THE VELIGER

The Veliger 46(4):332–350 (October 6, 2003)

Acanthina Fischer von Waldheim, 1807 (Gastropoda: Muricidae), an Ocenebrine Genus Endemic to South America

THOMAS J. DEVRIES

Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington 98195, USA[1]

Abstract. The endemic South American muricid genus, *Acanthina* Fischer von Waldheim, 1807, is re-evaluated using characters of fossil and Recent shells. Three new taxa from Peru and Chile are described: *A.* ***triangularis***, sp. nov. (late Pliocene), *A.* ***obesa***, sp. nov. (late Miocene to early Pliocene), and *A.* ***rugosa***, sp. nov. (late Miocene). These species and the late Oligocene to middle Miocene *A. katzi* Fleming, 1972, are found in deposits that indicate nearshore environments like those favored by the extant *A. unicornis* (Bruguière, 1789) and *A. monodon* (Pallas, 1774). The pace of acanthinine evolution matches that of contemporaneous muricid genera in western South America.

INTRODUCTION

Acanthina Fischer von Waldheim, 1807, comprises species of ovate ocenebrine muricids (Kool, 1993) with a labral tooth that range from southern Peru to southeastern Argentina (Dall, 1909; Carcelles, 1954; Figure 1). Most authorities recognize two modern subspecies or species (Carcelles, 1954; Dell, 1971; Wu, 1985). Absent biological data, the two taxa, largely disjunct geographically, are herein treated as separate species. *Acanthina monodon* (Pallas, 1774) [synonym: *A. calcar* (Martyn, 1784)], the type species, encompasses specimens from Argentina and southern Chile with imbricate spiral cords and a relatively thin outer lip. *Acanthina unicornis* (Bruguière, 1789) [synonym: *A. crassilabrum* (Lamarck, 1816)] includes specimens from southern Peru to southern Chile that generally lack imbrication and possess a thick, often dentate outer lip.

Fossils of *Acanthina* have long been known from Pleistocene and upper Pliocene strata of Chile (Philippi, 1887; Herm, 1969). Most were assigned to one of many Recent forms (Sowerby, 1835) that are best synonymized with *A. monodon* or *A. unicornis*. An older species, *A. katzi* Fleming, 1972, occurs in lower Miocene deposits of Chiloe, Chile (Watters & Fleming, 1972) and lower to middle Miocene deposits of southern Peru (DeVries & Vermeij, 1997).

This paper describes three new species of *Acanthina* from upper Miocene and Pliocene strata in Peru and Chile, documents a range extension of the genus into northernmost Peru during the late Pliocene, and summarizes the evolutionary history of the genus.

[1] Mailing address: Box 13061, Burton, Washington 98013, USA.

GEOLOGY

The Cenozoic stratigraphy and paleontology of forearc basins with *Acanthina*-bearing deposits was described by Muizon & DeVries (1985), DeVries (1988, 1998), and Dunbar et al. (1990) for Peru and by Tavera (1979) for Chile. The geological setting of Lo Abarca, an upper Miocene Chilean locality with *Acanthina,* was discussed by Covacevich & Frassinetti (1990).

MATERIALS AND METHODS

Specimens described in this study were found by the author, V. Alleman, and J. Macharé. Comparative material was provided by the California Academy of Sciences, Los Angeles County Museum of Natural History, and Museo Nacional de La Plata (Argentina).

Locality descriptions are in the appendix. Lengths (L) are measured from the apex of the spire to the end of the siphonal canal, parallel to the axis of coiling. Widths (W) are measured at right angles to the length between the farthest points left and right of the coiling axis. Both are reported in millimeters (mm). Dimensions diminished by breakage are enclosed by parentheses. Types and figured specimens are deposited at the Burke Museum of Natural History and Culture (University of Washington, Seattle, Washington); Departamento de Vertebrados, Museo de Historia Natural (Universidad de San Marcos, Lima, Peru); the Museo de Historia Natural, Universidad Ricardo Palma (Lima, Peru); and the Museo Nacional de Historia Natural (Santiago, Chile).

Abbreviations used for museums and collections are as follows: LACM—Los Angeles County Museum of Natural History, Los Angeles, California, USA; MUSM INV—Departamento de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, Lima, Peru; OSU—Orton Museum, Ohio State University, Columbus, Ohio, USA; SGO.PI.—Museo Nacional de Historia Natural, Santiago, Chile; UCMP—University of California at Berkeley, Museum of Paleontology, Berkeley, California, USA; UNLP—Museo Nacional de La Plata, Universidad de La Plata, Argentina; USNM—Department of Paleobiology, United States National Museum, Washington, D.C., USA; UWBM—Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA; VE—Private collection, V. Alleman, Facultad de Biología, Universidad Ricardo Palma, Lima, Peru.

SYSTEMATIC PALEONTOLOGY

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossman, 1903
Genus *Acanthina* Fischer von Waldheim, 1807

Acanthina Fischer von Waldheim, 1807:174.

Type species: *Buccinum monodon* Pallas, 1774:33, pl. 3, figs. 3, 4.

Original description: "Coquille ovale. Ouverture se terminant inférieurement en un canal très court, oblique, peu échancré à l'extrèmité. Bord gauche calleux, formant un bourrelet distinct de la columelle. Lèvre droite épaisse, munie près de la base d'une épine très longue."

Diagnosis: Shell with short, unconstricted or slightly constricted base. Two primary spiral cords on early whorls, one at shoulder, the other anterior to first; these and additional spiral cords evident on adult body whorl, if not subdued or obsolete. Columella excavated. Thin spiral groove near base ending in labral tooth inside outer lip.

Additional description: Shell to 60 mm long; trigonal, biconic, or fusiform; anterior slightly constricted or unconstricted. Spire 10 to 30 percent of shell length. Sutures impressed to appressed, usually adherent just below shoulder. Protoconch heterostrophic, submerged, absent on fossils. Teleoconch with three to five whorls. Shoulder angulate or rounded. Periphery near or posterior to midpoint of body whorl. Growth lines prosocline, sometimes lamellose. Axial sculpture lacking or, rarely, with irregular swellings. Spiral sculpture of two rounded primary cords on juveniles, one at shoulder, the other anterior to first; both sometimes obsolete or joined by other spiral cords of equal or lesser strength on adults. Thin spiral groove near base, ending in labral tooth emerging from within outer lip. Aperture ovate. Outer lip sometimes thickened, beveled, dentate within, and/or crenulate at outer edge. Parietal callus weak. Columella concave to straight, smooth, excavated along entire length. Fasciole short, arched, usually bordered posteriorly by sharp ridge of growth-line chevrons. Siphonal canal short, narrow, open.

Discussion: Species from Central and North America once placed in *Acanthina* are notable for combinations of prominent and regular axial sculpture, glossy apertures, labral teeth at the edge of the outer lip, and/or broad primary spiral cords not seen in species from South America. Hence, they have been assigned by others to different genera or subgenera: *A. brevidentata* (Wood, 1828) to *Thais* Röding, 1798, by Cooke (1919) and Wu (1985) or *Acanthais* Vermeij & Kool, 1994, based on anatomy and radular characters; *A. tuberculata* (Sowerby, 1835) to *Mancinella* Link, 1807, by Wu (1985) based on similar criteria (Vermeij & Kool, 1994); and *Acanthina angelica* Oldroyd, 1918, *A. punctulata* (Sowerby, 1835), *A. lugubris* (Sowerby, 1821), and *A. paucilirata* (Stearns, 1871) to *Acanthina* (*Acanthinucella*) or simply *Acanthinucella* Cooke, 1918, based on shell morphology and radular features (Cooke, 1918; Wu, 1985; Vermeij, 1993). *Acanthina spirata* (Blainville, 1832) has both been grouped with and separated from *A. punctulata* (e.g., Grant & Gale, 1931; McLean, 1969). *Acanthina emersoni* Hertlein & Allison, 1959, a Pliocene species from California, was thought by its authors to be related to *A. spirata*. *A. angelica* and *A. lugubris* have recently been placed in the new genus *Mexacanthina* Marko & Vermeij, 1999.

Toothed specimens from Chile and Peru with a deeply constricted base assigned to *Nucella* (*Acanthinucella*) by Herm (1969) and *Acanthina* (*Acanthinucella*) by DeVries (1986) are now placed in *Herminespina* DeVries & Vermeij, 1997.

Occurrence: Uppermost Oligocene to upper Miocene: southern Peru to southern Chile. Pliocene: northern Peru to central Chile. Pleistocene to Recent: southern Peru to southeastern Argentina (Figure 1).

Acanthina monodon (Pallas, 1774)

(Figures 2–7)

Buccinum monodon Pallas, 1774:33, pl. 3, figs. 3, 4.
Buccinum calcar Bruguière, 1789:253, volume 1, figure 10; volume 2, figure 50 [attributed to Martyn (1784)].
Nucella (*Acanthina*) *calcar* (Martyn). Carcelles, 1954:pl. 1, figs. 5–11; pl. 2, figs. 12–22. (See extensive synonymy.)
Not *Nucella* (*Acanthina*) *crassilabrum calcar* (Martyn). Herm, 1969:pl. 17, figs. 7–9. (correct identification is *Acanthina unicornis*).
Acanthina monodon monodon (Solander, 1786). Wu, 1985: 56, figs. 13–14, 24, 34, 52–58, 71.
Acanthina monodon (Pallas, 1774). Kool, 1993:229, figs. 27A–D.

Diagnosis: Sculpture typically imbricate; primary and secondary spiral cords numerous. Outer lip usually not thickened.

Description: Shell to 60 mm long, thin to moderately thick-shelled; adults ovate, spire 20–30 percent of length. Sutures slightly to moderately impressed. Shoulder evenly, broadly rounded, rarely with weak sutural platform. Spiral sculpture imbricate; about 13 primary cords between shoulder and spiral groove, variably alternating with secondary cords of varying strength. Five to seven

Figure 1. Distribution of Recent *Acanthina unicornis* and *A. monodon*. Pacific Neogene forearc basins with *Acanthina*-bearing marine sediments are also shown.

secondary spiral cords on base, three to four posterior to shoulder, with or without a single primary spiral cord. Outer lip in adults generally less than 4 mm thick, thin or slightly thickened and weakly beveled; outer edge crenulate; inner edge weakly dentate (seven to 12 teeth) or smooth. Labral tooth well developed. Columella straight to concave; excavated but not broadly. Fasciolar ridge poorly developed.

Whorls of small juveniles with five to seven primary spiral cords posterior to spiral groove. Two spiral cords, one at shoulder and another anterior to shoulder, sometimes more prominent (LACM 72-157-2e, Figure 5).

Discussion: *Acanthina monodon* at present occupies intertidal and shallow subtidal habitats from the Chonos Archipelago of southern Chile to Santa Cruz Province, Argentina (Carcelles, 1954). The species has been found on upper Pleistocene terraces in Argentina (UNLP 1407b and UNLP 1407c, Figures 6, 7), but not in older deposits (Pastorino, 1994). Some Recent specimens from southern Chile have a slightly thickened and dentate outer lip (LACM 54679a, Figure 2), characters shared with many specimens of *A. unicornis*.

Material: LACM 72-157.2a, L 52.7, W 39.0; LACM 72-157.2b, L 39.4, W 28.6; LACM 72-157.2c, L 30.6, W 22.4; LACM 72-157.2d, L 28.0, W 21.1; LACM 72-157.2e, L 11.1, W 7.5; LACM 72-157.2f, L 9.5, W 5.7; LACM 54679a, L 50.0, W 35.3; LACM 54679b, L 46.0, W 31.4; UNLP 1407a, L 42.9, W 28.9; UNLP 1407b, L 42.9, W 28.8; UNLP 1407c, L 27.5, W 18.4; UNLP 1398, lot of six fragments.

Occurrence: Upper Pleistocene to Recent. Southern Chile to southeastern Argentina.

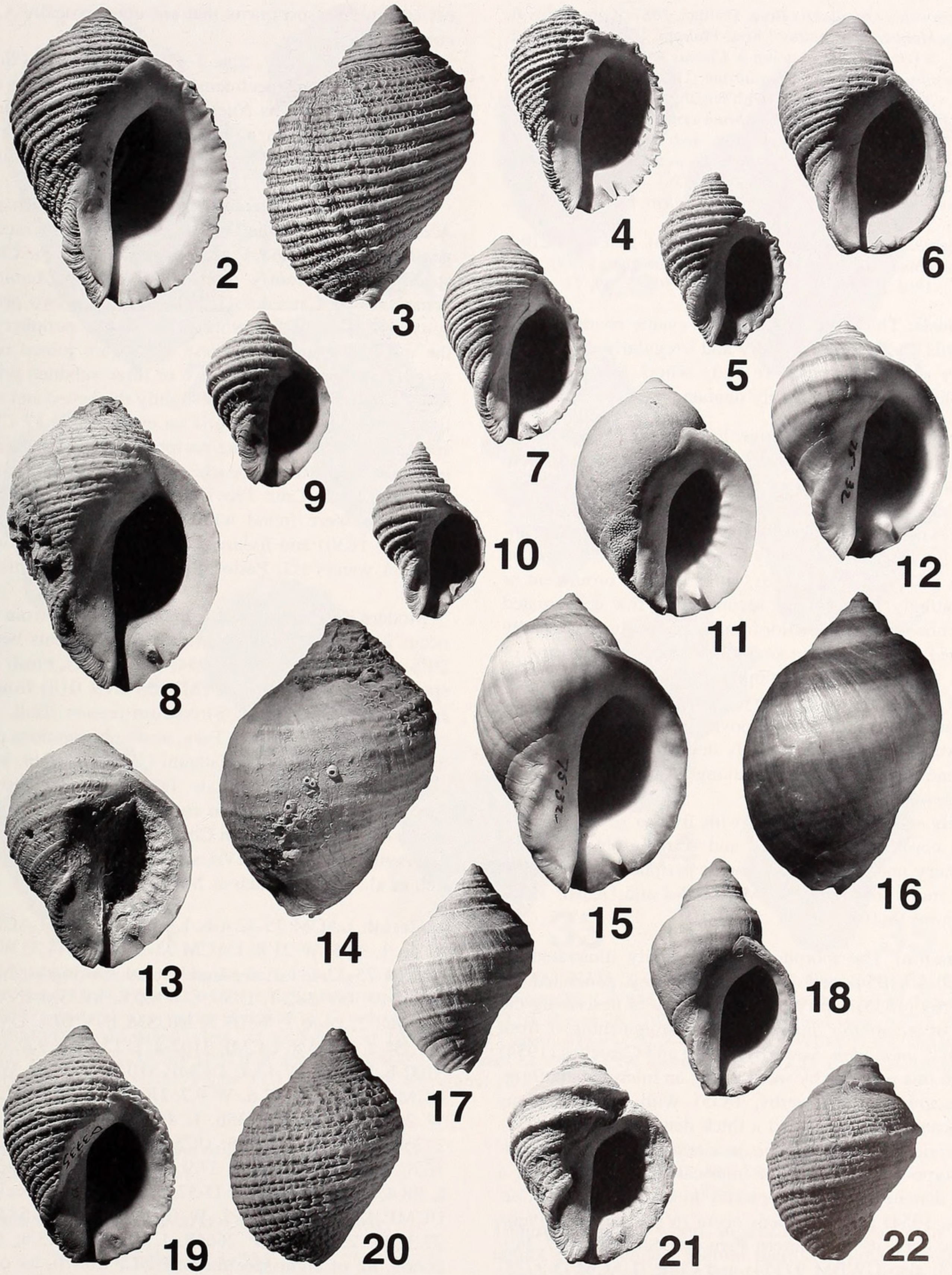
Acanthina unicornis (Bruguière, 1789)

(Figures 8–22)

Buccinum unicorne Bruguière, 1789:254.
Monoceros crassilabrum Lamarck, 1816:pl. 396, figs. 2a,b.
Monoceros acuminata Sowerby, 1835:50.
Monoceros citrinum Sowerby, 1835:51.
Monoceros costatum Sowerby, 1835:50.
Monoceros globulus Sowerby, 1835:50.
Monoceros ambiguus Sowerby, 1846:261, pl. 4, figs. 66, 67.
Monoceros unicorne Sowerby. Hupé, 1854:194.
Monoceros ambiguus Sow. Philippi, 1887:56, pl. 7, fig. 1.

→

Figures 2–7. *Acanthina monodon*. Figure 2. LACM 54679a, apertural view, ×1.0. Figure 3. LACM 54679a, abapertural view, ×1.0. Figure 4. LACM 72-157.2c, apertural view, ×1.12. Figure 5. LACM 72-157.2e, apertural view, ×2.69. Figure 6. UNLP 1407b, apertural view, ×0.96. Figure 7. UNLP 1407c, apertural view, ×1.25.
Figures 8–22. *Acanthina unicornis*. Figure 8. UWBM 97373, apertural view, ×1.0. Figure 9. UCMP 3102-d, apertural view, ×2.18. Figure 10. UCMP 3102-a, apertural view, ×1.87. Figure 11. LACM 75-32.4-b, apertural view, ×1.02. Figure 12. LACM 75-32.4-c, apertural view, ×1.30. Figure 13. MUSM INV 017, apertural view, ×1.0. Figure 14. UWBM 97373, abapertural view, ×1.0. Figure 15. LACM 75-32.4-d, apertural view, ×1.13. Figure 16. LACM 75-32.4-d, abapertural view, ×1.07. Figure 17. UCMP 3102-b, abapertural view, ×1.81. Figure 18.



UNLP 26668, apertural view, ×0.92. Figure 19. UCMP D-3735a, apertural view, ×0.96. Figure 20. UCMP D-3735a, abapertural view, ×0.96. Figure 21. UCMP D-3735f, apertural view, ×1.25. Figure 22. UCMP D-3735f, abapertural view, ×1.25.

Monoceros crassilabris Brug. Philippi, 1887:56, pl. 6, fig. 6.
Not *Monoceros costatus* ? Sow. Philippi, 1887:56, pl. 5, fig. 9 (correct identification is *Chorus* sp.).
Nucella (*Acanthina*) *crassilabrum* (Lam.). Carcelles, 1954: 257, pl. 1, figs. 1–4 (with lengthy synonymy).
Nucella (*Acanthina*) *crassilabrum crassilabrum* (Lamarck). Herm, 1969:138, pl. 17, figs. 4a,b 6a,b.
Nucella (*Acanthina*) *crassilabrum acuminata* (Sowerby). Herm, 1969:140, pl. 17, figs. 5a,b.
Nucella (*Acanthina*) *crassilabrum calcar* (Martyn). Herm, 1969:pl. 17, figs. 7–9.
Acanthina crassilabrum (Lamarck, 1816). Dell, 1971:210.
Acanthina monodon crassilabrum (Lamarck, 1789). Wu, 1985:58, figs. 15–17, 23, 35–37, 50–51, 59, 71.

Diagnosis: Thick-shelled; shoulder evenly rounded. Spiral cords numerous, unequally and irregularly developed, usually subdued over entire body whorl. Inner edge of outer lip sometimes strongly dentate.

Description: Shell to 60 mm long, broadly fusiform to ovate, base of body whorl usually slightly constricted. Adults thick-shelled. Spire 25–30 percent of length. Sutures appressed to impressed. Shoulder evenly rounded, rarely with sutural platform; periphery at or slightly anterior to midpoint of body whorl. Spiral sculpture on adults of 20–25 spiral cords, either equally prominent or alternatingly primary and secondary, a few accentuated with chocolate brown color in modern specimens; usually subdued or obsolete but sometimes strongly imbricate or rarely with two well developed primary spiral cords between shoulder and periphery. Three to five subdued spiral cords anterior to spiral groove. Outer lip thick, strongly beveled, sometimes strongly dentate, with eight to 11 elongate teeth evenly spaced along aperture. Labral tooth well developed.

Early whorls in juveniles with five to seven primary spiral cords between suture and spiral groove; cord at periphery and another anterior to peripheral cord sometimes more prominent (UCMP 3102-d and UCMP 3102-a, Figures 9, 10).

Discussion: The morphological diversity illustrated by Carcelles (1954) and lengthy synonymy generated by Sowerby (1835) testify to the difficulty of describing the shell of *Acanthina unicornis* and distinguishing it from that of *A. monodon.* Sowerby (1835) and Carcelles (1954) solved this problem by recognizing an intermediate form, "*A. acuminata*" (Sowerby, 1835), with both numerous imbricate spiral cords and a thick dentate outer lip.

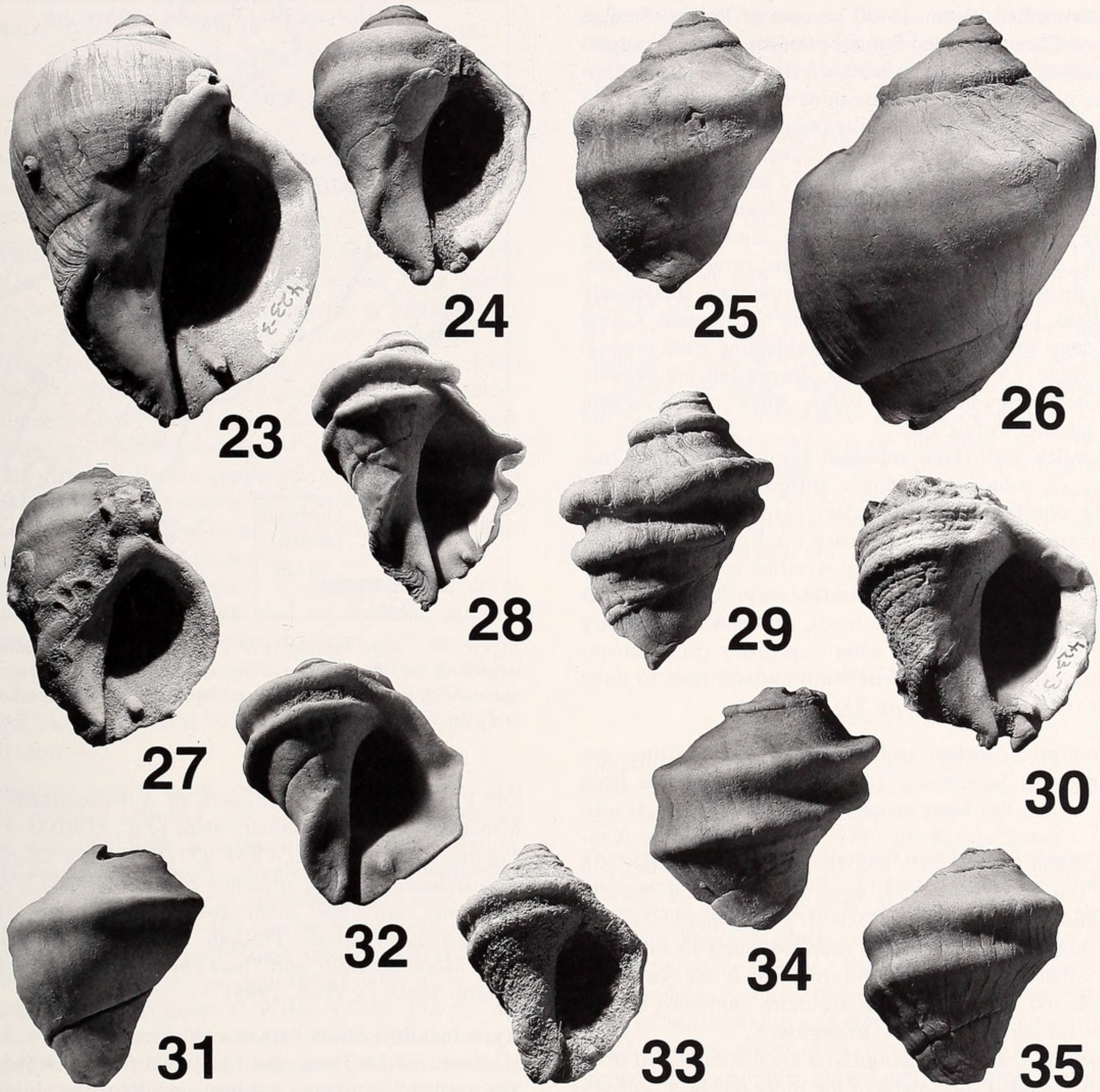
Individuals of *Acanthina unicornis* with the "*acuminata*-type" combination of imbricate spiral cords and a thick dentate outer lip live today in southern Chile (Carcelles, 1954) and specimens occur in Pliocene and Pleistocene deposits of southern Peru (MUSM INV 017, Figure 13; also UWBM 97374) and Chile (LACM D-3735-a; Figures 19, 20). In Peru, imbricate adult specimens of *Acanthina* occur in upper Pliocene strata (UWBM 97373, Figures 8, 14; also UWBM 97374) together with the oldest acanthinine specimens that are unequivocally *A. unicornis.*

Herm (1969: pl. 17, figs. 7–9) illustrated two Pliocene "*acuminata*-type" specimens of *A. unicornis* from Chile but identified them as *Nucella* (*Acanthina*) *crassilabrum calcar,* reserving the name "*N.* (*A.*) *crassilabrum acuminata*" for an early Pleistocene specimen that should be assigned to his *N.* (*A.*) *crassilabrum costata.*

Pleistocene specimens of non-imbricate, high-spired *Acanthina* from marine terraces in Chubut Province, Argentina (UNLP 26668, Figure 18) resemble some Chilean specimens erroneously referred to *Nucella* (*Acanthina*) *acuminata* by Carcelles (1954). They have two primary spiral cords on earlier whorls, one at the periphery and the other anterior to the first. These are joined on the anterior of later whorls by two or three subdued primary spiral cords. The outer lip is slightly thickened and sometimes finely dentate. There is no evidence on 17 Chubut specimens of the imbricate sculpture that characterizes *A. monodon* from Recent beaches or Pleistocene marine terraces in Santa Cruz Province, Argentina. The Chubut specimens were found with specimens of *Tegula atra* (Lesson, 1830) and fissurellids now encountered only in Chilean waters (G. Pastorino, personal communication, 2002).

Modern specimens of *Acanthina unicornis* from Chile occur in intertidal and sublittoral environments between 29°S and 42°S (Carcelles, 1954; Dell, 1971). Fresh beach specimens of *A. unicornis* (MUSM INV 018) from San Juan de Marcona (15°27′S) confirm reports (Dall, 1909) of the species in southern Peru, as do observations of live intertidal individuals at Matarani (17°S; M. Rabi, written communication, 1997). Late Pliocene and Pleistocene specimens are known from coarse-grained bioclastic deposits throughout northern Chile (Herm, 1969) and southern Peru (Muizon & DeVries, 1985; DeVries, 1986; Ortlieb et al., 1990; Ortlieb & Macharé, 1990).

Material: LACM 75-32.4-b, L 37.0, W 28.4; LACM 75-32.4c, L 30.5, W 21.8; LACM 75-32.4-d, L44.3, W 29.8; LACM 75-32.4, lot of 14 additional specimens; MUSM INV 017, DV 382-1, L 39.9, W 30.8; MUSM INV 018, DV 468-2, L 46.7, W 37.8; MUSM INV 019, DV 812-1, L 54.2, W 43.8; UCMP 3102-a, L 15.1, W 9.4; UCMP 3102-b, L 18.8, W 13.1; UCMP 3102-c, L 31.2, W 22.8; UCMP 3102-d, L 13.6, W 9.2; UCMP D-3735a, L 40.9, W 29.2; UCMP D-3735b, L 45.1, W 31.0; UCMP D-3735c, L (34.3), W 26.6; UCMP D-3735d, L (18.4), W 16.6; UCMP D-3735e, L 37.9, W 27.5; UCMP D-3735f, L 28.4, W 21.8; UCMP D-3735, lot of two specimens; UCMP D-5826a, L 44.5, W 31.0; UCMP D-5826b, L 27.3, W 22.3; UNLP 26668, L 43.0, W 25.6; UNLP 26669, lot of eight specimens; UNLP 26670, lot of nine specimens; UWBM 97372, DV 468-2, L 36.0, W 27.1; UWBM 97373, DV 812-1, L 48.0, W 34.1; UWBM 97374, JM84 319B, L 35.1, W 25.7.



Figures 23–35. *Acanthina* ***triangularis*** DeVries, sp. nov. Figure 23. UWBM 97375, apertural view, ×0.98. Figure 24. OSU 37358, apertural view, ×1.04. Figure 25. OSU 37358, abapertural view, ×1.04. Figure 26. UWBM 97375, abapertural view, ×0.98. Figure 27. OSU 37359, apertural view (suture distorted by growth of balanids), ×1.05. Figure 28. UWBM 97376, apertural view, ×1.32. Figure 29. UWBM 97376, abapertural view, ×1.32. Figure 30. UWBM 97377, apertural view, ×0.94. Figure 31. UWBM 97378, abapertural view, ×1.70. Figure 32. UCMP D-3735-d, apertural view, ×1.83. Figure 33. OSU 37360, apertural view, ×2.23. Figure 34. UCMP D-3735, abapertural view, ×1.83. Figure 35. UWBM 97379, abapertural view, ×1.62.

Occurrence: Upper Pliocene to Recent. Southern Peru to southern Chile.

Acanthina ***triangularis*** DeVries, sp. nov.

(Figures 23–35)

Acanthina triangularis DeVries, 1986:592, pl. 33, figs. 9, 12; pl. 34, figs. 2, 6, 7, 10, 12; pl. 35, figs. 1, 2, 3 (unpublished dissertation).

Nucella (*Acanthina*) *crassilabrum costata* (Sowerby). Herm, 1969:139, pl. 17, figs. 2a, 2b, 3. Not *Monoceros costatum* Sowerby, 1835.

Diagnosis: Body whorl angulate or biangulate in both adults and juveniles. Sutural platform planar or slightly concave. Two primary spiral cords or keels; other spiral sculpture usually subdued or absent.

Description: Shell to 70 mm long; biconic. Adults thin to thick shelled. Spire 25–30 percent of length. Sutures appressed near shoulder. Sutural platform planar or slightly concave, broad, inclined 30–45 degrees. Shoulder angulate; periphery located one-third to one-half length of body whorl from suture, usually coincident with shoulder. Spiral sculpture of primary spiral cord at shoulder, subdued to keeled; another primary cord anterior to first, often reduced to spiral swelling or obsolete. Additional weakly developed secondary spiral cords and tertiary threads, usually obsolete or nearly so; rarely, imbricate. Outer lip angulate or biangulate; sometimes moderately thickened, beveled, neither crenulate nor dentate. Labral tooth deep within outer lip, often projecting from internal spiral ridge. Columella concave, deeply but not broadly excavated. Pseudumbilical callus thick, with arching ridge parallel to fasciole.

Juveniles with three subequal primary cords on first whorls of teleoconch; cords differentiating on later whorls, one becoming secondary cord on expanded sutural platform, another a primary cord on shoulder, and third a primary cord anterior to shoulder cord. Additional secondary cords on larger juveniles and subadults inserted on sutural platform (one cord), between two primary cords (one cord), between anterior primary cord and spiral groove (four to five cords), and on base (two to three cords) (OSU 37360, Figure 33).

Discussion: *Acanthina* ***triangularis*** is not the same costate taxon as Sowerby's (1835) *Acanthina costata* from Chile, which has been synonymized herein with *A. unicornis.* Costate specimens of *A. unicornis,* modern (Carcelles, 1954:figs. 36–43; UCMP 3102-a, unfigured) and fossil (Herm, 1969:pl. 17, figs. 5a, b, termed *Nucella* (*Acanthina*) *acuminata*; UCMP 3735-f, Figures 21, 22) have shoulders that are more rounded, outer lips that are more often dentate, anterior profiles that are less constricted, and spiral cords that are more numerous than is typical for specimens of *A.* ***triangularis***.

Adults of Acanthina ***triangularis*** are distinguished from broadly rounded specimens of the more recent *A. unicornis* and smooth-shelled, tightly rounded specimens of the older *A.* ***obesa*** by their planar sutural platform and two prominent primary spiral cords (or rarely, one: UWBM 97378, Figure 31). Juveniles of *A.* ***triangularis*** and *A.* ***obesa*** are identical, whereas those of *A. unicornis* are more evenly rounded and have several primary spiral cords, rather than two.

The type locality for *Acanthina* ***triangularis,*** north of the Río Chira, northern Peru (4°40′S), is a significant northward range extension for *Acanthina.* Specimens (OSU 37358, Figures 24, 25; OSU 37359, Figure 27) are found in the lowest pebbly sandstone beds of the Taime formation (DeVries, 1986, 1988) with other mollusks, e.g., *Chorus blainvillei* (d'Orbigny, 1842) and *Herminespina mirabilis* (Möricke, 1896), that suggest a late Pliocene age (DeVries, 1997a; DeVries & Vermeij, 1997). A late Pliocene age for specimens of *A.* ***triangularis*** from a marine terrace in southern Peru (e.g., UWBM 97375, Figures 23, 26, and UWBM 97376, Figures 28, 29) is also indicated by the presence of the mollusks *Trachycardium procerum domeykoanum* (Philippi, 1887), *Amiantis domeykoana* (Philippi, 1887), *Concholepas nodosa* Möricke, 1896, and *Thais chocolata* (Duclos, 1832) (Herm, 1969; DeVries, 1995).

Figure 36. Type locality (DV 272/DV 273) of *Acanthina* ***triangularis*** DeVries, sp. nov. Outcrops of basal bioclastic sandstones with *A.* ***triangularis*** occur in quebradas between La Brea and Amotape.

Type locality: Strata between Quebrada Songora, 14 km southeast of La Brea, and Quebrada Cardo Grande, 10 km north of Amotape, northwestern Peru (localities DV 272/273; Figure 36).

Material: OSU 37358, holotype, DV 272/273, L 38.0, W 28.7; OSU 37359, paratype, DV 272/273, L 38.1, W 28.4; OSU 37360, paratype, DV 273-1, L 15.3, W 11.8; MUSM INV 013, DV 423-3, L (30.5), W 24.6; MUSM INV 014, DV 423-3, L (37.2), W 26.5; MUSM INV 015, DV 423-3, L (53.5) W 41.4; MUSM INV 016, DV 423-3, L 26.6 W 22.0; UCMP D-3735-d, Coquimbo, Chile, L (17.6) W 17.6; UWBM 97375, DV 423-3, L 60.9, W 44.5; UWBM 97376, DV 423-3, L (31.2), W 23.1; UWBM 97377, DV 423-3, L 41.6, W 36.0; UWBM 97378, DV 423-3, L (19.8), W 16.3; UWBM 97379, DV 423-3, L 21.1, W 17.6.

Occurrence: Late early to late Pliocene, northern Peru to northern Chile.

Acanthina ***obesa*** DeVries, sp. nov.

(Figures 37–52)

Acanthina obesa DeVries, 1986:591, pl. 34, figs. 1, 2 (unpublished dissertation).

Diagnosis: Shell broadly trigonal; shoulder tightly rounded; usually smooth. Spire usually low. Juveniles with two prominent spiral cords at and anterior to shoulder.

Description: Shell to 50 mm long; broad, width and height of body whorl usually about equal. Base barely constricted. Shell thin to moderately thick. Spire usually 10 to 20 percent of shell length. Sutures appressed. Sutural platform broad, slightly convex, typically inclined less than 30°. Shoulder usually tightly rounded, periphery at midpoint of body whorl. Spiral sculpture usually absent or consisting of weakly developed spiral cords separated by thin grooves. Rarely, sculpture with mix of 25–35 scaly secondary cords and tertiary threads. Outer lip thin or thick, often beveled if latter, inside edge smooth. Columella broadly, deeply excavated.

Juveniles with three primary or secondary spiral cords on sutural platform; primary cord on shoulder; primary cord anterior to shoulder cord with intercalated secondary spiral cord; five or six secondary cords on body whorl; three secondary spiral cords on base (OSU 37368, Figures 38 and 40; UWBM 97380, Figure 41; MUSM INV 012, Figure 43).

Discussion: A low spire, broad sutural platform, and tightly rounded shoulder give specimens of *Acanthina* ***obesa*** a profile with a distinctive posterior inflation. Adults are usually entirely smooth, in contrast with other species of *Acanthina*. Large specimens with high spires (UWBM 97381, Figure 49) can be distinguished from specimens of *A. unicornis* by their smooth shell and thinner, non-dentate outer lips. Specimens with more fully developed spiral sculpture (UWBM 97382, Figures 42, 44) can be separated from those of older *A. katzi* and younger *A. unicornis* by their posterior inflation. Strongly sculptured early Pliocene specimens (OSU 37361, 37362, 37363, Figures 50–52), however, do resemble those of the younger *A.* ***triangularis***.

The oldest Peruvian specimens of *Acanthina* ***obesa*** come from beach coquinas on the eastern flank of Quebrada Riachuelo (Figures 42, 44) that overlie middle Miocene strata containing specimens of *A. katzi*. Farther south, specimens of *A.* ***obesa*** (Figures 37, 39) overlie ash beds at Alto Grande and Aguada de Lomas with ^{40}K-^{39}Ar dates of 9.5 Ma and 8 to 8.8 Ma, respectively (Muizon & DeVries, 1985; Muizon & Bellon, 1986). Numerous specimens of *A.* ***obesa*** (UWBM 97383, Figures 45, 46) are found in lowermost Pliocene strata at Sud-Sacaco (Muizon & DeVries, 1985). The single specimen of *A.* ***obesa*** known from Chile (SGO PI 5750, Figures 47, 48) was found by the author in upper Miocene shell and gravel banks at Lo Abarca (Covacevich & Frassinetti, 1990).

Type locality: Aguada de Lomas, east of intersection of Panamerican Highway with road to Lomas. East slope, south of abandoned HierroPeru road (locality DV 369; Figure 53).

Material: OSU 37361, DV 361-5, L 25.3, W 19.2; OSU 37362, DV 361-5, L 27.4, W 21.7; OSU 37363, DV 361-5, L 24.9, W 20.4; OSU 37365, holotype, DV 369-3, L 40.9, W 36.3; OSU 37366, paratype, DV 370-2, L 35.5, W 31.3; OSU 37368, paratype, DV 370-2, L 16.2, W 13.1; MUSM INV 010, DV 571-1, L (39.3), W 31.9; MUSM INV 011, DV 1230-1, L 38.4, W 31.3; MUSM INV 012, DV 571-1, L 19.6 W 14.8; SGO.PI.5750, Lo Abarca, L 18.7, W 15.0; VE09261a, Aguada de Jahuay, L (46.2), W 40.9; VE09261b, Aguada de Jahuay, L (40.4), W 32.1; VE09261c, Aguada de Jahuay, L 29.7, W 25.8; VE09313, Aguada de Jahuay, L 29.4, W 23.5; VE09262, Cerro Alto, L 34.3, W 27.9; UWBM 97380, DV 571-1, L 20.2 W 15.8; UWBM 97381, DV 571-1, L (49), W 35.4; UWBM 97382, DV 1230-1, L 36.0, W 31.8; UWBM 97383, DV 360-2, L 29.8, W 24.6.

Occurrence: Upper Miocene to lower Pliocene, southern Peru to central Chile.

Acanthina ***rugosa*** DeVries, sp. nov.

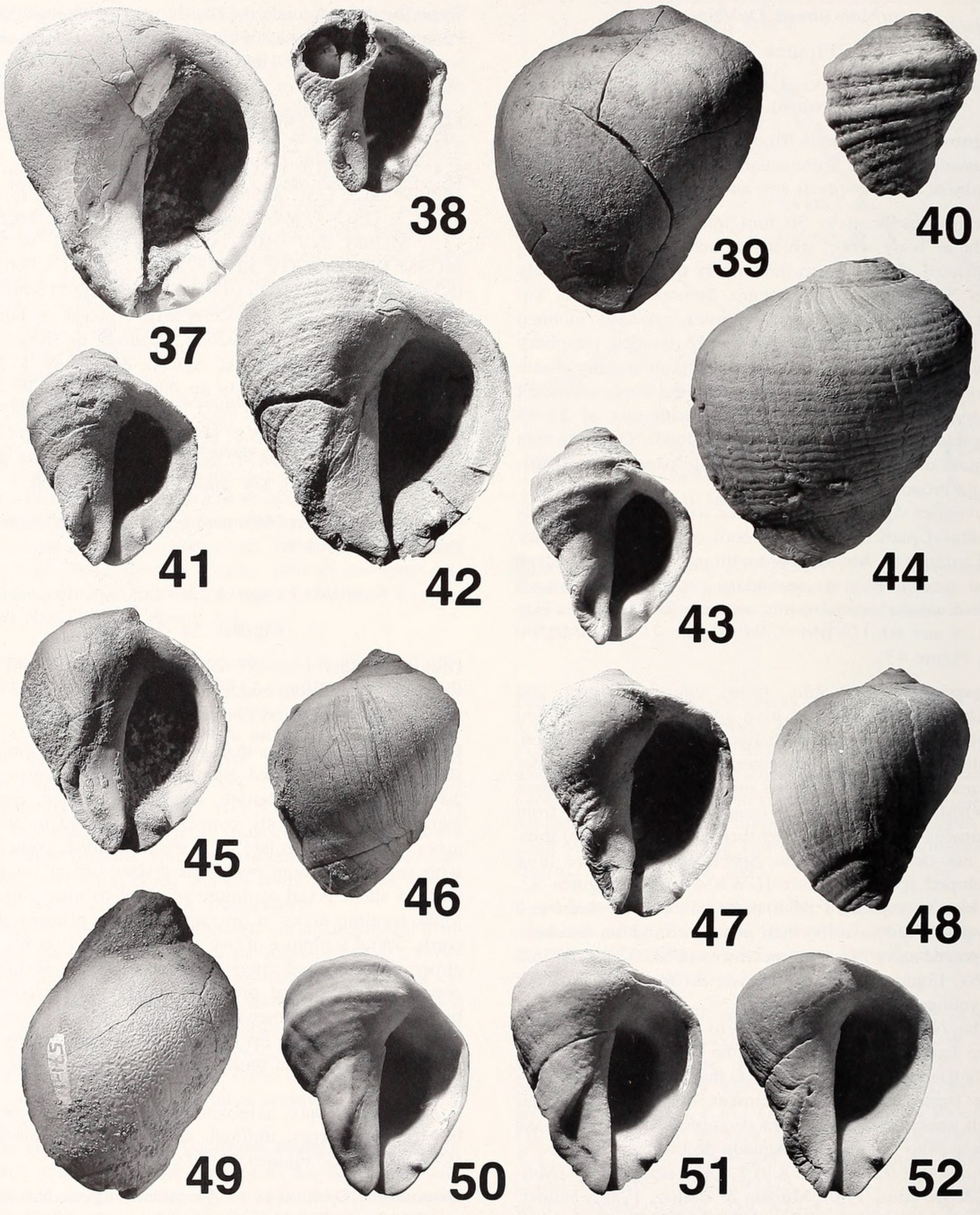
(Figures 54–57)

Diagnosis: Shell globose. Axial sculpture of eight to nine weak collabral folds; nodes at intersections of axial folds and two primary spiral cords.

Description: Shell less than 40 mm long, thick, globose. Base slightly constricted. Spire moderately elevated, 15–20 percent of shell length. Sutures appressed. Sutural platform broad, slightly convex, inclined 40 to 50 degrees. Shoulder angulate to sharply rounded, coincident with periphery, about two-fifths distance from suture to base of shell. Axial sculpture of eight to nine collabral folds, forming nodes at intersections with primary spiral cords. Spiral sculpture of two subdued primary cords, one at periphery, second anterior to first; two weak secondary cords, one on sutural platform, another at midpoint of body whorl; and numerous tertiary threads between suture and base. Outer lip thick, beveled, usually smooth, rarely dentate. Labral tooth short. Columella broadly excavated.

Juveniles biconic; axial and spiral sculpture as above, but more sharply defined and generally imbricate (UWBM 97385, Figures 56, 57).

Discussion: Specimens of *Acanthina* ***rugosa*** are distinguished from all other species of *Acanthina* except those of the oldest, *A. katzi,* by possessing numerous collabral folds. Like specimens of *A. katzi,* they have well developed, well differentiated, and imbricate primary and lesser spiral cords, but unlike those of *A. katzi,* they have a broadly excavated columella and a broader sutural plat-



Figures 37–52. *Acanthina* ***obesa*** DeVries, sp. nov. Figure 37. OSU 37365, apertural view, ×1.21. Figure 38. OSU 37368, apertural view, ×1.91. Figure 39. OSU 37365, abapertural view, ×1.21. Figure 40. OSU 37368, abapertural view, ×1.91. Figure 41. UWBM 97380, apertural view, ×1.71. Figure 42. UWBM 97382, apertural view, ×1.37. Figure 43. MUSM 012, apertural view, ×1.77. Figure 44. UWBM 015, abapertural view, ×1.37. Figure 45. UWBM 97383, apertural view, ×1.32. Figure 46. UWBM 97383, abapertural view, ×1.32. Figure 47. SGO.PI.5750, apertural view, ×2.10. Figure 48. SGO.PI.5750, abapertural view, ×2.10. Figure 49. UWBM 97381, abapertural view, ×0.98. Figure 50. OSU 37361, apertural view, ×1.57. Figure 51. OSU 37362, apertural view, ×1.41. Figure 52. OSU 37363, apertural view, ×1.56.

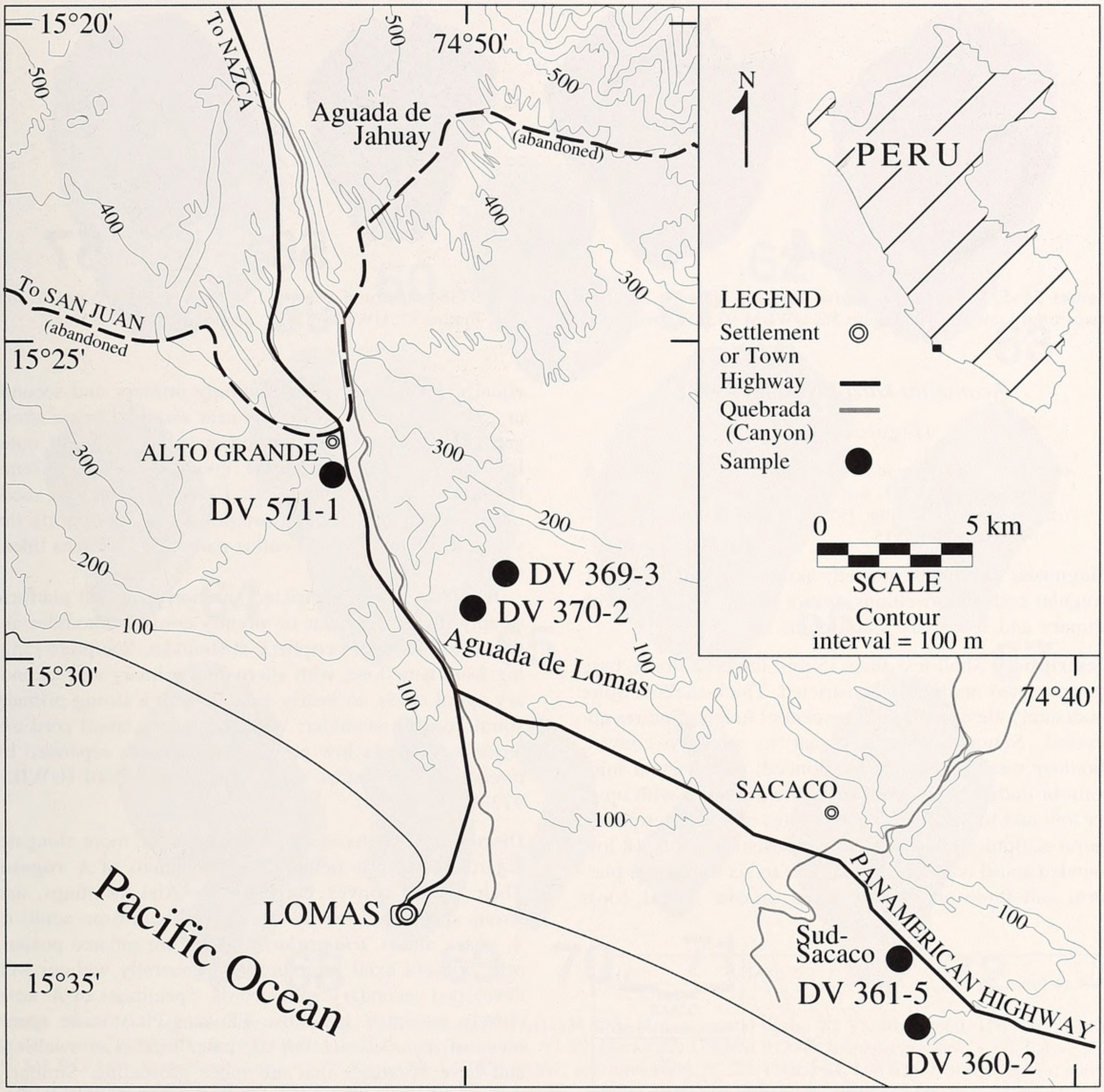


Figure 53. Type locality (DV 369) of *Acanthina* ***obesa*** DeVries, sp. nov.

form, characters shared with specimens of the younger *A.* ***obesa***.

The only collection of *Acanthina* ***rugosa*** comes from bioclastic conglomerates very near the base of a Neogene section on the south side of Quebrada Huaricangana (Figure 58). The conglomerate bed rests close to igneous basement that rears 500 meters up to the peak of Cerro Huaricangana, which served at the time of deposition as a peninsular buffer between the deposit and the open Pacific Ocean. Other mollusks from the same horizon [*Chorus frassinetti* DeVries, 1997; *Herminespina philippi* (Möricke, 1896)] suggest a late Miocene age (DeVries, 1997a; DeVries & Vermeij, 1997).

Type locality: South side of Quebrada Huaricangana, above basement platform. Sample DV 387-3 (Figure 58).

Material: UWBM 97384, holotype, DV 387-3, L (29.6), W26.1; UWBM 97385, paratype, DV 387-3, L (20.0), W 17.4; MUSM INV 008, paratype, DV 387-3, L (26.5), W 20.5; MUSM INV 009, DV 387-3, lot of 5.

Occurrence: Upper Miocene to lower Pliocene, southern Peru.

Figures 54–57. *Acanthina* ***rugosa*** DeVries, sp. nov. Figure 54. UWBM 97384, apertural view, ×1.31. Figure 55. UWBM 97384, abapertural view, ×1.31. Figure 56. UWBM 97385, apertural view, ×1.64. Figure 57. UWBM 97385, abapertural view, ×1.64.

Acanthina katzi Fleming, 1972

(Figures 59–67)

Acanthina crassilabrum katzi Fleming, 1972, in Watters & Fleming, 1972:397, figs. 6m–6s.
Acanthina katzi Fleming, 1972. DeVries & Vermeij, 1997: 613, figs. 2.13–2.15.

Diagnosis: Shoulder rounded; axial sculpture of broad, irregular collabral swellings. Entire surface of adults with primary and secondary spiral cords.

Description: Shell less than 35 mm long, fusiform, base unconstricted or slightly constricted. Thick-shelled. Spire moderately elevated, 20–25 percent of height. Sutures appressed. Sutural platform planar to strongly convex; shoulder weakly angulate to rounded; periphery at midpoint of body whorl. Axial sculpture absent or with up to six low and broad collabral swellings near the periphery. Spiral sculpture often lamellose, consisting of 15–18 low rounded spiral cords, including five to six on sutural platform and three anterior to spiral groove. Spiral cords equally developed, or alternatingly primary and secondary, or with one or two cords near shoulder being stronger. Labral tooth short, located at or near edge of outer lip. Outer lip beveled inward, crenulate; inside of outer lip with six to nine short teeth. Columella concave, moderately excavated. Ridge posterior to fasciole poorly developed. Pseudumbilical callus narrow, sometimes thickened.

Juveniles more constricted anteriorly; sutural platform steeply inclined, planar or slightly convex. Shoulder angulate to rounded; periphery at shoulder. Sculpture ranging from lamellose, with alternating primary and secondary spiral cords, to nearly smooth with a strong primary spiral cord on shoulder; weaker primary spiral cord anterior to first; six low primary spiral cords separated by threadlike interspaces anterior to second cord (UWBM 97389, Figure 60).

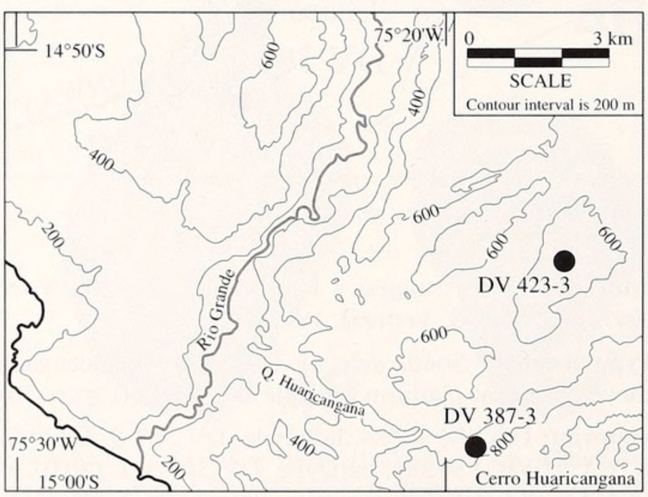
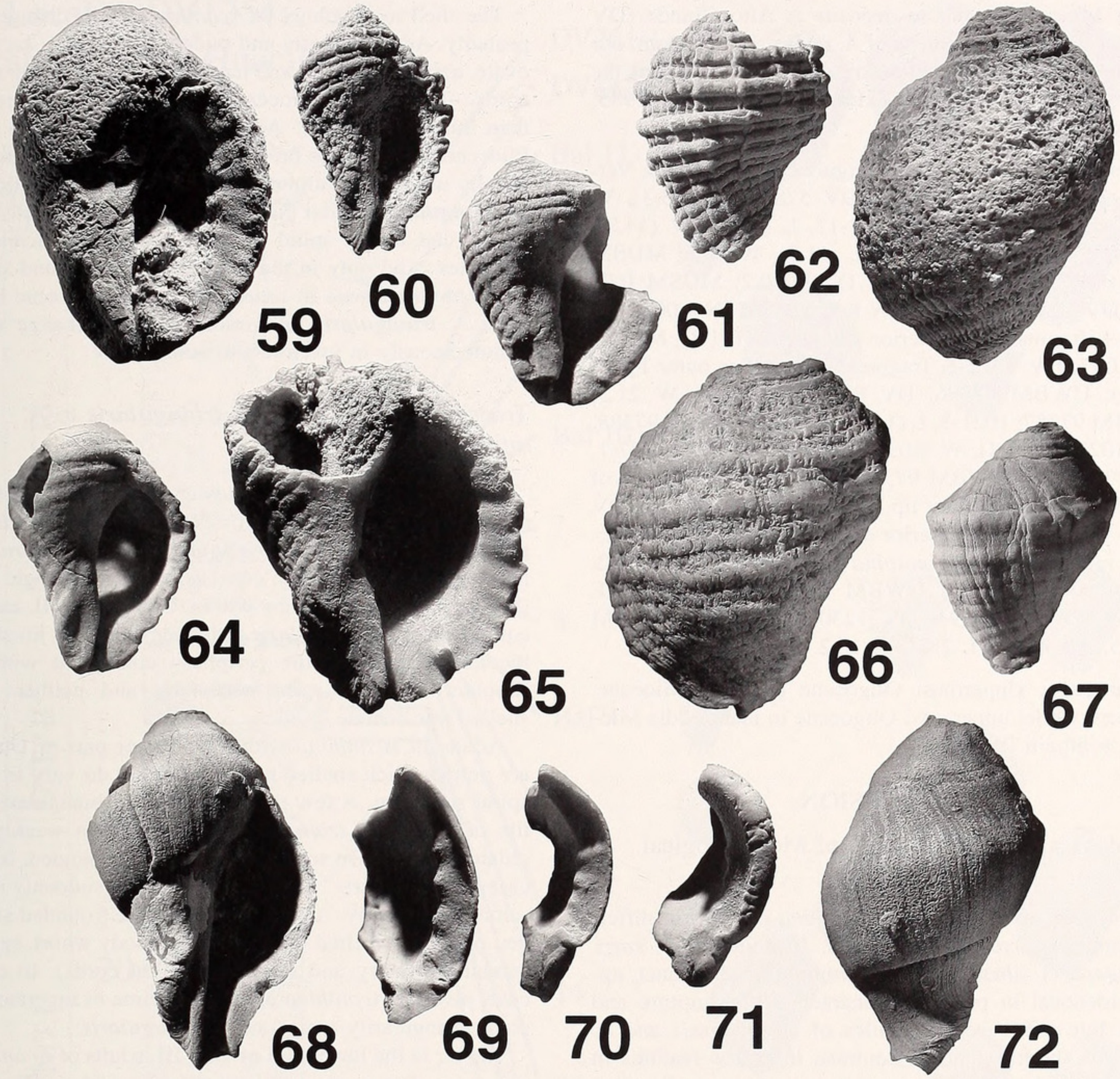


Figure 58. Type locality of *Acanthina* ***rugosa*** DeVries, sp. nov. Also shown is sample DV 423-3 with *A.* ***triangularis*** DeVries, sp. nov. from upper Pliocene marine terrace northwest of Cerro Huaricangana.

Discussion: Adults of *Acanthina katzi* are more elongate, regardless of spire height, than specimens of *A.* ***rugosa***. Their evenly convex body whorl, axial swellings, and strong spiral cords easily distinguish them from adults of *A.* ***obesa*** and *A.* ***triangularis***, which are inflated posteriorly, without axial sculpture, and generally without well developed secondary spiral cords. Specimens of *A. katzi* closely resemble lamellose Pliocene-Pleistocene specimens of *A. unicornis*, but the latter lack axial swellings and have apertures that are more prosocline. Similarly sculpted *A. monodon* are much larger and thinner-shelled than the thick-shelled *A. katzi*.

The early Miocene record of *Acanthina katzi* in Chile is discussed by DeVries & Vermeij (1997). Recent field work has clarified the record in southern Peru. The oldest Peruvian specimens of *A. katzi* are fragments of outer lips in a 25-Ma coquina (UWBM 97390) near Caravelí (Noble et al., 1985; DeVries, 2001a). Younger specimens were found at the type locality of the Chilcatay formation (DV 478-2) below a regional angular unconformity with an age estimated at 15–16 Ma and above strata dated with diatoms at 18–19 Ma (Dunbar et al., 1990; DeVries, 1998). Other late early Miocene specimens were found in deltaic deposits at Quebrada Gramonal (USNM 447143,



Figures 59–67. *Acanthina katzi* (Fleming, 1972). Figure 59. MUSM INV 004, apertural view, ×1.72. Figure 60. UWBM 97389, apertural view, ×3.31. Figure 61. USNM 447143, apertural view, ×1.89. Figure 62. UWBM 97388, abapertural view, ×3.0. Figure 63. MUSM INV 004, abapertural view, ×1.72. Figure 64. UWBM 97387, apertural view, ×2.28. Figure 65. UWBM 97386, apertural view, ×1.90. Figure 66. UWBM 97386, abapertural view, ×1.90. Figure 67. MUSM INV 005, abapertural view, ×3.09.
Figures 68–72. *Herminespina philippi* (Möricke, 1896). Figure 68. UWBM 97385, apertural view, ×1.73. Figure 69. UWBM 97392, outer lip, ×1.62. Figure 70. UWBM 97393, outer lip, ×1.53. Figure 71. UWBM 97394, outer lip, ×1.76. Figure 72. UWBM 97395, abapertural view, ×1.73.

Figure 61; also DV 574-2), also just below the lower/middle Miocene regional unconformity (DeVries, 1998), and in strata above the unconformity (e.g., UWBM 97389, 97388, 97387, and MUSM INV 005, Figures 60, 62, 64, and 67, respectively). Specimens above the unconformity occur with other mollusks (*Turritella infracarinata* Gryzbowski, 1899; *Concholepas unguis* DeVries, 1995; *Concholepas chirotensis* DeVries, 2000; *Anadara sechurana* Olsson, 1932) that indicate a middle Miocene age (DeVries, 1995, 1997b, 2000). Middle Miocene specimens of *A. katzi* are especially common in basal transgressive bioclastic sandstones of the Pisco formation (MUSM INV 004, Figures 59, 63; also DV 1322-1). Farther south, a specimen (UWBM 97386, Figures 65, 66) was encountered near Camaná in lower to middle Miocene beds from Quebrada Chiroteo (DeVries, 2000).

Specimens of *Acanthina katzi* have never been found with the diverse and well preserved molluscan fauna from upper Miocene nearshore deposits at Alto Grande (DV 571-1), in which specimens of *A.* ***obesa*** are abundant, nor in upper Miocene and Pliocene deposits throughout the Pisco and Sacaco basins (Muizon & DeVries, 1985; DeVries, 1998).

Material: (USNM specimens figured by DeVries & Vermeij, 1997) USNM 447142, DV 578-12, L (15.3), W 13.5; USNM 447143, DV 578-12, L (17.7), W (14.2); USNM 447144, DV 578-12, L (11.7), W 10.6; MUSM INV 004, DV 1325-1, L (27.1), W 20.2; MUSM INV 005, DV 1307-1, L (11.2), W 8.5; MUSM INV 006, DV 1258-1, fragment of posterior outer lip, L (11.8); MUSM INV 007, DV 1322-1, fragment of anterior outer lip, L (16.6); UWBM 97386, DV 815-1, L (26.6), W 21.3; UWBM 97387, 1021-3, L (15.1), W 11.2; UWBM 97388, DV 1021-3, (11.4), W 9.0; UWBM 97389, DV 1307-1, L 10.2, W 6.5; UWBM 97390, DV 1258-1, fragment of anterior portion of outer lip, L (8.2); UWBM 97391, DV 1322-1, fragment of anterior outer lip, L (15.8). Comparative material of *Herminespina philippi*: UWBM 97392, DV 1230-3 L (21.7); UWBM 97393, DV 1230-3, L (22.9); UWBM 97394, DV 1230-3, L (20.0); UWBM 97395, DV 426-3, L 28.3, W 18.2.

Occurrence: Uppermost Oligocene to lower Miocene, southern Chile; uppermost Oligocene to late middle Miocene, southern Peru.

DISCUSSION

Ontologically Varying Rates of Morphological Change

The shell morphology of *Acanthina* evolved at different rates for juveniles and adults. Juveniles of *A. katzi, A.* ***rugosa****, A.* ***obesa****, and A.* ***triangularis****,* all extinct, appear identical in prominent characters of sculpture and form, but differ from juveniles of *A. unicornis* and *A. monodon,* both extant. In contrast, the same features in *Acanthina* adults underwent numerous changes between the late Oligocene and present.

Juveniles of extinct *Acanthina* species have two strong primary cords, and the sutural platform is nearly planar. The resulting profile is distinctly biconic. Juveniles of *A. unicornis* and *A. monodon* are ovate to fusiform with five to seven primary spiral cords between the suture and spiral groove. The convex sutural platform merges with a rounded shoulder. The periphery is located at the midpoint of an inflated body whorl.

The shell morphology of *Acanthina* adults changed repeatedly. Adults of early and middle Miocene *A. katzi* are ovate, axially sculpted, and have numerous primary spiral cords. Adults of late Miocene *A.* ***rugosa*** are much broader than those of *A. katzi.* Adults of late Miocene to early Pliocene *A.* ***obesa*** are broad, but lack axial sculpture and usually all spiral sculpture. Only adults of late Pliocene *A.* ***triangularis*** exhibit the biconic profile, bicarinate body whorl, and muted spiral sculpture of extinct *Acanthina* juveniles. And only in the evolution of the round-shouldered multi-carinate *A. unicornis* from the biconic bicarinate *A.* ***triangularis*** does morphological change occur simultaneously in juvenile and adults.

Transition from *Acanthina* ***triangularis*** to *A. unicornis*

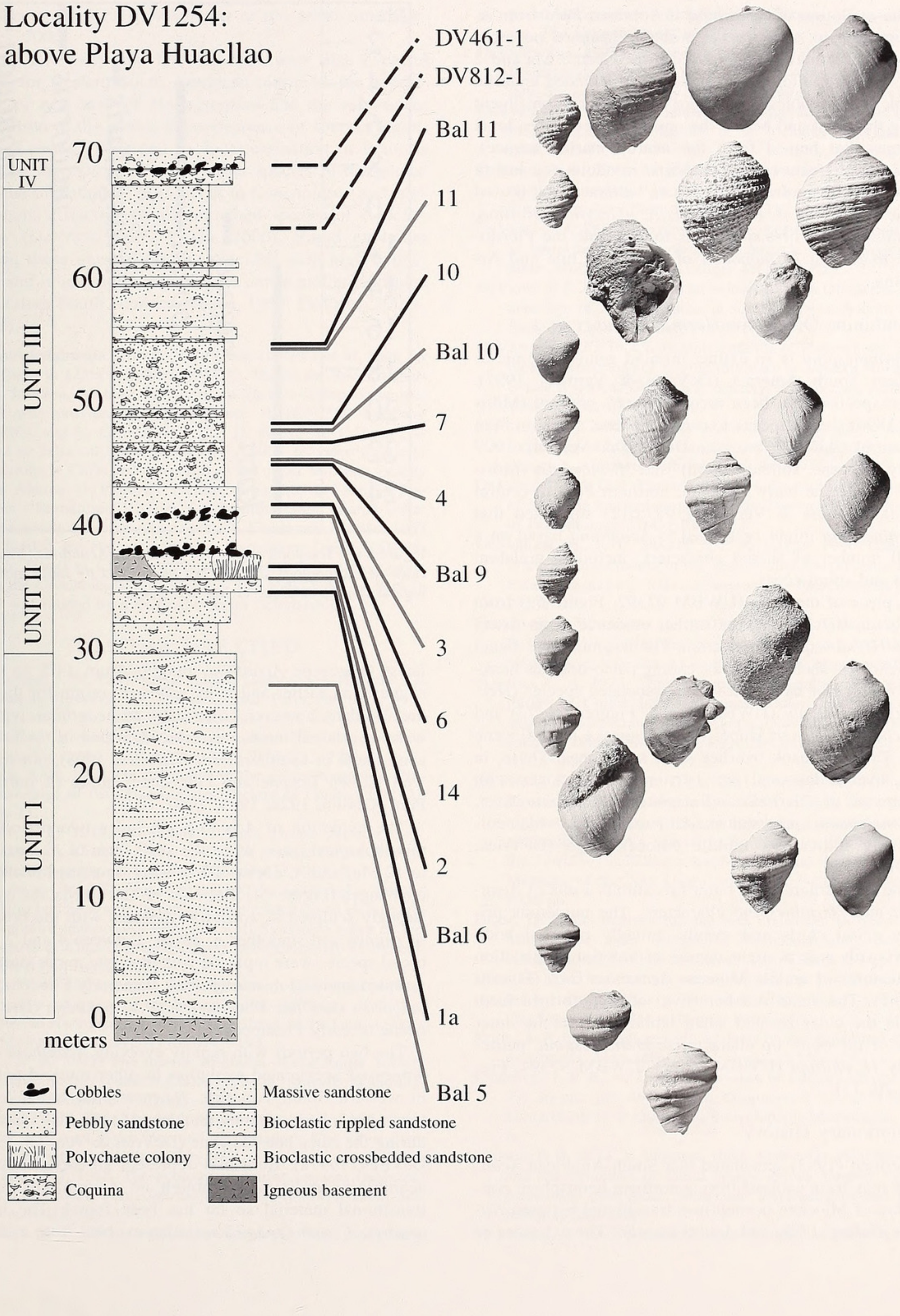
Outcrops of Pliocene and lower Pleistocene nearshore deposits near Chala have provided a series of specimens grading from *Acanthina* ***triangularis*** to *A. unicornis.* A nearly continuous section consists of four lithologic units (Figure 73). Acanthinines within Units I and II are unequivocally *A.* ***triangularis****,* whether adults or juveniles: biconic, biangulate, the periphery coincident with the shoulder, minimal spiral sculpture, and neither thick shelled nor dentate.

Adults of *Acanthina* within the lower part of Unit III are neither thick shelled nor dentate, but do vary in their spiral sculpture. A few retain the biconic biangulate profile of typical *A.* ***triangularis***. Most have a weakly angulate shoulder. On some, the shoulder is rounded. In rare cases, "triangularis" sculpture is replaced suddenly in the same specimen by "unicornis" sculpture (rounded shoulder, periphery shifted to mid-point of body whorl, several subdued primary and secondary spiral cords). In every case, juvenile *Acanthina* exhibit the same exaggerated biconic biangularity typical of *A.* ***triangularis***.

Higher in the lower half of Unit III, adults of *Acanthina* are more often ovate and less often biangulate. The first adults appear with the multi-corded imbricate sculpture of *A. unicornis* var. *acuminata.* Juveniles, however, are still biconic and biangulate. Only in the upper half of Unit III do typical juveniles of *A. unicornis* appear: fusiform, with several primary spiral cords between the suture and spiral groove. The shoulders of adults are entirely rounded; the cords, numerous, moderately well developed, differentiated in size, and sometimes imbricate; and the outer lip, thickened and sometimes dentate.

→

Figure 73. Distribution of acanthinine morphology in measured section DV 1254. Specimens from Units I and II are *Acanthina* ***triangularis*** DeVries, sp. nov. Adults with the rounded shoulder of *A. unicornis* first appear above 39 meters in the section, while juveniles and adults unequivocally referable to *A. unicornis* first appear above 50 meters. Additional samples from correlative horizons in nearby sections, DV 4161 and DV 812, are indicated with dashed lines. Images of small to large specimens standardized at lengths of 1.25, 1.9, and 2.5 cm.


Locality DV1254:
above Playa Huacllao
UNIT IV
UNIT III
UNIT II
UNIT I
70
60
50
40
30
20
10
0
meters
DV461-1
DV812-1
Bal 11
11
10
Bal 10
7
4
Bal 9
3
6
14
2
Bal 6
1a
Bal 5
Cobbles
Pebbly sandstone
Polychaete colony
Coquina
Massive sandstone
Bioclastic rippled sandstone
Bioclastic crossbedded sandstone
Igneous basement

The evolution of *Acanthina* in southern Peru from *A.* ***triangularis*** to *A. unicornis* probably spanned no more than a few hundred thousand years between 3 Ma and 2 Ma, occurring after the introduction of rounded andesite pebbles and cobbles as a major sedimentary constituent along the coast and before the onset of extreme sea level changes that helped form the nearby marine terraces. "Unicornis" features appeared first in adults and last in the smallest juveniles. "Acuminata" characters appeared at the end of the *A.* ***triangularis****-A. unicornis* transition, constituting the first specimens to resemble the Pleistocene to Recent *A. monodon* of southern Chile and Argentina.

Acanthinine Origin for *Herminespina*

Herminespina is an extinct muricid genus endemic to western South America (DeVries & Vermeij, 1997). Three species have been recognized: *H. philippi* (Möricke, 1896) (late Miocene to early Pliocene, southern Peru to central Chile), *H. saskiae* DeVries & Vermeij, 1997 (early Pliocene, southern Peru), and *H. mirabilis* (Möricke, 1896) (late early Pliocene, northern Peru to central Chile). DeVries & Vermeij (1997:612) suggested that *Herminespina* might be related to *Acanthina* based on a small number of shared characters, including collabral folds and spiral cords.

A piece of outer lip (UWBM 97392, Figure 69) from Quebrada Riachuelo gives further credence to an *Acanthina-Herminespina* connection. The fragment was found in the lowest shell bank of ascending paleo-beaches flanking outcrops of basement rock. Associated species (*Herminespina philippi* (UWBM 97395, Figures 68, 72) and *Concholepas kieneri* Hupé, 1854) suggest a late Miocene age. The shell bank overlies shelf sandstones. These, in turn, overlie lagoonal and barrier-bar sandstones with specimens of *Turritella infracarinata. Acanthina katzi, Concholepas unguis,* and *Anadara sechurana,* which collectively indicate a middle Miocene age (DeVries, 1997b).

The worn fragment of outer lip exhibits a mix of *Acanthina* and *Herminespina* characters. The numerous primary spiral cords and evenly, broadly rounded body whorl with only a slight degree of anterior constriction are features of middle Miocene *Acanthina katzi* (Figures 59, 65). The small number (five) of well formed teeth inside the outer lip and small labral tooth at the outer edge of the outer lip characterize *Herminespina,* particularly *H. philippi* (UWBM 97393, UWBM 97394, Figures 70, 71).

Evolutionary History

Vermeij (1993) speculated that South American *Acanthina* may have evolved from a northern hemisphere population of Miocene ocenebrines transitional between *Nucella* Röding, 1798, and *Acanthinucella.* The existence of

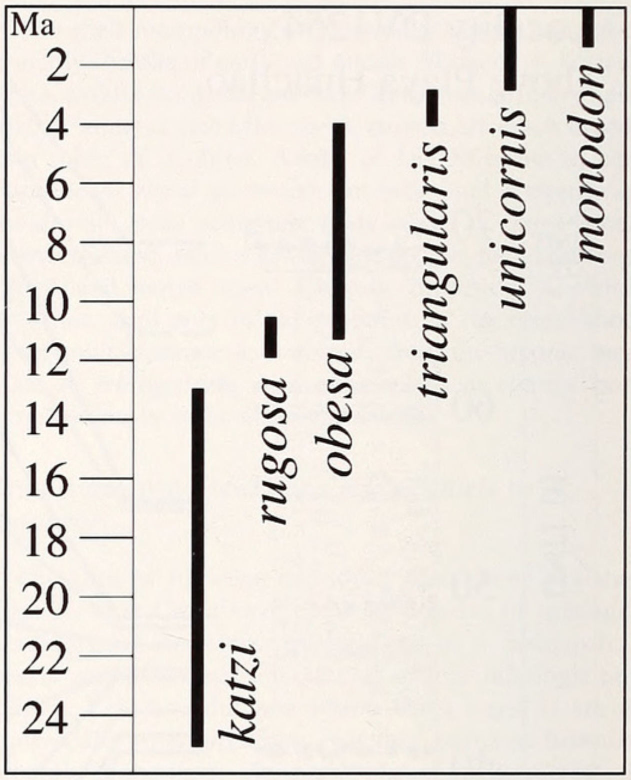


Figure 74. Temporal ranges for species of *Acanthina.* Two periods of morphological stasis are interrupted by rapid morphological change at about 11 Ma and 3 Ma.

latest Oligocene *Acanthina* ranging from 14°S to 41°S suggests an earlier and more southerly origin for the genus. To date, however, no ancestor to *Acanthina,* with or without a labral tooth, has been identified in the Oligocene fauna of southern Peru (DeVries, 1998), nor in the well known Eocene and Oligocene faunas of northern Peru (Olsson, 1928, 1929, 1930, 1931).

The evolution of *Acanthina* includes two periods of morphological stasis when the shell form of *A. katzi* (25 to 12 Ma) and *A.* ***obesa*** (10 to 4 Ma) remained relatively unchanged (Figure 74). Between 12 and 10 Ma, the ovate, strongly sculpted *A. katzi* was replaced with the broader *A.* ***rugosa*** and smoother *A.* ***obesa***. Between 4 and 2 Ma, broad species were replaced with elongate, more strongly sculpted species: *A.* ***triangularis*** (late early Pliocene), *A. unicornis* (late late Pliocene), and *A. monodon* (late Pliocene or early Pleistocene).

The two periods with rapidly evolving *Acanthina* also witnessed accelerated evolution in other muricid genera in western South America. *Herminespina* and *Chorus* Gray, 1847, both genera with a labral tooth, first appeared during the early late Miocene (DeVries & Vermeij, 1997; DeVries, 1997a). Both may represent an early Miocene acanthinine radiation, although no *Acanthina-Chorus* transitional material so far has been found. The large quadrate *Concholepas kieneri* also evolved from a much smaller species of *Concholepas* at the same time (DeVries, 2000).

The late early and late Pliocene were also eventful times for western South American muricids: the appearance of new taxa of *Herminespina* and the subsequent extinction of the genus; the appearance of *Chorus giganteus* (Lesson, 1830) and its local extinction in Peru, as well as the extinction of all other species in the genus; and the evolution of labral teeth in *Concholepas* and concomitant extinction of all untoothed species of *Concholepas* (DeVries, 1995, 1997a, 2000). Rapid evolution within these muricid clades coincided with high extinction and immigration rates for the entire molluscan fauna in western South America (Herm, 1969; DeVries, 2001b, 2002).

Acknowledgments. I thank V. Alleman (URP) and M. Rabi for their help in Lima and the late Sr. C. Martin de Buey and his wife, Josefina, for their hospitality in Sacaco. Comparative material was provided by A. Riccardi (UNLP), D. Lindberg (UCMP), and L. Groves (LACM). D. Frassinetti (Museo Nacional de Historia Natural, Santiago, Chile) provided access to collections in Chile and directions to the upper Miocene locality at Lo Abarca. G. Pastorino (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires) shared information about *Acanthina* in Argentina. Fieldwork in 1986–1987 was funded by National Science Foundation Grant EAR-85-03886. Travel to Chile in 1993 was funded in part by a grant from the Conchologists of America, Inc. Field work in Peru in 1999 was funded by a Fulbright Senior Scholarship.

LITERATURE CITED

Bruguière, J. G. 1789. Encyclopédie Méthodique. Histoire Naturelle des Vers. Vol. 1. Panckoucke: Paris. 344 pp.

Carcelles, A. R., 1954. Observaciones sobre los generos *Nucella, Chorus,* y *Concholepas.* Instituto Nacional de Investigación de las Ciencias Naturales 2(16):255–275.

Cooke, A. H. 1918. On the radula of the genus *Acanthina.* Proceedings of the Malacological Society of London 13(1–2): 6–11.

Cooke, A. H. 1919. The radula in *Thais, Drupa, Morula, Concholepas, Cronia, Iopas,* and allied genera. Proceedings of the Malacological Society of London 13:90–110.

Covacevich, V. & D. Frassinetti. 1990. La fauna de Lo Abarca: Hito biochronoestratigráfico y paleoclimático en el Terciario superior marino de Chile central. II Symposio sobre el Terciario de Chile (Universidad de Concepción), 10–12 December 1990, Actas:51–71.

Dall, W. H. 1909. Report on a collection of shells from Peru, with a summary of the littoral marine Mollusca of the Peruvian zoological province. Proceedings of the United States National Museum 37(1704):147–194.

Dell, R. K. 1971. The marine Mollusca of the Royal Society expedition to southern Chile, 1958–59. Records of the Dominion Museum 7(17):155–233.

DeVries, T. J. 1986. The geology and paleontology of tablazos in northwest Peru. Doctoral Dissertation, The Ohio State University, Columbus, Ohio. 964 pp.

DeVries, T. J. 1988. The geology of marine terraces (tablazos) of Northwest Peru. Journal of South American Earth Sciences 1(2):121–136.

DeVries, T. J. 1995. *Concholepas* Lamarck, 1801 (Neogastropoda: Muricoidea): A Neogene genus native to South America. The Veliger 38(4):284–297.

DeVries, T. J. 1997a. A review of the genus *Chorus* Gray, 1847 (Gastropoda: Muricidae) from western South America. Tulane Studies in Geology and Paleontology 30(3):125–147.

DeVries, T. J. 1997b. Middle Miocene marine sediments in the Pisco Basin (Peru). Boletín de la Sociedad Geológica del Perú 87:1–13.

DeVries, T. J. 1998. Oligocene deposition and Cenozoic sequence boundaries in the Pisco Basin (Peru). Journal of South American Earth Sciences 11(3):217–231.

DeVries, T. J. 2000. Two new Neogene species and the evolution of labral teeth in *Concholepas* Lamarck, 1801 (Neogastropoda: Muricoidea). The Veliger 43(1):43–50.

DeVries, T. J. 2001a. Molluscan evidence for an Oligocene-Miocene age of 'Paracas' beds in southern Peru. Boletín de la Sociedad Geológica del Perú 92:57–65.

DeVries, T. J. 2001b. Contrasting patterns of Pliocene and Pleistocene extinctions of marine mollusks in western North and South America. Geological Society of America, Abstracts with Programs 33(3):A–35.

DeVries, T. J. 2002. Patterns of diversity in Cenozoic marine mollusks from the Peruvian Province. Geological Society of America, Abstracts with Programs 34(5).

DeVries, T. J. & G. J. Vermeij. 1997. *Herminespina:* New genus of Neogene muricid gastropod from Peru and Chile. Journal of Paleontology 71(4):610–615.

Dunbar, R. B., R. C. Marty & P. A. Baker. 1990. Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru. Palaeogeography, Palaeoclimatology, Palaeoecology 77: 235–261.

Fischer von Waldheim, G. 1807. Catalogue Systématique et Raissoné des Curiositées de la Nature et de l'Art, Vol. 3. Végétaux et Animaux. Museum Démidoff: Moscow. 339 pp.

Fleming, C. A. 1972. Contributions to the geology and paleontology of Chiloe Island, southern Chile. Part II. Pliocene marine invertebrates from Chepu District, Chiloe. Philosophical Transactions of the Royal Society of London (series B) 263:380–408.

Grant, U. S., IV, & H. R. Gale, 1931. Catalogue of the marine Pliocene and Pleistocene mollusca of California and adjacent regions with notes on their morphology, classification, and nomenclature and a special treatment of the Pectinidae and the Turridae (including a few Miocene and Recent species): Memoirs of the San Diego Society of Natural History 1. 1036 pp.

Herm, D. 1969. Marines Pliozän und Pleistozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen: Zitteliana 2:159 pp.

Hupé, H. 1854. Malacologia y conquiliogia. Pp. 1–499 in C. Gay (ed.), Historia Fisica y Politica de Chile. Vol. 8. and Atlas (Zoologica). Maulde et Renou: Paris.

Kool, S. P. 1993. Phylogenetic analysis of the Rapaninae (Neogastropoda: Muricidae). Malacologia 35:155–259.

Lamarck, J. P. B. A. 1816. Mollusques et polypes divers. Part 23, 16 pp., pls. 391–488 in Bruguière, J. G., J. P. B. A. Lamarck, & G. P. Deshayes, Encyclopédie Méthodique. Paris.

Marko, P. B. & G. J. Vermeij. 1999. Molecular phylogenetics and the evolution of labral spines among Eastern Pacific ocenebrine gastropods. Molecular Phylogenetics and Evolution 13:275–288.

McLean, J. H. 1969. Marine Shells of Southern California. Natural History Museum of Los Angeles County, Science Series 24:104 pp.

MUIZON, C. DE & H. BELLON. 1986. Nouvelles données su l'âge de la formation Pisco, Pérou. Comptes Rendues Acadamie Sciences (Paris) series D 303:1401–1404.

MUIZON, C., DE & T. J. DEVRIES. 1985. Geology and paleontology of the Pisco Formation in the area of Sacaco, Peru. Geologische Rundschau 74:547–563.

NOBLE, D. C., M. SEBRIER, F. MEGARD & E. MCKEE. 1985. Demonstration of two pulses of Paleogene deformation in the Andes of Peru. Earth and Planetary Science Letters 73:345–349.

OLSSON, A. A. 1928. Contributions to the Tertiary paleontology of northern Peru: Part 1, Eocene Mollusca and Brachiopoda. Bulletins of American Paleontology 14(52):47–154.

OLSSON, A. A. 1929. Contributions to the Tertiary paleontology of northern Peru: Part 2, Upper Eocene Mollusca and Brachiopoda. Bulletins of American Paleontology 15(57):67–116.

OLSSON, A. A. 1930. Contributions to the Tertiary paleontology of northern Peru: Part 3, Eocene Mollusca. Bulletins of American Paleontology 17(62):1–96.

OLSSON, A. A. 1931. Contributions to the Tertiary paleontology of northern Peru: Part 4, The Peruvian Oligocene. Bulletins of American Paleontology 17(63):97–264.

ORTLIEB, L. & J. MACHARÉ. 1990. Geochronología y morfoestratigrafía de terrazas marinas del pleistoceno superior: el caso de San Juan-Marcona, Peru. Boletín de la Sociedad Geológica del Perú 81:87–106.

ORTLIEB, L., T. DEVRIES & A. DÍAZ. 1990. Ocurrencia de *Chione broggi* (Pilsbry and Olsson, 1943) (Pelecypoda) en depositos litorales cuatermarios del sur del Perú: implicaciones tectónicas. Boletín de la Sociedad Geológica del Perú 81:121–126.

PALLAS, P. S. 1774. Spicilegia Zooligica. Vol. 1. Part 10. Lange: Berolini. 41 pp.

PASTORINO, G. 1994. Los gastropodos de las terrazas marinas Cuaternarias de Rio Negro y Chubut. Doctoral Dissertation, Facultad de Ciencias Naturales, Universidad Nacional de La Plata, Argentina. 205 pp.

PHILIPPI, R. A. 1887. Fósiles terciarios i cuatarios de Chile. BrockHaus: Leipzig. 312 pp.

SOWERBY, G. B., I. 1835. Characters of new genera and species of Mollusca and Conchifera, collected by Hugh Cuming. Proceedings of the Zoological Society of London 1835:49–51.

SOWERBY, G. B., II. 1846. Appendix. Description of Tertiary fossil shells from South America, Pp. 249–268 in C. Darwin, Geological Observations on South America, pt. 3. The Geology of the Voyage of the Beagle. Smith, Elder, and Co: London.

TAVERA, J. 1979. Estratigrafía y paleontología de la Formación Navidad, Provincia de Colchagua, Chile (Lat. 30°50'S). Museo Nacional de Historia Natural (Santiago, Chile) Boletín 36:176 pp.

VERMEIJ, G. J. 1993. *Spinucella,* a new genus of Miocene to Pleistocene muricid gastropods from the eastern Atlantic. Contributions to Tertiary and Quaternary Geology 30:19–27.

VERMEIJ, G. J. & S. P. KOOL. 1994. Evolution of labral spines in *Acanthais,* new genus, and other rapanine muricid gastropods. The Veliger 37:414–424.

WATTERS, W. A. & C. A. FLEMING. 1972. Contributions to the geology and paleontology of Chiloe Island, southern Chile. Philosophical Transactions of the Royal Society of London (series B) 263:369–408.

WU, S.-K. 1985. The genus *Acanthina* (Gastropoda: Muricidae) in West America. Special Publication of the Mukaishima Marine Biological Station 1985:45–66.

APPENDIX

List of Samples and Localities

Latitudes and longitudes followed by the designation "GPS" were obtained from replicated or averaged non-differential values obtained from global positioning satellites using a Magellan 2000XL instrument. Repeated GPS measurements rarely varied by more than one second and were checked against the appropriate 1:100,000 topographic map.

Aguada de Jahuay	Probably where about 100 m upstream from where access road cuts across Quebrada Jahuay, lower 5 m of section at base of quebrada. 15°21′20″S, 74°53′06″W (Acarí 1: 100,000 quadrangle). Locality of V. Alleman, designated samples DV 024 and DV 028 by the author. Uppermost Miocene to Lower Pliocene.
Cerro Alto	Km 22 carretera Acarí, Sacaco. Locality of V. Alleman, designated sample DV 025 by the author. Lower Pliocene.
Lo Abarca	About 10 km northeast of San Antonio, outcrop of indurated sandstone and conglomerate near foot of hill on south side of road from San Sebastian at western edge of village of Lo Abarca, Chile. 33°32′S, 71°33′W. Upper Miocene to lower Pliocene.
DV 272	2.5 km southwest village of La Brea, Quebrada Songora. 4°42′49″S, 81°05′35″W.
DV 273	14 km southeast village of La Brea; northwest arm of Quebrada Cardo Grande. 4°48′21″S, 81°01′49″W. Taime Formation, upper Pliocene.
DV 360-2	Sud Sacaco, western end of ridge extending from Panamerican Highway. 15°34′43″S, 74°43′17″W (Yauca 1:00,000 quadrangle). Pisco Formation, lower Pliocene.
DV 361-5	Sud Sacaco: northeast depression near Panamerican Highway. 15°34′17″S, 74°43′26″W (Yauca 1:100,000 quadrangle). Pisco Formation, lower Pliocene.
DV 369-3	East slope Aguada de Lomas,

south of abandoned HierroPeru road. 15°28′32″S, 74°47′30″W (Acarí 1:100,000 quadrangle). Pisco Formation, upper Miocene.

DV 370-2 West side Aguada de Lomas, terraced surface. 15°29′S, 75°49′W (Acarí 1:100,000 quadrangle). Pisco Formation, upper Miocene.

DV 382-1 San Juan/Lomas road, kilometer marker 50, flat-topped knoll south of highway. 15°22′02″S, 75°05′26″W (San Juan 1:100,000 quadrangle). Remnant of marine terrace, upper Pleistocene.

DV 387-3 South side of Quebrada Huaricangana, above basement rock platform, second resistant horizon above white diatomaceous bed. 14°58′44″S, 75°19′23″W (Palpa 1: 100,000 quadrangle). Pisco Formation, lower Pliocene.

DV 423-3 Mollusk bed capping south side of northeast knob of double-knobbed mesa north of Quebrada Huaricangana. 14°55′33″S, 75°17′41″W (Puerto Caballas Quadrangle 1: 50,000). Marine terrace, uppermost Pliocene to lowermost Pleistocene.

DV 426-3 West Gulch, Quebrada Huaricangana, about 130 meters above base of section, in mixture of sand, boulders, and cobbles (Palpa 1: 100,000 quadrangle).

DV 468-2 Playa Yanyarina, about 22 km southeast of San Juan de Marcona. 15°27′S, 74°59′W (Acarí 1: 100,000 quadrangle). Recent.

DV 478-2 Lomas Chilcatay, northeast end of outcrop. 14°11′42″S 76°06′57″W (Punta Grande 1:100,000 quadrangle). Chilcatay Formation, lower Miocene.

DV 571-1 El Jahuay, hillside west of Panamerican Highway, south of intersection with road northwest to San Juan de Marcona. In fact, place name is a misnomer—maps label the area Alto Grande. (Area disturbed following highway construction in early 1990s.) 15°26′57″S, 74°52′06″W (Yauca 1:100,000 quadrangle). Pisco Formation, upper Miocene.

DV 574-2 Quebrada Gramonal, east side of canyon headwall, top of deltaic foreset beds of coarse-grained bioclastic sandstone. 14°45′13″S 75°30′39″W (Lomitas 1:100,000 quadrangle). Chilcatay Formation, lower Miocene.

DV 578-12 Double-knobbed hill N of Fundo Santa Rosa, E side of Rio Ica, top of cross-bedded sandstone sets. 14°46′28″S, 75°30′43″W (Lomitas 1:100,000 quadrangle). Lower to middle Miocene.

DV 579-2 One kilometer east of double knobbed hill, south of mouth of Quebrada Gramonal, east side of the Río Ica. 14°46′30″S, 75°30′06″W (Lomitas 1:100,000 quadrangle). Chilcatay Formation, lower Miocene.

DV 812-1 South side of Quebrada Huacllaco, roadcut along Panamerican Highway. 15°52′S, 74°11′W (Chala 1: 100,000 quadrangle). La Planchada Formation, upper Pliocene.

DV 815-1 Head of Quebrada Chiroteo, Panamerican Highway, where it turns into Quebrada del Toro, at an elevation of about 500 m (Camaná 1: 100,000 quadrangle). Camaná Formation, Middle Miocene.

DV 1019-1 About 0.5 km north of pass where road to coast climbs out of Gramonal valley and passes toward Fundo Santa Rosa. 14°45′50″S, 75°30′22″W (GPS; Lomitas 1: 100,000 quadrangle). Pisco Formation, middle Miocene.

DV 1021-3 East side Quebrada Gramonal, hillside above point where road to coast crosses from western to eastern side of quebrada; 44.6 m in section. 14°44′19″S, 75°31′02″W (GPS; Lomitas 1:100,000 quadrangle). Pisco Formation, middle Miocene.

DV 1230-1 Fourth white shell bank from base of outcrop, flanking basement knoll, east side Quebrada Riacheulo. 14°40′45″S, 75°29′20″W (Palpa 1:100,000 quadrangle). Pisco Formation, lower upper Miocene.

DV 1230-3 As for 1230-1, lower three shell banks; *Acanthina*/*Herminespina* specimen from lowest shell bank. Pisco Formation, lower upper Miocene.

DV 1258-1 Altos de Gramadal, south of Caravelí, INGEMMET sect J from Pecho (1983); coquina block fallen from horizon 21. 15°56′35″S, 73°19′19″W (GPS; Caravelí 1: 100,000 quadrangle). Basal Camaná Formation, latest Oligocene.

DV 1307-1 Bluff east of the mouth of Quebrada Gramonal, overlooking road to Fundo Santa Rosa. 14°45′48″S, 75°30′23″W (GPS; Lomitas 1: 100,000 quadrangle). Middle Miocene.

DV 1322-1 Pass to Penon. 14°26′04″S, 75°51′00″W (GPS: Ica 1:100,000 quadrangle). Middle Miocene.

DV 1325-1 Outcrops in hills south of El Penon road. 14°27′44″S, 75°50′29″W (GPS: Ica 1:100,000 quadrangle). Middle Miocene.

JM84319B Toward coast from Palpa (Palpa 1: 100,000 quadrangle). Pleistocene.

LACM 72-157.2 Intertidal, Punta Alert, Isla Knocker, Magallanes Province, Chile (49°52′48″S, 75°13′18″W). Recent.

LACM 75-32.4 Intertidal, Punta El Lacho, north of Cartagena, Santiago Province, Chile (33°30′S, 71°39′W). Recent.

LACM 54679 Intertidal, Punta Baxa, Magallanes Province, Chile. Recent.

UCMP 3102 Chile. 35°S, 72°W. Recent.

UCMP D-3735 Along Panamerican Highway, about 11.2 km north of La Serena, from outcrops in deep roadcut along south side of deep quebrada; basal fine-grained sandstones with lenses of gravel. 29°48′30″S, 71°16′30″W (Coquimbo 1:50,000 quadrangle). Late Pliocene.

UCMP D-5826 Sandy outcrops along bank of stream, 1.5 km south of improved road at Estero El Ganso. 34°13′S, 71°45′W (Central Rapel 1:50,000 quadrangle). Pliocene.

UNLP 1398 Surface, Bahia Sanguinetti, Santa Cruz Province, Argentina. Holocene/Pleistocene.

UNLP 1407 Bahia Sanguinetti, Santa Cruz Province, Argentina. Holocene/ Pleistocene.

UNLP 26668 Uplifted marine terrace, Camarones, Chubut Province, Argentina. Pleistocene. Also UNLP 26669, 26670.