perpendicular to the shell axis. Height 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 Paijmans (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).

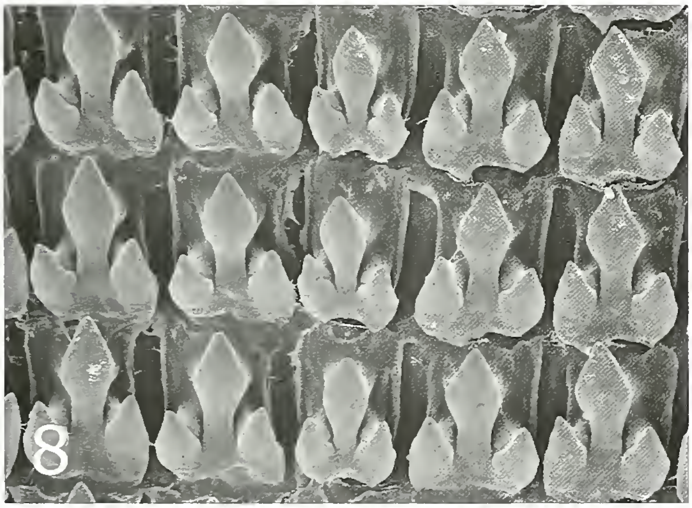
SYSTEMATICS

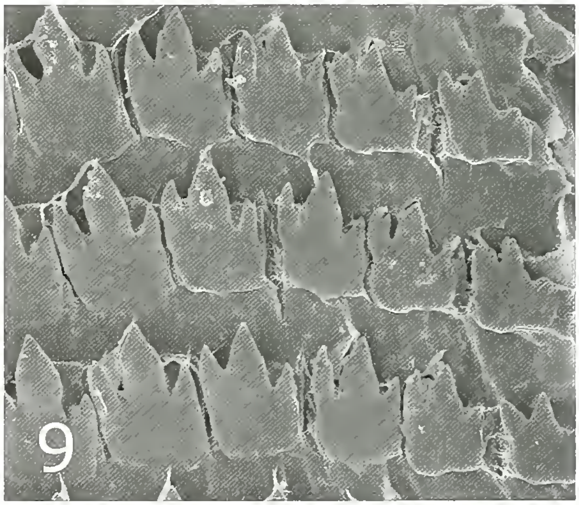
Family Charopidae Hutton, 1884
Genus *Paryphantopsis* Thiele, 1928

Type species: *Flammulina* (*Paryphantopsis*) *lamelligera* Thiele, 1928, by original designation.

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







Figures 2–9. *Paryphantopsis louisiadarum.* **2–4.** Photographs of shell, UF 353425, diameter 10.6 mm. **5.** Photograph of live animal. **6–7.** Camera lucida drawing of genitalia, UF 353426, maximum width 11.6 mm. **8–9.** Scanning electron micrograph of radula, UF 353426, field width of central and lateral teeth 61 μm, marginals 70 μm.

Paryphanta louisiadarum Möllendorff, 1899: 89; Möllendorff and Kobelt, 1902–1905: 17, pl. 3, figs. 1–3.

Illonesta louisiadarum (Möllendorff, 1899).—Iredale, 1941: 92–93.

Paryphantopsis louisiadarum (Möllendorff, 1899).—Solem, 1958: 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 0.0–0.2 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 continue 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 periostracal 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 pigment 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 fades 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 rapidly towards its base. Penis is sculptured with four pilasters two of these are wide and two narrower. Each pilaster is regularly plicated perpendicular to the length of the penis (Figure 7). The penial retractor muscle originates from the diaphragm and inserts on the basal 0.30 of the epiphallus. The spermathecal duct is robust, narrowing gradually from the basal 0.25 to the apical 0.25 and remaining narrow until joining the ovate spermatheca. The free oviduct joins the short vagina just above the spermatheca.

The central teeth of the radula (Figure 8, center row) are tricuspid, 12–13 µm wide and 15–16 µm long, roughly 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 laterals 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 posterior 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 ectocones 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 grade in shape and are difficult to classify as either laterals or marginals. The last five are clearly marginal teeth and are dorsoventrally compressed and tricuspid, 11–12 µm wide and 12–18 µm long (Figure 9). The endocones of the marginal teeth are 0.70 to nearly the same height as the mesocones and the ectocones 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 *Paryphanta louisiadarum* included a single set of measurements: major diameter 9.5 mm, minor diameter 6.5 mm, and altitude 6 mm. However, these measurements are difficult to match to either of the two now slightly broken shells of *P. louisiadarum* donated from his collection to Natur-Museum Senckenberg, Frankfurt, and originally cataloged together as SMF 137274. One specimen has patterns of missing periostracum similar to the shell figured by Möllendorff and Kobelt (1902–1905). Labeling with this shell indicates it was separated from the other specimen and marked "Lectotype" based on its similarity to the shell figured by Möllendorff; later, Solem (1970) formally published this lectotype designation. The other specimen in the lot, now the paralectotype, was recatalogued as SMF 165564. Möllendorff's specimens of *Paryphanta louisiadarum* came from Strubell, who also

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

Species	N		H	D	SH	SD	AH	AD	W
P. louisiadarum	50	Mean ± SD	7.5 ± 0.7	10.3 ± 0.7	0.1 ± 0.1	3.6 ± 0.3	6.2 ± 0.4	6.6 ± 0.5	2.8 ± 0.1
		Range	6.7–9.0	9.3–11.9	0.0–0.2	3.0–4.0	5.7–6.9	5.8–7.6	2.7–3.0
P. misimensis	11	Mean ± SD	6.0 ± 0.3	8.0 ± 0.5	0.1 ± 0.1	2.6 ± 0.2	5.1 ± 0.3	5.3 ± 0.2	2.5 ± 0.1
		Range	5.7–6.6	7.2–8.7	0.0–0.3	2.3–3.1	4.7–5.5	4.8–5.5	2.3–2.7
P. vanatinensis	50	Mean ± SD	5.8 ± 0.5	7.9 ± 0.7	0.1 ± 0.1	2.8 ± 0.3	4.9 ± 0.4	4.9 ± 0.6	2.6 ± 0.2
		Range	5.1–6.9	7.0–9.6	0.0–0.3	2.5–3.6	4.4–6.0	3.9–6.0	2.4–2.9
P. yelensis	10	Mean ± SD	2.7 ± 0.3	3.9 ± 0.3	0.1 ± 0.1	1.6 ± 0.2	1.9 ± 0.2	2.4 ± 0.1	2.8 ± 0.1
		Range	2.4–3.1	3.6–4.5	0.0–0.2	1.3–1.9	1.6–2.1	2.3–2.6	2.7–3.0

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).

Other Material Examined: Papua New Guinea, Milne Bay Province, Louisiade Islands, UMMZ 127616 (1 specimen): Rossel Island: ANSP 109257 (1 specimen); UF 339009 (27 specimens), base of Taclm Gap, 569 meters altitude, 11.353° S, 154.223° E, J. Slapcinsky, 5 May 2004; UF 339012 (15 specimens) PNGNM 005-001 (5 specimens), Lipuwopu at Lipu River, 320 meters altitude, 11.346° S, 154.221° E, J. Slapcinsky, 12 May 2004; BPBM 268733 (5 specimens), MNHW MN 998 (5 specimens), UF 339011 (16 specimens), UF 353425 (1 specimen), UF 353426 (1 specimen), Lubwe Creek at base of Taclm Gap, 638 meters altitude, 11.354° S, 154.223° E, J. Slapcinsky, 6 May 2004; UF 339015 (29 specimens), Taclm Gap below summit of Mount Rossel, 679 meters altitude, 11.356° S, 154.243° E, J. Slapcinsky, 4 May 2004; UF 339010 (4 specimens), W of former site of Gobubop Village, 285 meters altitude, 11.336° S, 154.221° E, J. Slapcinsky, 16 May 2004; UF 339013 (8 specimens), Wopu River upstream of trail crossing near abandoned Yela Village, 280 meters altitude, 11.338° S, 154.224° E, J. Slapcinsky, 14 May 2004; SFM (5 specimens), QM MO76144 (5 specimens), UF 339014 (12 specimens), Yelebop Mountain S of Mount Rossel, 777 meters altitude, 11.357° S, 154.222° E, J. Slapcinsky, 8 May 2004.

Habitat: Observed above 280 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.

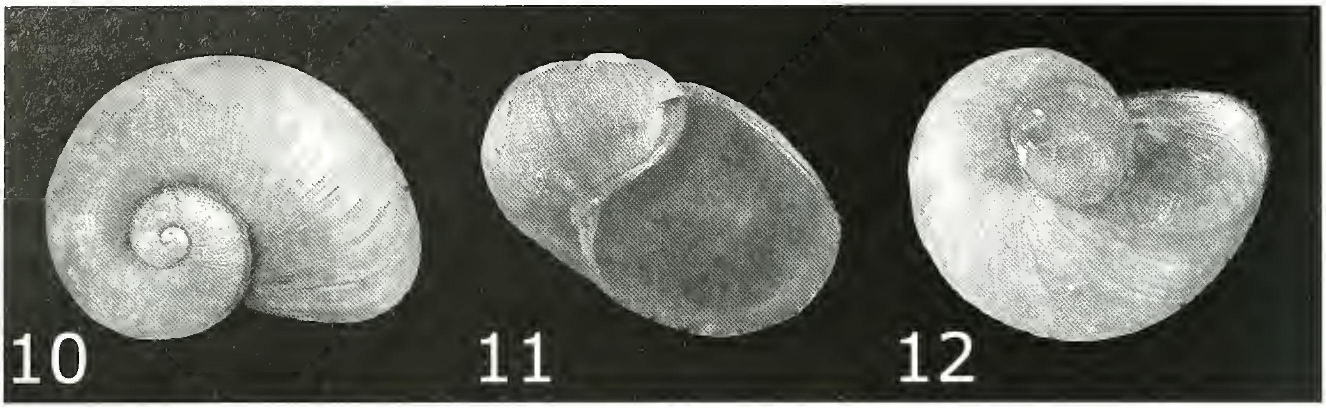
Remarks: Within *Paryphantopsis*, *P. louisiadarum* is similar only to *P. globosa*, *P. misimensis*, *P. ubwamensis*, and *P. vanatinensis* in lacking all traces of periostracal extensions on the growth lines. *Paryphantopsis louisiadarum* differs from *P. globosa* in being smaller, having a closed umbilicus and fewer whorls and differs from *P. misimensis* and *P. vanatinensis* 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. misimensis* that extend to the sole of the foot unlike those of *P. vanatinensis*. The shell of *P. louisiadarum* is usually irregularly maculated with darker pigment unlike the more uniformly colored *P. misimensis* and *P. vanatinensis*. *Paryphantopsis ubwamensis* differs from *P. louisiadarum* in having a more tightly coiled shell with a higher spire and an apical diverticulum on the epiphallus.

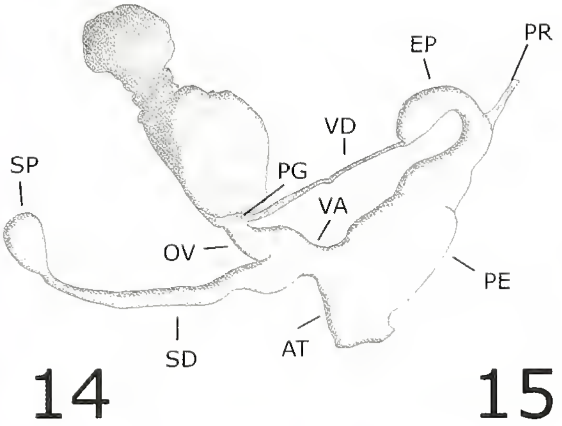
Paryphantopsis misimensis new species
(Figures 10–17, Table 1)

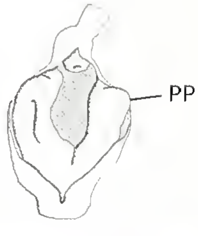
Description: The adult shell is globose, large for the genus, 7.2–8.7 mm (mean = 8.0, see Table 1 for sample size and standard deviation) in diameter and 5.7–6.6 mm (mean = 6.0) in height, with 2.3–2.7 (mean = 2.5) rapidly expanding whorls (Figures 10–12). The suture is deeply impressed and the shell 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 0.68–0.81 (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).

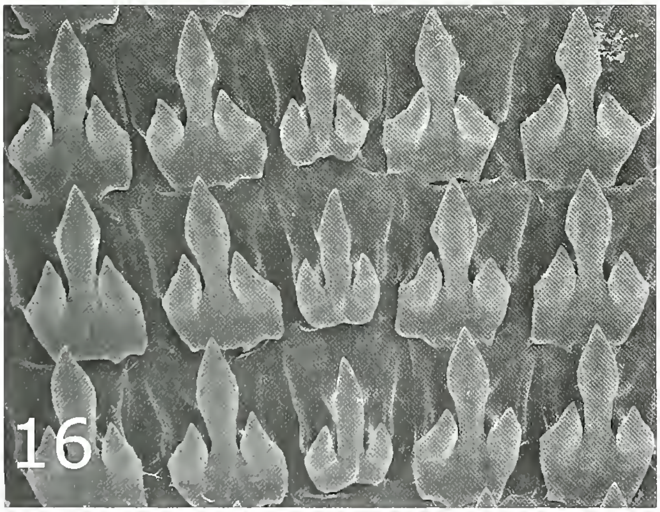
The body color is uniform yellow that fades to cream in specimens preserved in ethanol; there are no lateral bands on the foot or pigment on the eyestalks (Figure 13). The vas deferens narrows rapidly after the prostate gland and remains narrow until entering the slightly swollen head of the epiphallus (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 larger 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.

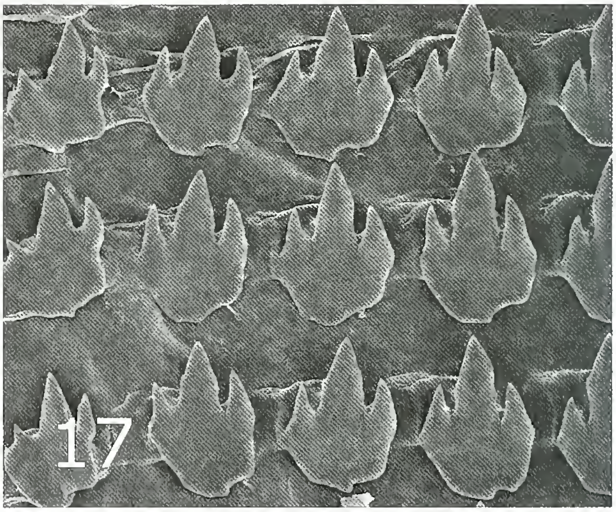
The central teeth of the radula (center row) are tricuspid, 9–10 µm wide and 16–17 µm long, smaller than the first lateral teeth, which are 13–14 µm wide, 21–22 µm long (Figure 16). The mesocones of the central teeth do not project beyond the basal plate while those of the lateral teeth do. The ectocones 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 grade in shape and are 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.

Holotype: UF 308234, F. Kraus, 17 January 2003.

Paratypes: BPBM 268734 (2 specimens), PNGNM 005-002 (5 specimens), UF 303579 (19 specimens), UF 303580 (7 specimens), UF 353424 (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 Tau, 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 Tau.

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

Remarks: *Paryphantopsis misimensis* is similar only to *P. globosa*, *P. louisiadarum*, *P. ubwamensis*, and *P. vanatinensis* in lacking all traces of periostracal extensions on the growth lines. *Paryphantopsis misimensis* differs from *P. globosa* 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 radular teeth with endocones and ectocones that point towards the mesocones. *Paryphantopsis ubwamensis* differs from *P. misimensis* in having a more tightly coiled shell with a higher spire and an apical diverticulum on the epiphallus.

Paryphantopsis vanatinensis new species
(Figures 18–25, Table 1)

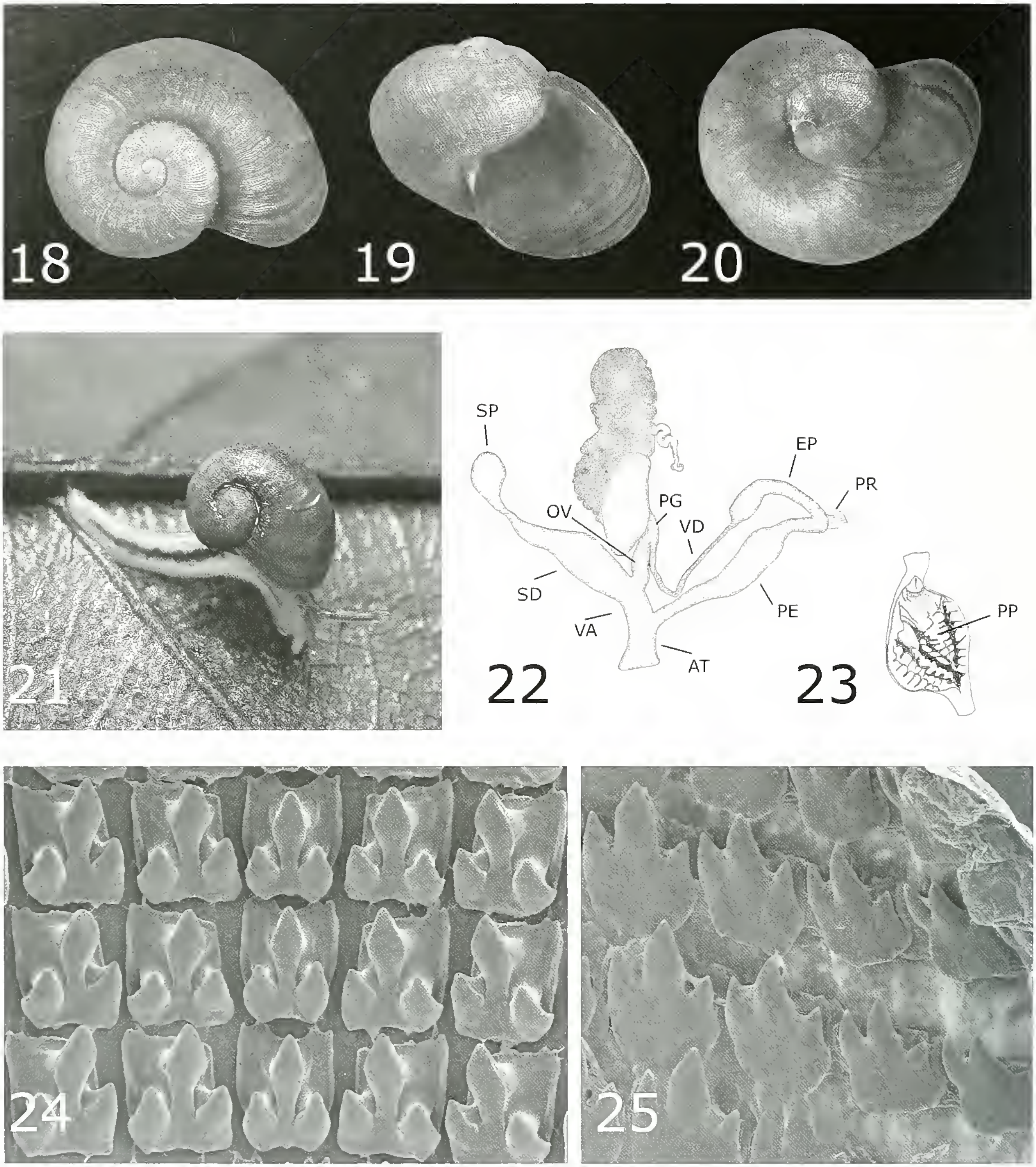
Description: The adult shell is globose, larger than average for the genus, 7.0–9.6 mm (mean = 7.9, see Table 1 for sample size and standard deviation) in diameter and 5.1–6.9 mm (mean = 5.8) in height, with 2.4–2.9 (mean = 2.6) rapidly expanding whorls (Figures 18–20). The suture is deeply impressed 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 striae. Spiral striae 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 ventral 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 epiphallus (Figure 22). The epiphallus 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 epiphallus. The penis is about the same length as the epiphallus, and sculptured with several rows of regularly plicate pilasters (Figure 23). The atrium is moderate in size and of consistent width. The spermatheceal 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 spermatheceal 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 conical 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 heights of the mesocones while the ectocones are slightly shorter, about 0.70 the height of the mesocones.

Holotype: UF 353421, J. Slapcinsky, 19 April 2004.

Paratypes: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Sudest Island (Vanatinai, Tagula): BPBM 268735 (10 specimens), MNHW MP 989 (5 specimens), PNGNM 005-003 (10 specimens), SFM (10 specimens), QM MO76145 (5 specimens), UF 339019 (68 specimens), UF 347729 (3 specimens), UF 353420 (1 specimen), UF 353423 (1 specimen), type locality, J. Slapcinsky, 19 April 2004; UF 339018 (41 specimens), base of Mount Riu (Mount Rio) on the Esiraba River, 120 meters altitude, 11.492° S, 153.413° E, J. Slapcinsky, 15 April 2004; UF 339017 (37 specimens), near Avarumolo Rock Shelter, 150 meters altitude, 11.490° S, 153.420° E, J. Slapcinsky, 23 April 2004.



Figures 18–25. *Paryphantopsis vanatinensis.* **18–20.** Photographs of shell, Holotype UF 353421, diameter 7.6 mm. **21.** Photograph of live animal. **22–23.** Camera lucida drawing of genitalia, UF 353423, maximum width 8.9 mm. **24–25.** Scanning electron micrograph of radula, UF 353423, field width of central and lateral teeth 87 μm, marginals 52 μm.

Type Locality: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Sudest Island (Vanatinai, Tagula). Emma Peak, just W of the summit of Mount Riu (Mount Rio), 725 meters altitude, 11.507° S, 153.431° 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: *Paryphantopsis vanatinensis* is similar only to *P. globosa*, *P. louisiadarum*, *P. misimensis*, and *P. ubwamensis* in lacking all traces of periostracal extensions on the growth lines. *Paryphantopsis vanatinensis* differs from *P. globosa* in being smaller, having a closed umbilicus and fewer whorls and differs from *P. louisiadarum* and *P. misimensis* 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. *Paryphantopsis ubwamensis* differs from *P. vanatinensis* in having a more tightly coiled shell with a higher spire and an apical diverticulum on the epiphallus.

Paryphantopsis yelensis 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 lirae can be seen on the apex of adult shells. These lirae 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 6–7 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 epiphallus. Immediately below the head of the epiphallus there is a finger shaped apical diverticulum that is roughly ½ the length of and nearly the same diameter as the epiphallus (Figure 29). The epiphallus 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 epiphallus. The epiphallus 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 oviduct, 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.

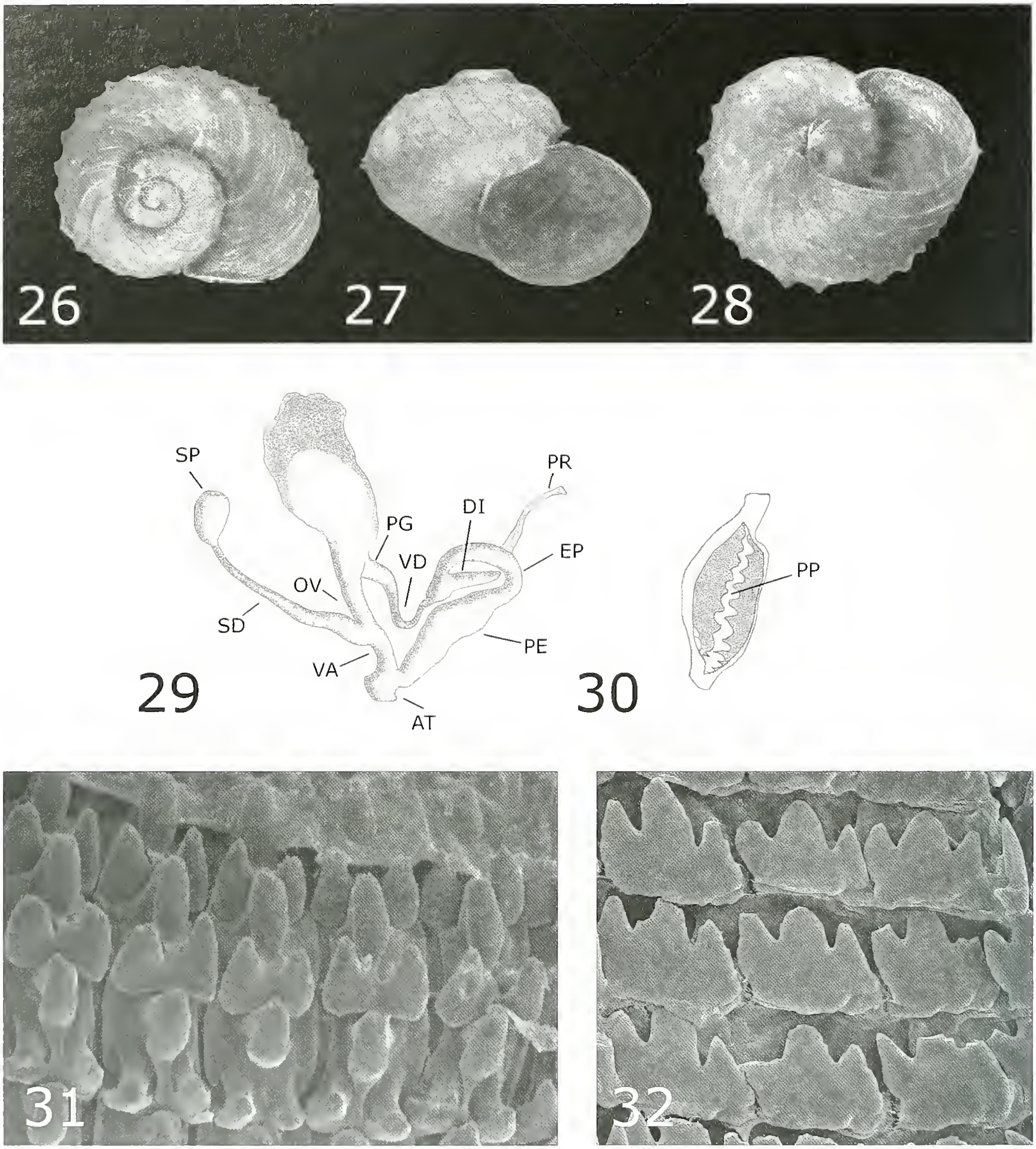
The central teeth of the radula (center row) are tricuspid, 7–8 μm wide and 12–13 μm long, of similar shape and length but slightly narrower than the first lateral teeth, 8–9 μm wide and 12–13 μm long (Figure 31). The mesocones of both the central and first lateral teeth are relatively short and blunt, 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.

Holotype: UF 353427, J. Slapcinsky, 12 May 2004.

Paratypes: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Yela Island (Rossel Island): UF 339016 (15 specimens), UF 353428 (1 specimen), type locality, J. Slapcinsky, 12 May 2004; UF 339120 (1 specimen), Wopu River upstream of trail crossing near abandoned Yela Village, 280 meters altitude, 11.338° S, 154.224° E, J. Slapcinsky, 14 May 2004; UF 339119 (1 specimen), former site of Gopubop Village, 275 meters altitude, 11.335° S, 154.222° E, J. Slapcinsky, 13 May 2004; UF 342911 (2 specimens), W of former site of Gopubop Village, 285 meters altitude, 11.336° S, 154.221° E, J. Slapcinsky, 16 May 2004.

Type Locality: Papua New Guinea, Milne Bay Province, Louisiade Archipelago, Yela Island (Rossel Island), Lipuwopu 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, mosses and lichens, and, less commonly, on dead logs and twigs near the ground.



Figures 26–32. *Paryphantopsis yelensis*. **26–28.** Photographs of shell, Holotype UF 353427, diameter 4.3 mm. **29–30.** Camera lucida drawing of genitalia, UF 353428, maximum width 4.7 mm. **31–32.** Scanning electron micrograph of radula, UF 353428, field width of central and lateral teeth 17 μm, marginal teeth 27 μm.

Remarks: *Paryphantopsis yelensis* differs from all other *Paryphantopsis* from the Louisiades, *P. louisiadarum*, *P. misimensis*, and *P. vanatinensis*, and from the lowland species from the mainland, *P. lebasii* and *P. yawii*, 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 radular 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. yawii*.

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. louisiadarum*, was previously described (Möllendorff, 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 charopid 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, 1983), 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. louisiadarum*, *P. misimensis*, and *P. vanatinensis* 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. louisiadarum*, *P. misimensis*, and *P. vanatinensis* lack periostracal extensions on the growth lines similar only to *P. globosa* and *P. ubwamensis* from mainland Papua New Guinea; however, they also lack an apical diverticulum similar only to *P. lebasii* and *P. yawii* 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. yawii*, 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.

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I thank the landowners of Araetha, Teheme, Damenu, 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. Kula 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 louisiadarum*; L. Appleton, P. Callomon, R. Jenssen, D. Potter, and M. Shea for facilitating my study of specimens in their care; and J. Worsfold 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.

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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, development of the epiphallus, thickness of the vas deferens at its junction with the prostate gland and 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 (I. 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, 1985). The species is placed in the *Polygyra plicata* group of the Polygyridae, Polygyrini (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, 1985), 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 squarish. The lip teeth are smaller and are not deeply immersed."

Hubricht (1985) described *D. lithica* and *D. dorfeuilliana* as "calciphiles 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 (1981b) placed the species in the genus *Millerelix* Pratt, 1981 "because of its position as a precise intermediate between *P[olygyra] mooreana* and *P[olygyra] dorfeuilliana* in shell characters"; both *Daedalochila mooreana* (Binney, 1857) and *D. dorfeuilliana* having been assigned to *Millerelix* on the basis of shell characters and genital anatomy (Pratt, 1981a, b). Subsequently, Emberton (1995) placed all members of the *Polygyra plicata* group into *Millerelix*, separating the species of *Millerelix sensu* Pratt, 1981b, from other members of the genus by erection of the subgenus *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 *Millerelix* 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 (1985). We were unable to examine material from the type locality of *D. dorfeuilliana* because that locality is unknown (Pilsbry, 1940).

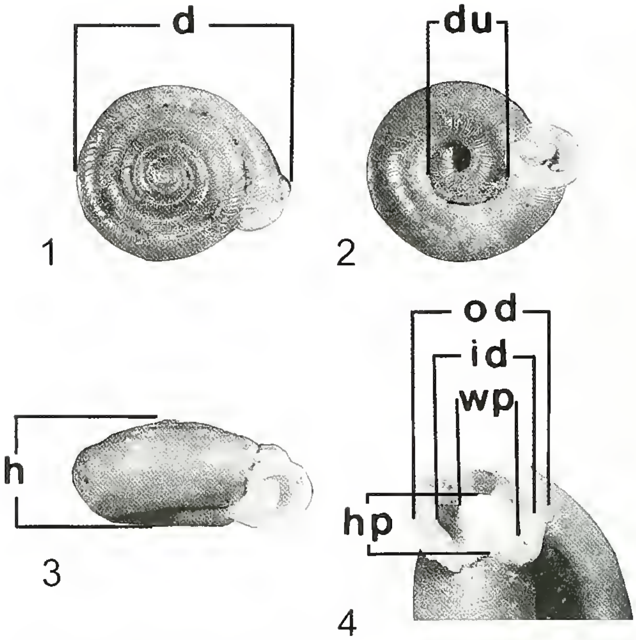
We have used type material of *D. lithica* plus material identified by Hubricht as *D. dorfeuilliana* and *D. lithica* to examine Hubricht's (1961) concept of the two species in more detail. Live material was obtained for study of the anatomy and habitat preferences so as to identify which characters 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 (UNMZ), Ann Arbor, Catalog Number UNMZ 205895; 19 lots (291 specimens of adult shells) collected between 10 April 1936 and 1978 (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 (132 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; 26 lots (142 adult shells) collected by the senior author between 12 June 1995 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 forms. 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.



Figures 1–4. Shell dimensions measured. **1.** d, diameter of shell; **2.** du, diameter of umbilicus; **3.** h, height of shell; **4.** od, outside diameter of aperture; id, inside diameter of aperture; wp, width of parietal lamella; hp, height of parietal lamella. *Daedalochila dorfeuilliana*, FMNH 308106, 8.4 mm diameter.

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 14, 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, NMW.Z.2005.011.03298, one specimen measured and illustrated (Figures 21, 22); NMW.Z.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

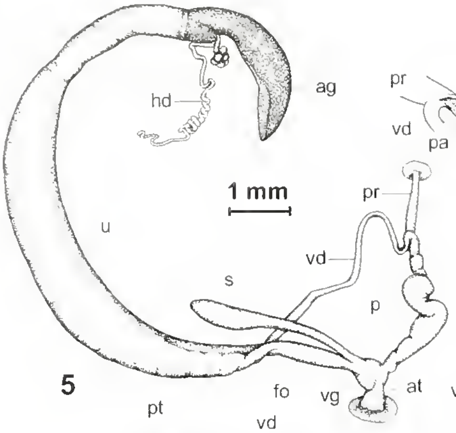
Shell Characters: Visual examination of Hubricht's material of *D. lithica* and *D. dorfeuilliana* in the FMNH confirmed the general features of his description of *D. lithica* and its comparison with *D. dorfeuilliana* (Hubricht, 1961). Thus, shells of the two species are similar in apical and umbilical 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 parietal 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 parietal lamella was often present in specimens identified as *D. lithica* (Figure 30), the shape being similar to the "squarish" parietal lamella of *D. dorfeuilliana* (Figure 31) as described by Pilsbry (1940). Conversely, the parietal 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, variously flexed (Figures 5, 14–16) or coiled (Figure 12) epiphallus, without appendix or flagellum; length 2.63–3.89 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 0.07–0.18 (mean = 0.13±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 2.82 ± 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



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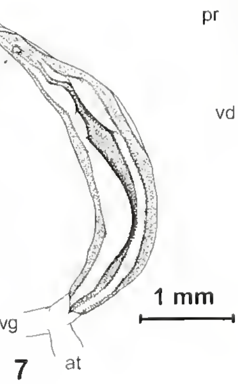

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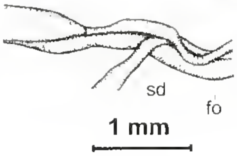

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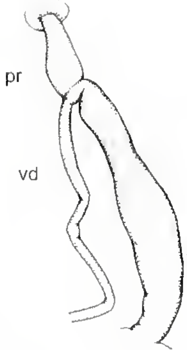

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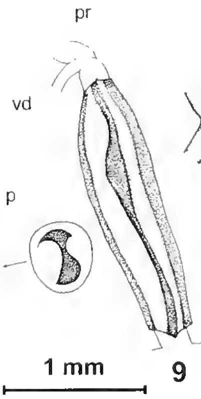

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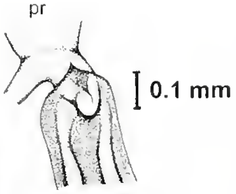

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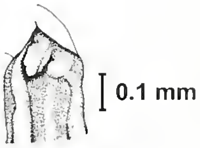

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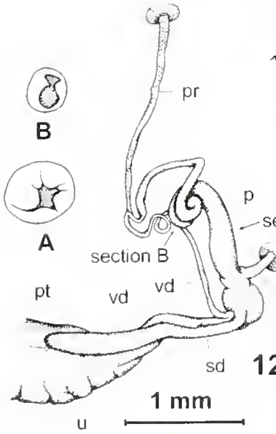

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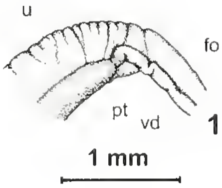

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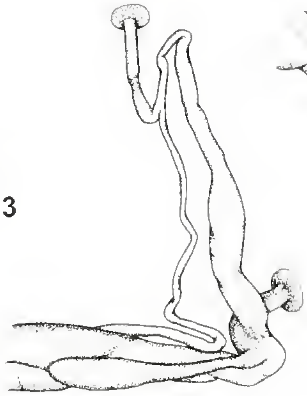

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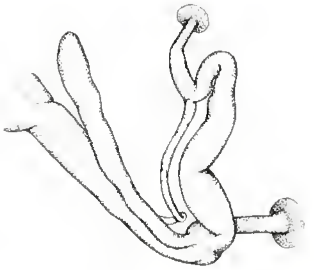

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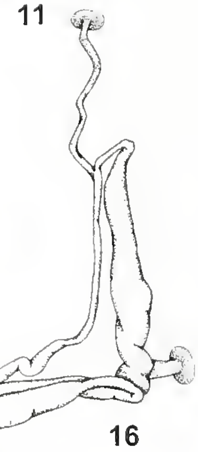

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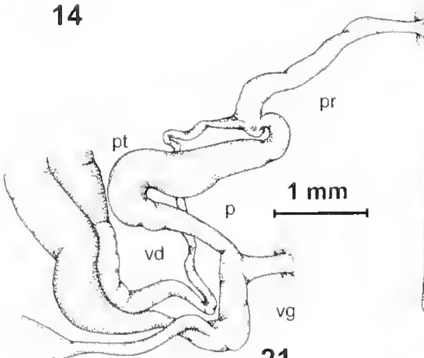

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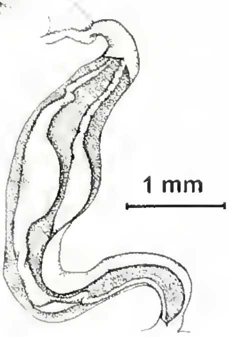

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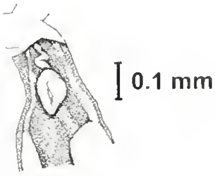

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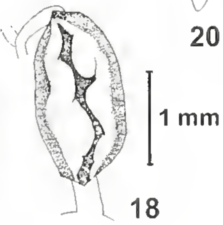

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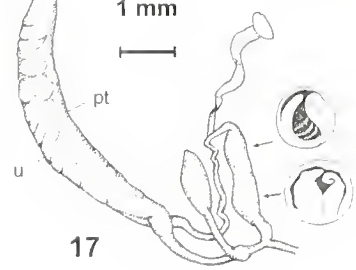

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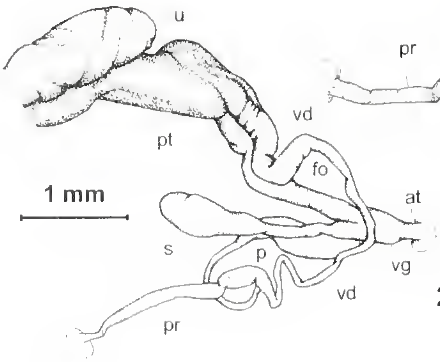

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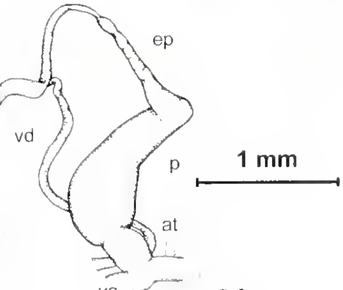

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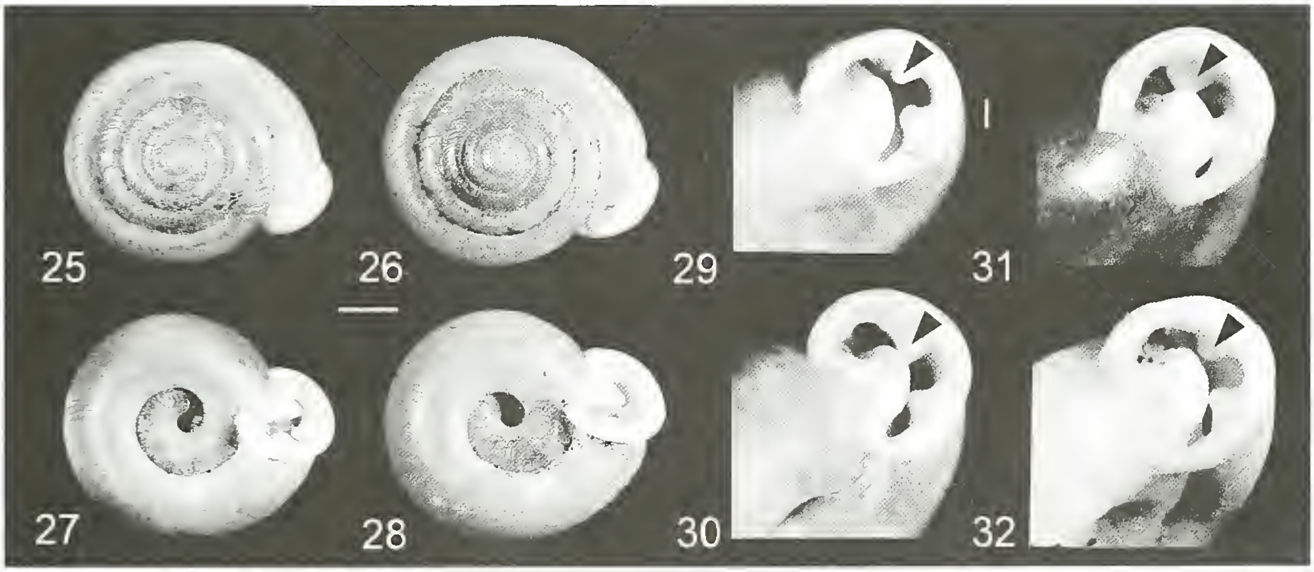
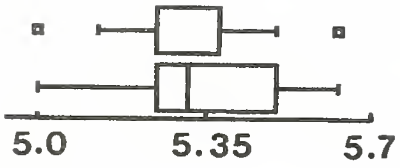
Figures 5–24. Genital anatomy of *Daedalochila lithica* (Figures 5–16) and *Daedalochila lithica* (Figures 17–24) from Arkansas. **5.** *D. lithica* Boone County, 29 April 2004, UF 376769. **6.** Same, detail of junction of vas deferens **(vd)** and prostate gland **(pt)**. **7.** Same, penis opened to show the two pilasters and the papilla (pa) in the terminal penis. **8.** *D. lithica*, Madison County, 22 September 2004, UF 376766, showing a stout penis **(p)** and a short penial retractor muscle **(pr)**. **9.** Same, detail of penis opened to near the penial retractor muscle. **10.** Same, apical penis opened to the penial retractor muscle, showing obsolete apical pilasters and detail of terminal penial papilla. **11.** *D. lithica*, Marion County, 20 January 2003, UF 376767, apical penis, opened, showing obsolete apical pilasters and detail of terminal penial papilla. **12.** *D. lithica*, Carroll County, 3 April 2004, UF 376816, 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 376816 (second specimen), detail of junction of vas deferens and prostate gland. **14–16.** *D. lithica*, distal genitalia showing variation of penis. **14.** From Boone County, 29 April 2004, UF 376769 (second specimen). **15.** From Madison County, 22 September 2004, UF 376766 (second specimen). **16.** From Boone County, 22 September 2004, UF 376765. **17.** *D. dorfeuilliana*, Hempstead County, 5 January 2003, FMNH293240 (reproduced from Coles and Walsh, 2006, fig. 35°), distal genitalia and penial sections. **18.** Same, opened to show pilasters (reproduced from Coles and Walsh, 2006, fig. 36°). **19.** *D. dorfeuilliana*, UF 376768 (second specimen), apical penis opened to penial retractor muscle to show the terminal end of the pilasters, with obsolete 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, NMW.Z.2005.011.03298, showing enlarged proximal vas deferens **(vd)** and vagina **(vg)** approximately twice as long as diameter. **22.** Same, penis opened to show pilasters. **23.** *D. dorfeuilliana*, Carroll County, 10/15 March 2005, UF 376770, distal genitalia showing enlarged vas deferens. **24.** Same, detail of penis. Abbreviations: **ag,** albumen gland; **at,** atrium; **ep,** epiphallus; **fo,** free oviduct; **hd,** hermaphrodite duct; **pa,** penial papilla; **p,** penis; **pr,** penial retractor muscle; **pt,** prostate gland; **s,** spermatheca; **sd,** spermatheca duct; **u,** uterus; **vd,** vas deferens; **vg,** vagina. ° Reproduced by permission of the American Malacological Bulletin.

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 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, UMMZ 205895, 8.0 mm diameter, six miles east of Mountain View, Stone County. **26.** *D. dorfeuilliana*, FMNH 308109, 8.2 mm diameter, Buffalo National River, Tyler Bend, Searcy County. **27.** Umbilical view, *D. lithica* same as above; **28.** *D. dorfeuilliana*, same as above; **29.** *D. lithica*, paratype, FMNH 256372, 7.8 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 308114, 8.2 mm diameter, Dogwood Trail at Beaver Dam Overlook, Carroll County. **32.** *D. dorfeuilliana*, FMNH 308119, 8.0 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).



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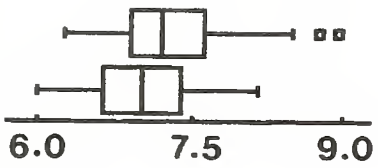

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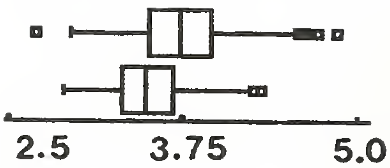

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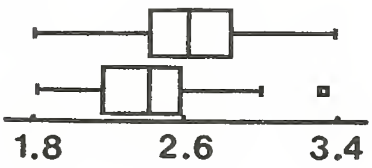

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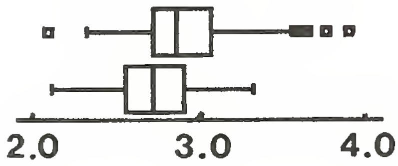

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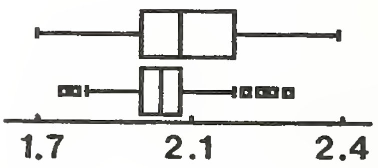

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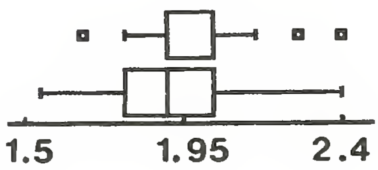

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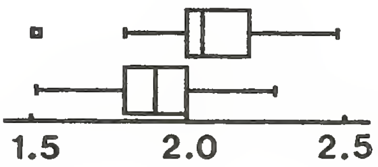

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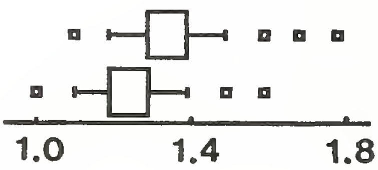

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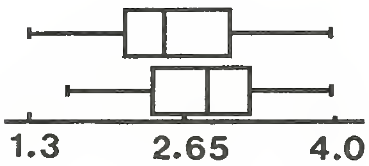

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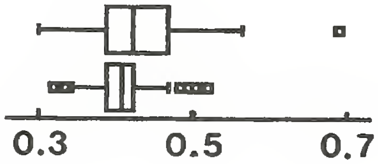

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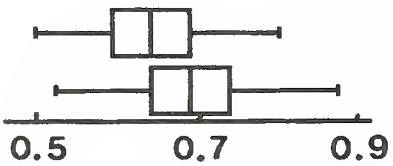

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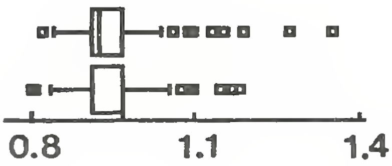

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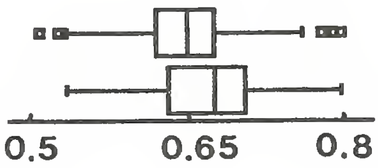

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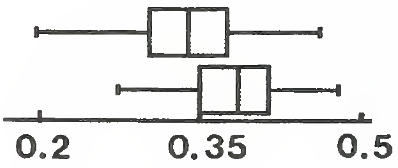

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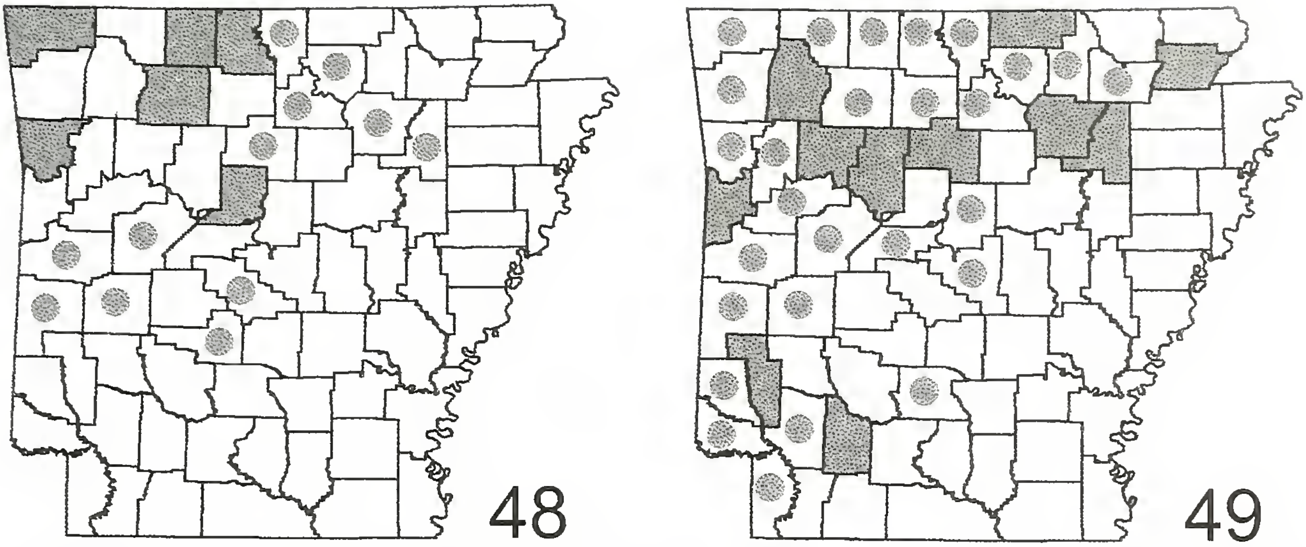
Figures 33–47. Box plot diagrams of shell measurements and ratios: *Daedalochila dorfeuilliana* (n=441) (above); *Daedalochila lithica* (n=427) (below). The 25th–50th percentiles of data fall within the boxes, the 10th–90th percentiles fall within the error bars, and data outside these ranges are plotted 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 (11.46). **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).



Figures 48–49. Distributions of *D. lithica* (Figure 48) and *D. dorfeuilliana* (Figure 49) in Arkansas. Dots: counties represented in this study; blackened: counties not represented in this study.

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 bisontes* 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*.

Feature	*D. lithica*	*D. dorfeuilliana*
Palatal lamella of aperture	not immersed (Figures 29, 30)	immersed (Figures 31, 32)
Penis	approximately uniform in diameter from base to mid length (Figures 5, 12, 14–16)	widest at mid length where the pilasters are well developed, with a narrow base (Figures 17, 21, 24)
Proximal vas deferens	not greatly enlarged, approximately twice its minimum diameter (Figures 6–13)	greatly enlarged, approximately 4 times its minimum diameter (Figures 21, 23)
Vagina length/diameter	approximately 1 (Figures 12, 14–16)	approximately 2 (Figure 21)

whether it is variable in development or was destroyed during dissection. Nevertheless, its presence agrees with Pratt's description of the anatomy of *D. dorfeuilliana* (Pratt, 1981b) and appears to be a "derivative" of the apical, pendant, conical projection (Emberton, 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. dorfeuilliana* (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 Emberton'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. dorfeuilliana* would be placed in the subgenus *Prattelix* because of the wider penis and greatly enlarged vas deferens (Emberton, 1995). Thus, these data give some support to the concepts of *Millerelix* as used by Pratt (1981a,b) and modified by Emberton (1995), but they do not change our conclusions concerning the inappropriate use of *Millerelix* for all members of the *D. plicata* group.

ACKNOWLEDGMENTS

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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. valenciai* new species and *P. mcleani* new species) extend the record of *Prisogaster* to the middle late Miocene and reveal its turbinine ancestry. A major morphological transformation during the late Pliocene 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 trochoidean 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 Pleistocene [Herm, 1969; not late Pliocene (Hickman and McLean, 1990)]. Individuals of *Prisogaster* live amongst wave-battered intertidal rocks and tide pools (Marincovich, 1973; Guzman et al., 1998), 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; Wenz, 1938), 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. stucchii* new species and *P. valenciai* new species. Specimens of the former were found near Sacaco in middle upper Miocene and lower Pliocene well-sorted cross-bedded 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

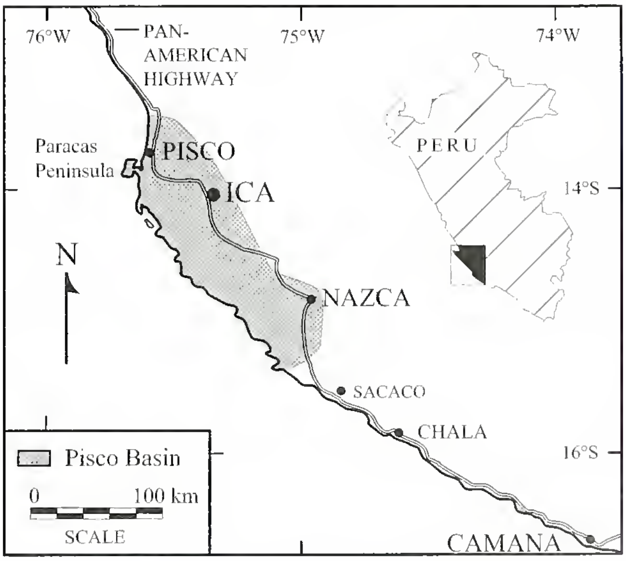

Figure 1. Location of the Pisco forearc basin in southern Peru. New fossil species of *Prisogaster* are from Cenozoic deposits near Sacaco and Chala.

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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 (Figure 3) 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* Hupé, 1854, *Acanthina triangularis* DeVries, 2003, and *Herminespina mirabilis* (Möricke, 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

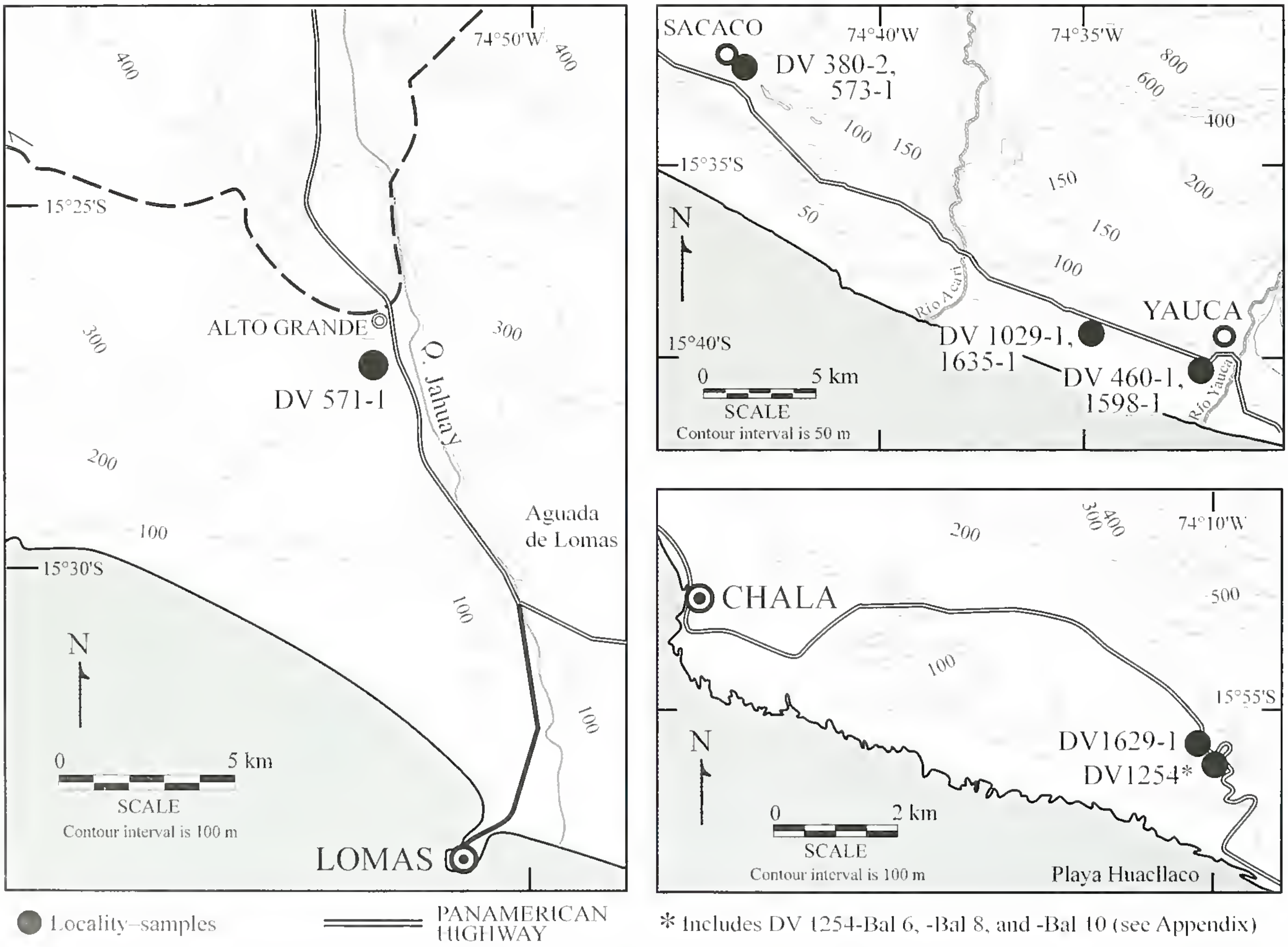


Figure 2. Type localities of *Prisogaster valenciai* new species (locality-samples DV 1254-Bal 6, Bal 8, and Bal 10) and *P. stucchii* new species (DV 571-1). Also shown are lower Pliocene locality-samples near Yauca (DV 1029-1, DV 1635-1, DV 460-1, DV 1598-1) and Sacaco (DV 380-2, DV 573-1) with *P. mcleani* and an upper Pliocene/lower Pleistocene marine terrace southeast of Chala with *P. niger* (DV 1629-1).

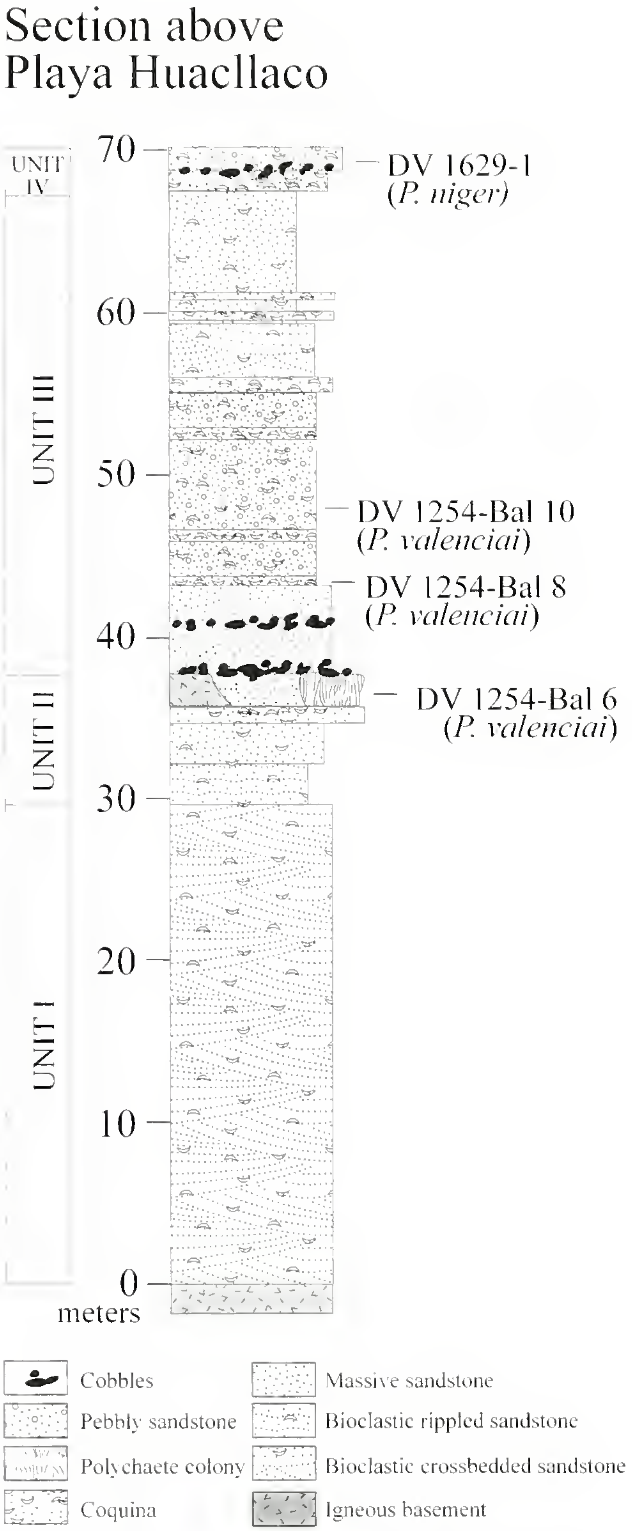


Figure 3. Huacllaco section southeast of Chala with stratigraphic position of type specimens of *P. valenciai* new species and other horizons with *Prisogaster* material.

Genus *Prisogaster* Mörch, 1850

Amyxa F. H. Troschel, 1852 (objective synonym)

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

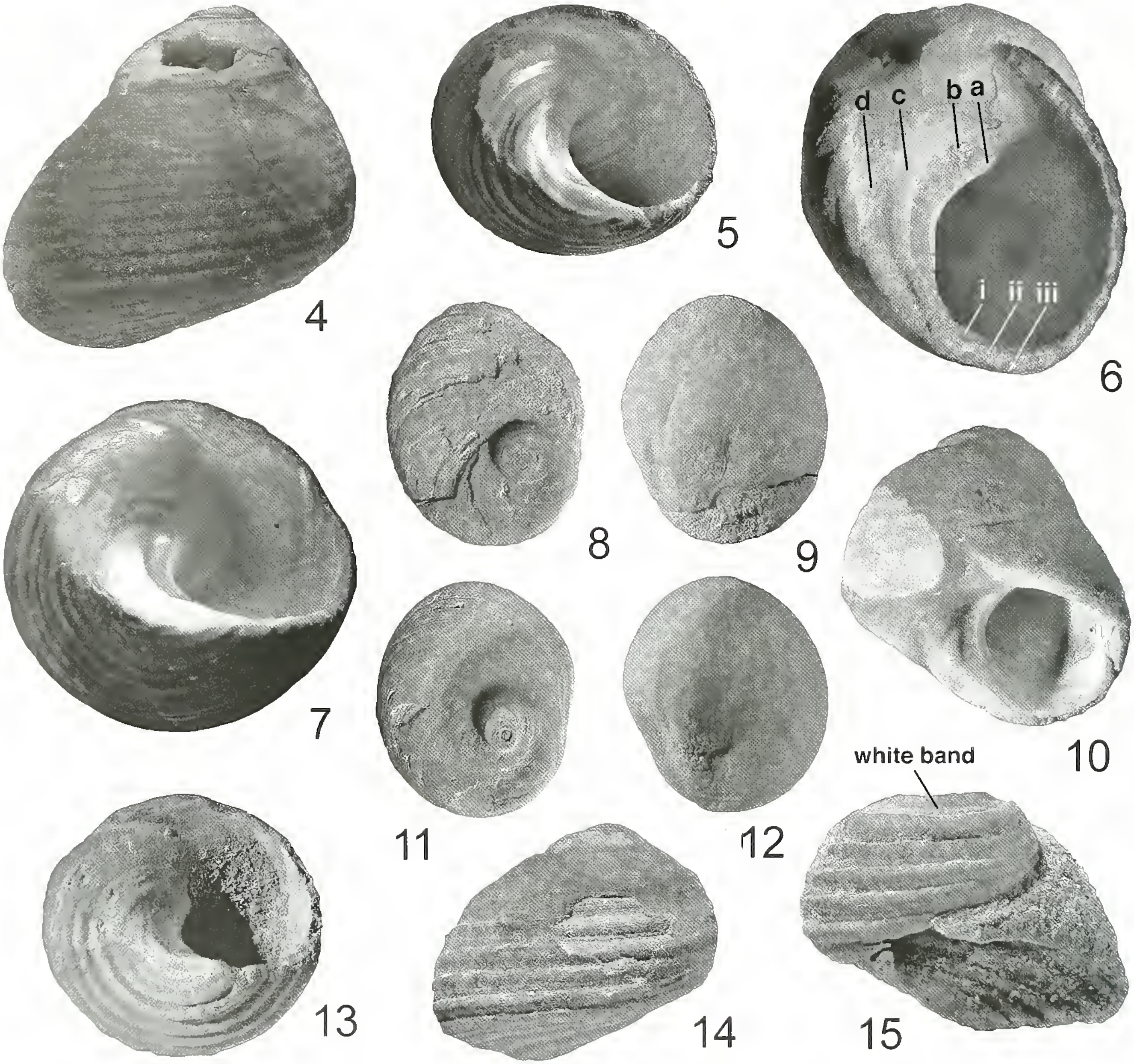
Discussion: Mörch (1850, p. 21) did not describe *Prisogaster*, but simply applied the new genus name without comment to *Turbo niger* Gray (= *Turbo niger* Wood, 1828), itself introduced with only a drawing and one-word description, "black" (Wood, 1828, p. 18). Hickman and McLean (1990) implicitly defined *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 quadripartite 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, 1909, p. 238.
Prisogaster niger Wood.—Mörch, 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; Ramirez, 1981, p. 130, fig. 154; Alamo and Valdivieso, 1997, p. 15, fig. 30; Guzmán et al., 1998, p. 37, fig. 27; Forcelli, 2000, p. 64, fig. 102; Aldea and Valdovinos, 2005, p. 390, fig. 8-H.
Prisogaster niger minor Mörch, 1850, p. 21.
Trochus gaudichaudii 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 twofold. Most posterior spiral cord wider, flatter, forming collar against preceding whorl. Interspaces narrower



Figures 4–15. *Prisogaster* spp. **4–10.** *Prisogaster niger* (Wood, 1828). **4.** UWBM 97829, Pisco Bay, Recent, abapertural view, length = 18.4 mm. **5.** UWBM 97830, Pisco Bay, Recent, oblique basal-apertural view, m. v. width = 15.7 mm. **6.** MUSM INV 116, DV 1629-1, latest Pliocene, oblique basal-apertural view showing quadripartite structure of columella, m. v. width = 17.9 mm. a = inner white column, b = medial nacreous band, c = outer white sinuous ridge, d = outermost elongate excavation, i = inner nacreous layer, ii = middle shell layer, iii = outer purple-black calcitic layer. **7.** UWBM 97829, basal view, width = 19.1 mm. **8.** UWBM 97837, DV 1629-1, operculum, interior view, length = 8.9 mm. **9.** UWBM 97837, operculum, exterior view. **10.** UWBM 97828, DV 398-1, Recent, apertural view showing outer layer and inner nacreous layer on body whorl, length = 18.3 mm. **11, 12.** *Prisogaster mcleani* new species. Early Pliocene. **11.** UWBM 97848, DV 573-1, operculum, interior view, length = 8.7 mm. **12.** UWBM 97848, exterior view. **13, 14.** *Prisogaster niger* (Wood, 1828). **13.** UWBM 97831, DV 461-1, latest Pliocene, basal view, m.v. width = 18.9 mm. **14.** UWBM 97831, abapertural view, length = 16.3 mm. **15.** *Prisogaster valenciai* new species. Late Pliocene. UWBM 97838, holotype, DV 1254-Bal 8, apertural view, width = 15.9 mm.

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 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 to 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 abaxial posterior corner; sinuous growth lines present on abaxial side. Interior nearly planar, coiled, changing from multispiral to paucispiral; all coils with long growing edge. Subsurface texture reticulate with elongate "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 464–1, 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 18.5; 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: Ipun, 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 (Herm, 1969; Valdovinos, 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. valenciai*. Specimens of *P. niger* differ from those of *P. valenciai* 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; Valdovinos, 1999), a distribution more extensive than ascribed to the species by Dall (1909) or Alamo and Valdivieso (1997). The Pleistocene record is limited to southern Peru and Chile, with no records from the marine *tablazos* of northern Peru (DeVries, 1986). The late Pliocene record is still more restrictive, with only southern Peruvian specimens known, including the oldest, which were found southeast of Chala (DV 1629-1) in the uppermost coquina (Unit IV) of the Huaclaco section (Figure 3), a shell bed dominated by thick disarticulated valves of the bivalve, *Mulinia edulis* (King, 1831).

A second modern species assigned to *Prisogaster* has been the Chilean *P. elevatus* (Eydoux 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, show a specimen with a blotchy purple-black color, elevated spire, absence of spiral sculpture, wavy growth lines, and evenly convex calcareous operculum visibly coiled on both sides, all features characteristic of *Tricolia* Risso, 1826 (Hickman and McLean, 1990), more particularly the Chilean *Tricolia mcleani* Marincovich, 1973. Neither the 14 mm length of Eydoux and Souleyet's "*Turbo elevatus*," however, nor the deep lunate columellar/parietal excavation, is characteristic of Chilean *Tricolia*, but rather suggest the Chilean trochid, *Diloma nigerrima* (Gmelin, 1791). The generic assignment of "*Turbo elevatus*" remains in doubt.

Prisogaster valenciai 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.

Description: Shell less than 15 mm long, globose, compressed axially. Thickness indeterminate (inner shell layers missing). Spire moderately elevated, length indeterminate (much of spire missing). Protoconch and early whorls of teleoconch unknown. Whorls broadly rounded posteriorly, weakly angulate anteriorly. Periphery usually anterior to axial midpoint of whorl. Sutures slightly impressed. Exterior gray to black, with interspaces sometimes cream-colored. Axial sculpture absent. Spiral sculpture of five to 14 broadly rounded primary cords, three to 10 posterior to base, two to four on base; spiral cords about equally wide except for broader, flatter, most posterior spiral cord forming low collar adjacent to suture. Interspaces usually narrower than spiral cords, sometimes filled with single secondary spiral cord. Strongly prosocline growth lines, sometimes lamellate. Aperture oblique, diagonally ovate. Outer lip strongly prosocline. Columella and umbilical area missing. Operculum unknown.

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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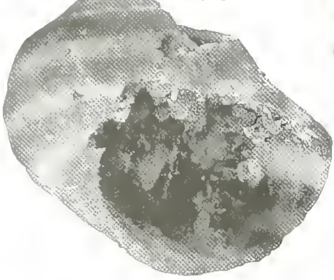
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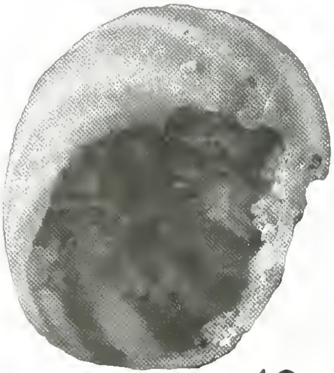
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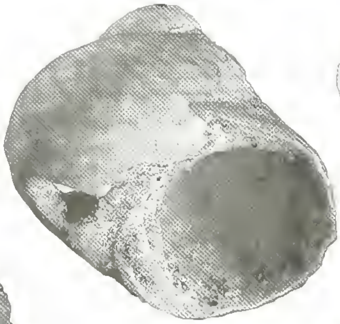
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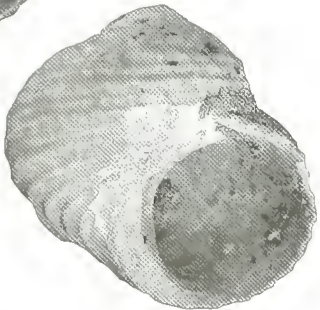
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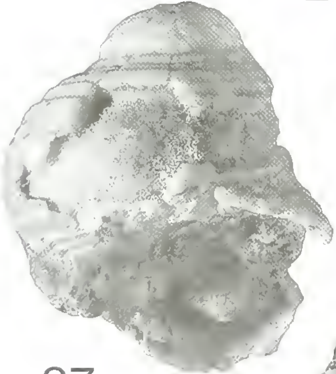
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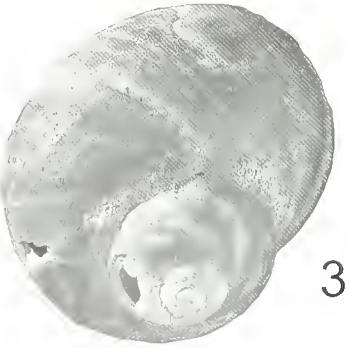
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118, paratype, DV 1254-Bal 8, fragment; MUSM INV 119, paratype, DV 1254-Bal 10, fragment.

Type Locality: Roadcut along the Panamerican Highway, 10 km southeast of Chala. Locality-samples DV 1254-Bal 6, DV 1254 Bal-8, DV 1254-Bal 10, late Pliocene, in section at 35, 42, and 47.5 meters, respectively, above crystalline basement (Figures 2, 3), 15°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 Valencia Chacón, director of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

Remarks: The incomplete specimens of *Prisogaster valenciai* 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. valenciai* is from the Pliocene section above Playa Huacllaco (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 valenciai* were found in Unit II and the lower part of Unit III of the Huacllaco 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; *Concholepas* spp.; *Choromytilus chorus* (Molina, 1782); and a new species of *Xanthochorus* Fischer, 1884 (DeVries, 2005a).

Prisogaster mcleani new species
(Figures 11, 12, 20, 21, 23–32)

Diagnosis: Globose, whorls broadly rounded anteriorly and posteriorly; tan-colored, often mottled, striped, or speckled with brown.

Description: Shell globose, about 20 mm long. Spire moderately to greatly elevated, about 30% to 40% of shell length. Protoconch unknown, teleoconch with about five whorls. Whorls convex, broadly rounded posteriorly and anteriorly, without anterior angulations. Sutures variably impressed. Exterior tan, often with mottling, prosocline flammules, or zig-zag patterns of brown. Axial sculpture absent. Spiral sculpture of ten to 15 rounded primary spiral cords between suture and umbilical area, subdued on smooth specimens; secondary spiral cords rarely interspersed. Entire surface often with tertiary spiral threads. Interspaces variably wide, crossed by strongly prosocline, colabral growth-line lamellae. Juveniles with three weaker spiral cords on base, four to five primary spiral cords on whorl. Aperture oblique, ovate to nearly circular, peristome incomplete. Umbilicus absent. Outer lip thin, strongly prosocline, inner edge smooth. Parietal and umbilical areas weakly excavated in adults. Columella with inner white column curving anteriorly; with a narrow, slightly excavated, nacreous band merging anteriorly with nacre-lined aperture; with a white ridge, slightly sinuous, outboard of the nacreous band, extending to base of aperture and coalescing with interspace between second and third basal spiral cords, with one or two short teeth abaxial; and with an outermost, narrow, white, excavation bordering the ridge at the outer margin of the columellar area, extending anteriorly just over half the length of columella.

OPERCULUM: Exterior convex, steeper posteriorly and adaxially; basal rim smooth, remainder of surface pustulose, more so peripherally than centrally. Two sub-axially elongate, anteriorly converging creases on adaxial side of diagonal bulge, inner crease extending to abaxial posterior corner; sinuous growth lines present on abaxial side. Interior nearly planar, coiled, multispiral changing to paucispiral; all coils with long growing edge. Larger coils with centered shallow, broad, flat-bottomed channel. Subsurface texture reticulate with elongate "cells" perpendicular to growth lines.

Figures 16–32. *Prisogaster* spp. **16–19.** *Prisogaster valenciai* new species. Late Pliocene. **16.** UWBM 97840, DV 1031-1, early late Pliocene, oblique spire view, width = 13.0 mm. **17.** UWBM 97840, apertural view. **18.** UWBM 97839, paratype, DV 1254-Bal 6, abapertural fragment, m. v. width = 12.7 mm. **19.** UWBM 97840, oblique basal-apertural view, m. v. width = 12.4 mm. **20, 21.** *Prisogaster mcleani* new species. **20.** MUSM INV 121, DV 1598-1, early Pliocene, oblique spire view showing change in color pattern and repaired break, m. v. width = 12.1 mm. **21.** MUSM INV 121, apertural view showing naticid drillhole to left of columella, width = 11.5 mm. **22.** *Prisogaster valenciai* new species. Late Pliocene. UWBM 97839, oblique basal view, m. v. width = 12.7 mm. **23–32.** *Prisogaster mcleani* new species. **23.** UWBM 97841, DV 571-1, holotype, middle late Miocene, apertural view showing quadripartite structure of columella (see text), length = 13.9 mm. **24.** UWBM 97842, DV 571-1, paratype, abapertural view, length = 21.1 mm. **25.** MUSM INV 120, DV 1598-1, apertural view showing quadripartite columella and prosocline color stripes, length = 12.4 mm. **26.** UWBM 97841, oblique spire view, m. v. width = 16.5 mm. **27.** UWBM 97842, abapertural view. **28.** UWBM 97844, DV 1598-1, abapertural view of juvenile showing bicarinate whorls and colabral growth-line lamellae, length = 9.4 mm. **29.** MUSM INV 124, DV 573-1, early Pliocene, abapertural view showing flecked stripes, length = 12.7 mm. **30.** MUSM INV 125, DV 571-1, abapertural view showing brown zig-zag pattern, length = 17.8 mm. **31.** UWBM 97843, oblique spire view, m. v. width = 19.7 mm. **32.** UWBM 97843, apertural view, length = 17.9 mm.

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 19.5.

Type Locality: Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona (= El Jahuay locality of Muizon and DeVries, 1985). Shell banks on south-facing slope, 15°26′57″ S, 74°52′06″ W (Acarí 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 8.9, 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 stucchii* differ from those of *P. niger* by being uncompressed axially, by having an outer calcitic layer that is tan, 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 mcleani* 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 subdued cords that barely rise above the neighboring wide interspaces (Figures 31, 32). Some Miocene and lower Pliocene juvenile specimens (Figures 28) have a pronounced biangulate 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 mcleani* 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 380-2) and Yauca (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 mcleani*, 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 bicarinate juvenile whorls that characterize many members of Turbininae. These similarities strengthen the case of Hickman and McLean (1990) that Prisogasterinae and Turbininae 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 molluscan 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 (Spieker, 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 multipartite 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 perimeter 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 globose tan-colored and brown-mottled *Prisogaster mcleani* to the axially compressed purple-black *P. niger* occurred during the time represented by Units II and III of the Huacllaco section (Figure 3), i.e., latest early Pliocene to late Pliocene, in the guise of *P. valenciai*. The oldest specimen of *P. valenciai* (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 relegated to spire whorls on the youngest specimens (Figure 15; DV 1254-Bal 10).

The late Pliocene appearance of a purple-black external calcitic 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-

rostoma) Swainson, 1840; *Tegula* (*Chlorostoma*) *atra* (Lesson, 1830); *T.* (*C.*) *luctuosa* (d'Orbigny, 1841); *T.* (*C.*) *tridentata* (Potiez and Michaud, 1838); 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 niger* 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. valenciai*, 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. mcleani* are found in well-sorted hummocky cross-bedded 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 foreshore environments with lower energies than typical for intertidal environments.

The late Pliocene was a time of morphological novelty for Mio-Pliocene taxa in Peru other than *Prisogaster*: *Acanthina* Fischer von Waldheim, 1807 (DeVries, 2003), *Concholepas* Lamarck, 1799 (DeVries, 2000), *Xanthochorus* Fischer, 1884 (DeVries, 2005a), and *Tegula* Lesson, 1835 (DeVries, unpublished data). It was during this time that the molluscan fauna of the Mio-Pliocene Peruvian 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 turbinine features suggest *Prisogaster* did arise from a middle Miocene species of *Turbo*, a possibility raised by Hickman and McLean (1990). 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. mcleani* (see Figures 20, 24, 30, 31). Alternatively, a stronger and more stable shell may have enabled individuals of *P. niger* to survive on rockier, higher-energy, intertidal substrates. Such environments became the norm for coastal Peru when much of the coast commenced a 200 m uplift during the latest Pliocene and protected embayments became fewer and much smaller (DeVries, 2001).

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APPENDIX

Locality-samples:

DV 380-2 Sacaco, in cross-bedded sandstones just below farmhouse, 15°32′29″ S, 74°43′53″ W (Acarí 1:100,000 quadrangle), Lower Pliocene.

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

DV 423-1 Terrace deposit capping Miocene strata west of Quebrada Huaricangana, 14°55′29″ S, 75°17′54″ W (Palpa 1:100,000 quadrangle), Pliocene.

DV 460-1 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 (same as DV 1598-1).

DV 461-1 Highest marine terrace about five km north of Chala, Peru, uppermost Pliocene/lowermost Pleistocene.

DV 463-1 Lower terrace, 5 km north of Chala (Chala 1:100,000 quadrangle), upper Pleistocene.

DV 464-1 Mid-level marine terrace, five km north of Chala (Chala 1:100,000 quadrangle), middle Pleistocene.

DV 571-1 Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south-facing hillside west of Panamerican Highway; one of several shell banks, 15°26′57″ S, 74°52′06″ W (Acarí 1:100,000 quadrangle), middle upper Miocene.

DV 573-1 Sacaco, shell banks and cross-bedded sandstone just below level of farmhouse (Acarí 1:100,000 quadrangle), lower Pliocene.

DV 720-1 Eastern major cobble ridge near Santa paleo-lagoon, northern Peru (see DeVries and Wells, 1990), Holocene.

DV 730-1 Between Ceros Pimenco and Mentiroso, mouth of Santa paleo-lagoon, northern Peru (see DeVries and Wells, 1990), Holocene.

DV 806-1 Southwest of Quebrada Usuaca, about 1.7 km west of Hacienda Tunga building, in middle of small natural amphitheater in hillside, highest shell bed. (Palpa 1:100,000 quadrangle), lower Pliocene.

DV 1029-1 Yauca Depression, west of Panamerican Highway, 15°39′29″ S, 75°35′08″ W (GPS, Yauca 1: 100,000 quadrangle). lower Pliocene.

DV 1031-1 Section along Panamerican Highway, Quebrada Huambo, about ten km west-northwest of Chala. Roadcut along Panamerican Highway, north face. 15°48′41″ S, 74°21′18″ W (GPS; Chala 1:100,000 quadrangle). Uppermost Pliocene / lowermost Pleistocene. [Note: This locality was mistakenly referred to as Morro Abra de los Chaparrinos (the "Huaellaco 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 Huaellaco. 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 8 Section along Panamerican Highway, ten km southeast of Chala and above Playa Huaellaco. 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 Huaellaco. 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 Huaellaco, 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

Discodoridid 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 radular morphology.

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

INTRODUCTION

Up to now, seven species of *Hoplodoris* Bergh, 1880 are known (Fahey and Gosliner, 2003). Some species had 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 (Fahey and Gosliner, 2003). Since the 1880s, different authors have compiled a list of the distinguishing characters of *Hoplodoris* (Thompson, 1975; Miller, 1991; Valdés, 2002). Fahey 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)

Description: External Anatomy (Figures 1, 2): Living animal measuring 27 mm length. Body oval, mantle covered with rounded tubercles. Coloration on central dorsum of living animal orange-brown, becoming whitish-orange toward mantle edge. Rounded orange-brown spots around median dorsum, among rounded tubercles. Opaque white ring present at base of tubercles, tubercle tip pale-orange. Rhinophores orange, terminally with pale-cream tip, rhinophores with approximately 15 lamellae. Branchial leaves six, tripinnate. Two anterior leaves yellowish-cream, two posterior leaves orange. Median leaves with orange base, upper half yellowish-cream. Foot narrow and elongated, with notch on anterior side. Oral tentacles two, short. Color of mantle underside whitish, with several brown orange spots on each side of foot.

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 radular 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.

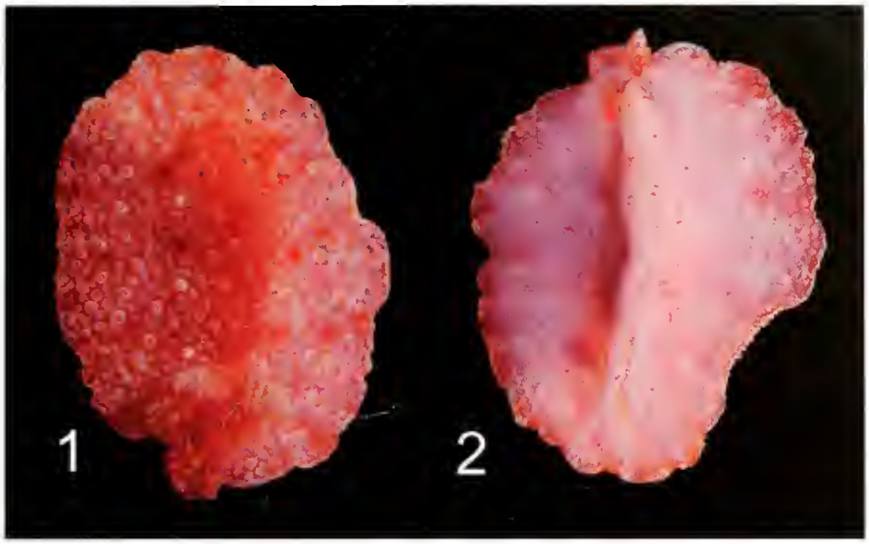
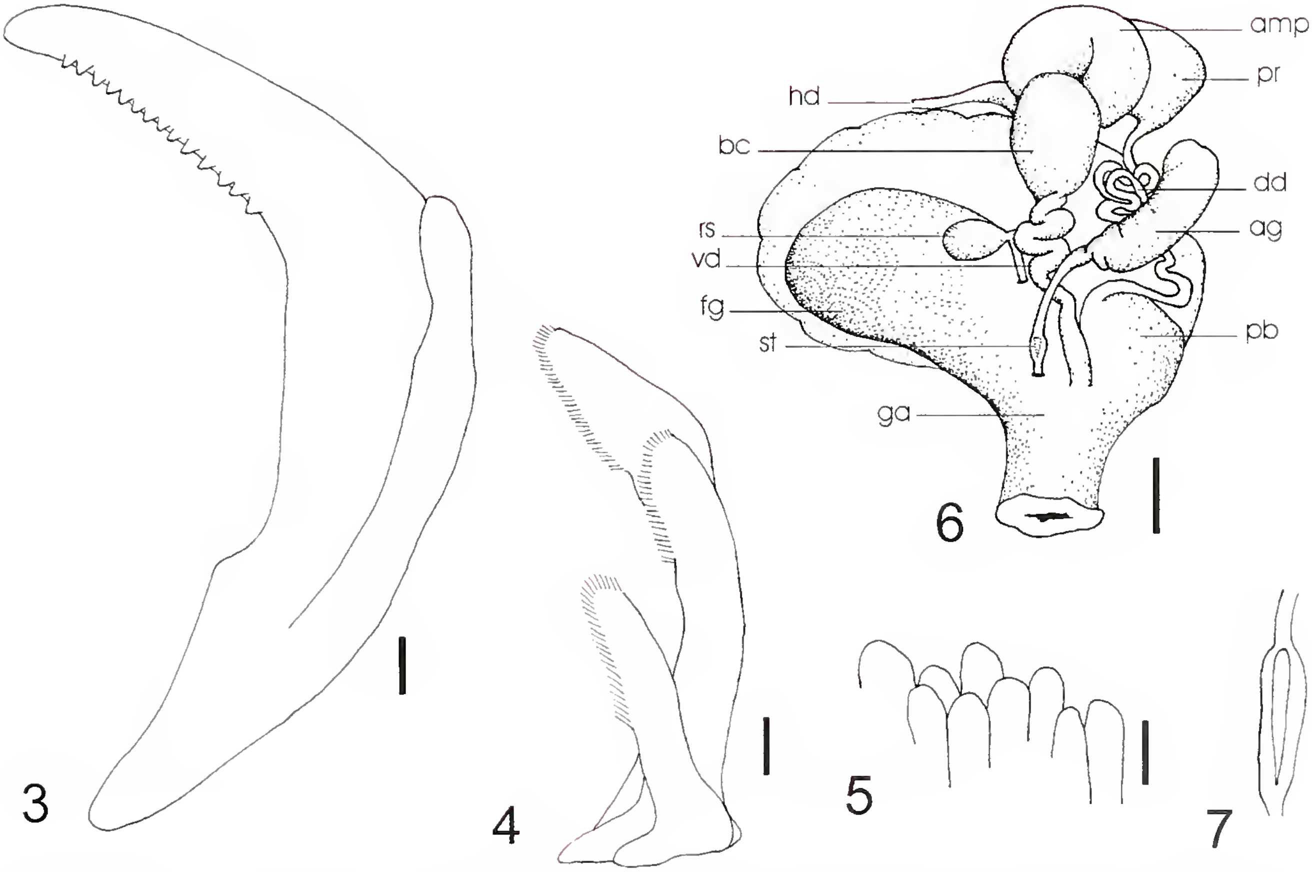
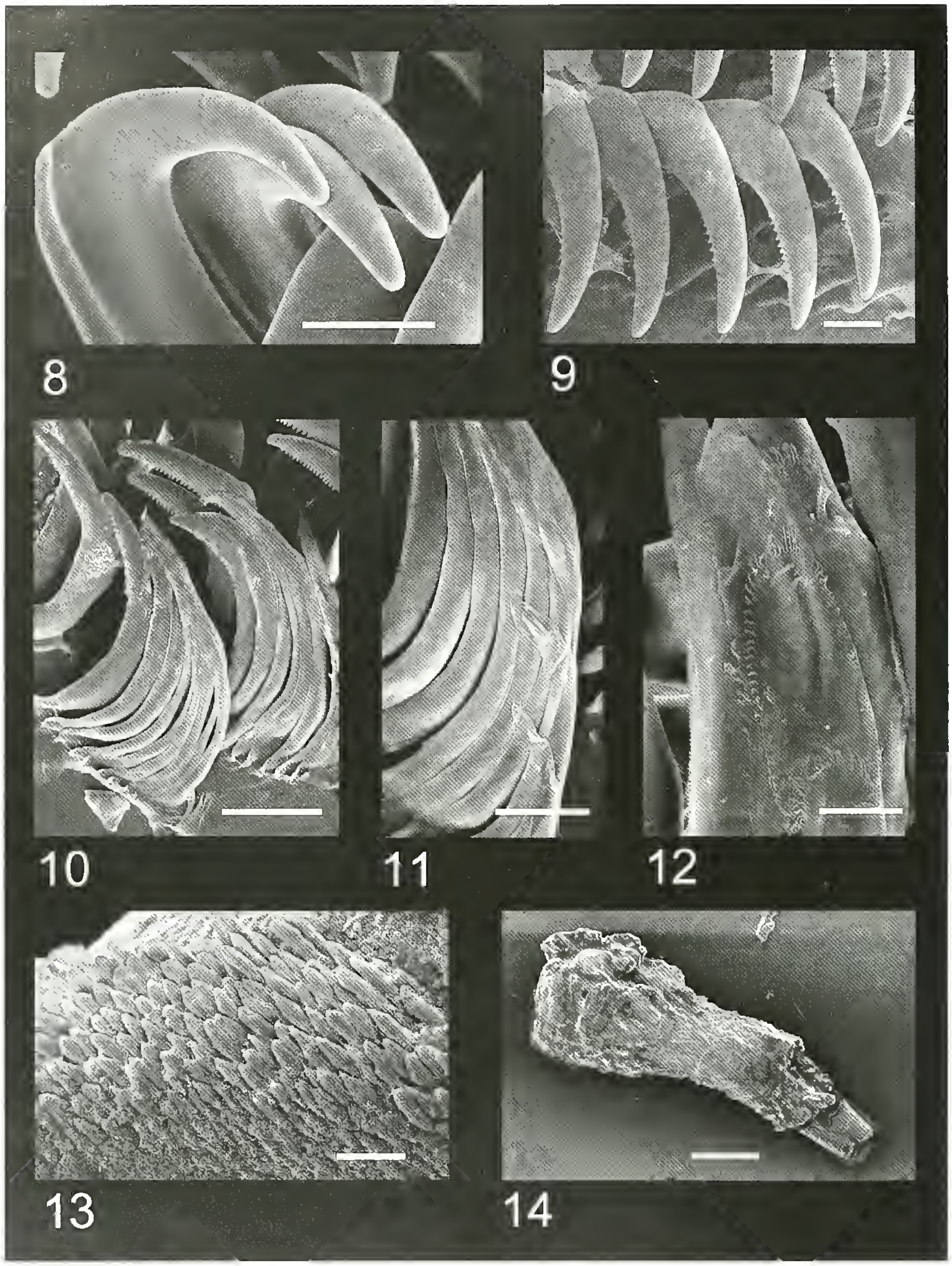


Figure 1–2. *Hoplodoris hansrosaorum*. Living holotype, 27 mm length. **1.** Dorsal view. **2.** Ventral view.



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 bulb; **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.



Figures 8–14. *Hoplodoris hansrosaorum*. **8.** Inner lateral teeth, showing the inner margin of the cusp. **9.** Middle lateral teeth. **10–12.** Outer lateral teeth. **13.** Jaw rodlets. **14.** Stylet with broken tip. Scale lines (8, 9, 11, 13) = 20 µm; (10, 14) = 50 µm; (**12**) = 10 µm.

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.*

	H. hansrosaorum	*H. armata*	*H. bifurcata*	*H. bramale*
References	Domínguez et al. (present study)	Baba, 1993	Fahey and Gosliner, 2003	Fahey and Gosliner, 2003
Distribution	Brazil	Japan	Hawaii, Japan, Philippines and Okinawa	Pacific Coast of Costa Rica
Ground color of dorsum	Brown orange central dorsum, and whitish orange towards the mantle edge	Yellowish gray with some brown flecks	Gray with mottled shades of darker grays and reddish-browns. Central red-brown band	Brown or tan
Tubercle color	Brown orange, with a white ring at the base	Brown with a white ring basally. Some specimens prominently capped with chocolate brown	With a white ring at the base, followed by a reddish-brown or tan ring, and a white tip	Brown with a white ring at the base
Tubercles morphology	Rounded	Rounded of different sizes	Large, round and tapered	Large and rounded
Rhinophore color	Orange with cream tip	Dark yellowish gray	Tan color with white tip	Brown with a white tip
Branchial leaf color	Anterior leaves, yellow and middle and posterior leaves orange	Darker yellowish gray leaves	Tan with whitish flecks the anterior leaves. Red-brown the posterior	Light tan
Radula	Formula: 24 × 31.0.31. Middle lateral teeth with about 14 denticles. The eight outermost lateral teeth are elongated plates with denticles. No hamate.	Formula: 45 × 50–60.0.50–60. Smooth teeth	Formula: 25 × 31.0.31. Innermost lateral tooth bifid. Middle radular teeth with 5–8 denticles. Two or three outermost teeth shorter and denticlate	Formula: 28 × 38.0.38. Innermost and middle teeth smooth. Two outermost teeth smaller and denticulate
Jaw rodlets	With rounded and irregular tip	Fibrous	Irregularly tipped	Irregularly tipped and with irregular edges
Accessory gland	One long large gland	Two glands	One large and bulbous gland	Two bulbous glands
Receptaculum seminis	Much smaller than the bursa copulatrix	Small and elongate	Much smaller than the bursa copulatrix	About the same size as the bursa copulatrix
Ampulla	Bulbous, doubled on itself	Elongated	Long, thin and tubular	Long, thin and tubular

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 Gosliner, 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 toward 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 rodlets 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 receptaculum seminis is about the same size as the bursa copulatrix. However, *H. hansrosaorum* has a thick ampulla, one accessory gland, and the receptaculum 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.*

H. estrelyado	*H. flammea*	*H. grandiflora*	*H. nodulosa*
Gosliner and Behrens, 1998; Fahey and Gosliner, 2003	Fahey and Gosliner, 2003	Fahey and Gosliner, 2003	Fahey and Gosliner, 2003
Philippine Islands, Western Australia, Vietnam, Indonesia, Marshall Islands, Solomon Islands, Coral Sea	Indonesia	Hawaii, Philippines, Tanzania, Palau, Mauritius, Kerama Island and Madagascar	Eastern Australia, Western Australia and New Zealand
Tan with brown and white specks	Reddish-mottled brown or tan. Bright red central dorsum, with white areas around them	Brown or tan. Some specimens with dark spots near the mantle edge. Others with a dark ring of tubercles on dorsum	Gray to yellows and reddish-browns, with mottled shades of darker hues. Color more distinct on the central dorsum
White patch with yellow center, surrounds a medial group of brown tubercles. Some white, and tan tubercles.	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.	Some specimens with areas of white tubercles as perpendicular rays along the mantle edge	On the central dorsum the tubercles have the same coloration of mantle. Tubercles with white ring at base towards the mantle edge
Large tapering tubercles	Large and rounded	Large and rounded	Large, round and tapered
Reddish brown with white specks	Tan and brown with white tip	Light tan with white tip	Tan with a white tip
Tan with brown and white specks	Light gray with tan tips	Light tan with frosted tips	Tan anterior leaves with whitish flecks. The posterior leaves can be a darker color
Formula: 26 × 65.0.65. Innermost lateral teeth with two denticles on outer edge. Middle teeth with up to 11 denticles. Outermost teeth with 6–11 denticles	Formula: 31 × 50.0.50. Innermost lateral tooth with a secondary cusp. Middle lateral teeth with about 8 denticles. Five outermost teeth small and denticulate	Formula: 26–40 × 40–116.0.116–40. Innermost lateral teeth with or without denticles. Middle lateral teeth with up 14 denticles. Two or three outermost teeth hamate with denticles.	Formula: 25 × 53.0.53. Smooth innermost and middle teeth. Four outermost lateral teeth short and denticulate
Irregularly tipped	Irregularly tipped and with knurls along the length	Irregularly tipped	Irregularly tipped
One very large irregularly-shaped gland	One bulbous gland	One long and tubular gland	Two long and bulbous glands
Smaller than the bursa copulatrix	About half the size of the bursa copulatrix	Much smaller than the bursa copulatrix	Much smaller than the bursa copulatrix
Thick and tubular	Long, thin and tubular	Thick and tubular	Long and tubular

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* (Baba, 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 radular morphology differs between these species. The innermost lateral tooth of *H. bifurcata* is bifid, the middle teeth have a cusp with 5–8 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 tan-colored rhinophores and tan gill leaves with whitish flecks. Furthermore, the four outermost radular teeth of *H. nodulosa* are denticulate (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. estrelyado* Gosliner and Behrens, 1998, *H. flammea* Fahey and Gosliner, 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.

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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 thiarid *Melanoides 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: Melanoides 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, Bronmark, 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 *Melanoides tuberculata* (Müller, 1774), which is native to the Middle East (Pointier, 1999), has invaded North America (Murray, 1964; Murray, 1971), South America (Pointier et al., 1994; De Marco, 1999; Giovanelli, 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 (7–40°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 superfamily Heterophyidae, which are vectors of intestinal flukes of animals and humans, e.g., *Metagonimus yokogawai* (Murray and Stewart, 1968). Other trematodes include *Philophthalmus megalurus* (family Philophthalmidae), which affects the nictating 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).

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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 χ^2 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 Tayuon, En um Sidra, En Saharon and Avoka (Figure 1). Since only three *T. granifera* individuals were found in En Tayuon 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 saulcyi* (Bourguignat, 1853) and *Theodoxus jordani* (Sowerby, 1836) (Figure 2). Additionally, there were two species of which only a few individuals were found, *Helcobaia contempta* (Dautzenberg, 1894) and *Melanopsis buccinoidea* (Olivier, 1901).

Species abundances differed significantly between En Saharon and Avoka (χ^2=389.3; df=5; P<0.001). Specifically, *T. granifera* (Fisher's exact test; P<0.001), *M. buccinoidea* (Fisher's exact test; P=0.004), *T. jordani* (Fisher'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 saulcyi* (Fisher's exact test; P<0.001) were more common in En Saharon.

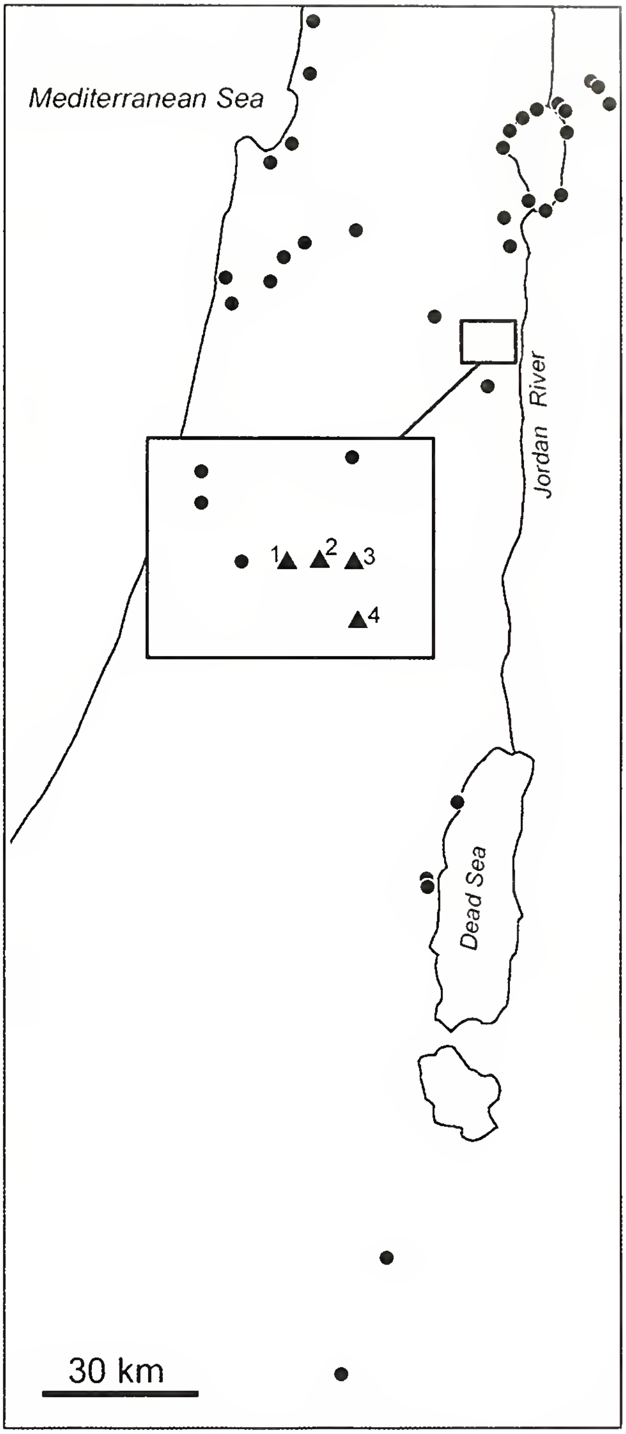

Figure 1. Distribution of sampling sites in Israel: (1) En Tayuon, (2) Avoka, (3) En um Sidra and (4) En Saharon. Due to the resolution of the map, some data points represent more than one sampling site.

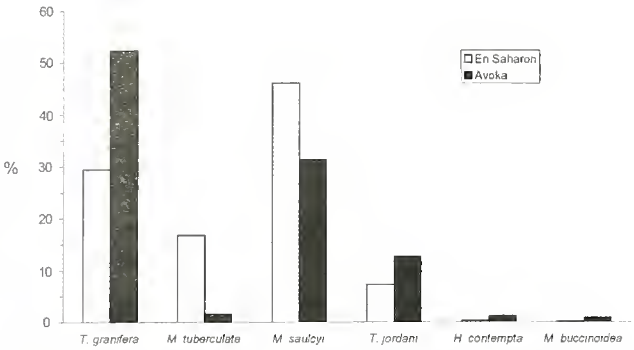

Figure 2. Relative species abundances in En Saharon and Avoka.

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

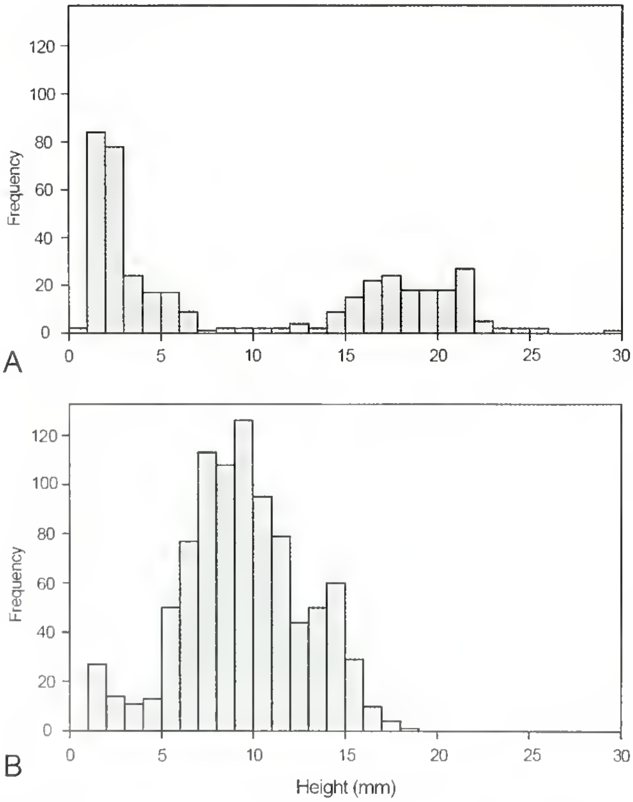

Figure 3. Size distribution (mm) of *Tarebia granifera* in (A) En Saharon and (B) Avoka.

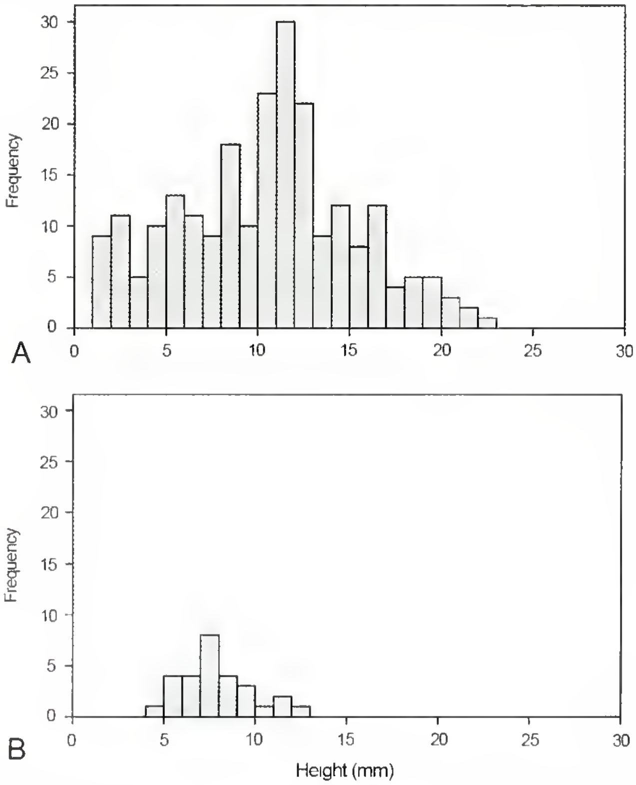

Figure 4. Size distribution (mm) of *Melanoides tuberculata* in (A) En Saharon and (B) Avoka.

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 Box-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 $F = 2.6$; $df_{1,2} = 3262$; $P = 0.054$.

Source	df	Sum of squares	F-ratio	*P*
Whole model	4	23585.5	56.3	<0.001
Shell height	1	9142.4	87.3	<0.001
Habitat	1	1587.6	15.2	<0.001
Species	1	34.5	0.3	ns
Habitat × Species	1	213.6	2.0	ns
Error	261	27344.6		

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/m^2; 52.4%) was more than twice that in En Saharon (511 snails/m^2; 29.5%), whereas the density of *M. tuberculata* in Avoka (35 snails/m^2; 1.6%) was almost tenfold less than in En Saharon (290 snails/m^2; 16.7%). 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 molluscivores in either site. Additionally, my 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 philophthalmid eye flukes. These parasites are known in Israel from both *M. tuberculata*, which hosts *Philophthalmus distomatosa* (Radev, Kanev, and Gold, 2000) and *M. buccinoidea*, 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 buccinoidea* were not found to be infected with *Philophthalmus*. Since *T. granifera* has been found to host *Philophthalmus megalurus* 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).

Tarebia 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 Wopschall, 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; Chrosciechowski, 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; Chaniotis *et al.*, 1980b). It has also been suggested that *T. granifera* is responsible for the disappearance of the endemic freshwater snail *Hemisinus cubanianus* (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 Nadasan, 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 snail hosts of schistosomiasis, *Biomphalaria glabrata* (Say, 1818) and *B. straminea* (Dunker, 1848) (Butler et al., 1980; 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; Cowie, 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.

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Notice

American
Malacological
Society

AMS 2007–Antwerp, Belgium
15–20 July 2007

WCM
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 Geiger)
- "Molluscs as models in evolutionary biology" (Matthias Glaubrecht and Thomas von Rintelen)
- "Inventorying 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 deeply 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 washbowl 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 €47.5 (singles) 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/zoology/unitas/congress.html#content.

Please join us in Antwerp!

Paula M. Mikkelsen
AMS President

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GASTROPODA

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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 8½ × 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.

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.

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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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