

The Late Cenozoic History of *Xanthochorus* Fischer, 1884 (Gastropoda: Muricidae) in Western South America

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Abstract. The South American muricid genus *Xanthochorus* Fischer, 1884, is reviewed in light of the discovery of late Cenozoic fossils from Peru. Four new species from southern Peru are described: *Xanthochorus xuster*, sp. nov. (late Pliocene), *X. eripepomis*, sp. nov. (early Pliocene), *X. ochuroma*, sp. nov. (late late Miocene to early Pliocene), and *Xanthochorus stephanicus*, sp. nov. (early late Miocene). Early late Pliocene specimens of the two extant species, *X. cassidiformis* (Blainville, 1832), and *X. buxeus* (Broderip, 1833), are documented from southern Peru, as are late Pliocene specimens of *X. cassidiformis* from northern Peru. *X. xanthostoma* (Broderip, 1833) is considered a synonym of *X. cassidiformis*. The oldest species of *Xanthochorus* has fluted lamellar axial ribs similar to those of modern South American species of *Trophon* Montfort, 1810. An evolutionary history for *Xanthochorus* is proposed based on shell morphology and stratigraphic occurrence.

INTRODUCTION

The muricid genus *Xanthochorus* Fischer, 1884, includes two living species, *Xanthochorus cassidiformis* (Blainville, 1832) and *X. buxeus* (Broderip, 1833). Both species are found in nearshore waters along the western coast of South America (Dall, 1909; Alamo & Valdivieso, 1997; Figure 1) and both have a reported stratigraphic range in Chile back to the early Pleistocene (Herm, 1969).

The discovery of four new species of fossil *Xanthochorus* in upper Miocene to upper Pliocene sandstones from southern Peru (Figure 2) extends the evolutionary history of the genus. The oldest of the four species, *X. stephanicus*, sp. nov., has features reminiscent of Recent austral species of *Trophon* Montfort, 1810. *X. ochuroma*, sp. nov., encompasses a morphological shift from *X. stephanicus* to the extant *X. cassidiformis* and *X. buxeus*. *X. eripepomis*, sp. nov., and *X. xuster*, sp. nov., are short-lived extinct Pliocene taxa. The pattern of evolution evidenced by the six species resembles that of other endemic muricid lineages in western South America.

GEOLOGY

The Cenozoic stratigraphy of the southern Peruvian Pisco and Sacaco forearc basins has been described by Muizon & DeVries (1985), Dunbar et al. (1990), and DeVries (1998). Upper Miocene and Pliocene marine deposits are assigned to the Pisco and La Planchada formations. They include thin-bedded tuffaceous and diatomaceous fine-grained sandstones, attributed to outer shelf environments, and massive tuffaceous coarser-grained sandstones from shallower shelf environments. Lying in contact with

outcrops of igneous rock are crossbedded and lenticular bioclastic conglomerates, the remnants of shallow subtidal and intertidal deposits that lapped onto pre-Eocene erosional platforms or against precipitous Andean foothills.

Deposits of the Pliocene Taime formation in northern Peru were described by DeVries (1986, 1988). Most Taime sediments are thought to have been deposited on the inner shelf, nearshore and intertidally, or within an elongate lagoon.

METHODS AND MATERIALS

Peruvian and Argentinian specimens described in this study were found by the author. Chilean specimens were collected by W. J. Zinsmeister (Purdue University, West Lafayette, Indiana, USA). Comparative material was studied at the Natural History Museum of Los Angeles County in California (LACM), the University of California Museum of Paleontology in Berkeley, California (UCMP), and the Museo Nacional de Historia Natural in Santiago, Chile.

Locality and sample descriptions are listed in the appendix. Lengths (L) and widths (W) are measured in millimeters (mm). Dimensions of broken specimens are enclosed by parentheses. Types and figured specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM), Ohio State University's Orton Museum in Columbus, Ohio (OSU), and the Departamento de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, in Lima, Peru (MUSM INV).

Radiometric dates and biochronostratigraphic ages for deposits from the Pisco Basin and outcrops to the south are discussed in Dunbar et al. (1990) and DeVries (1998).

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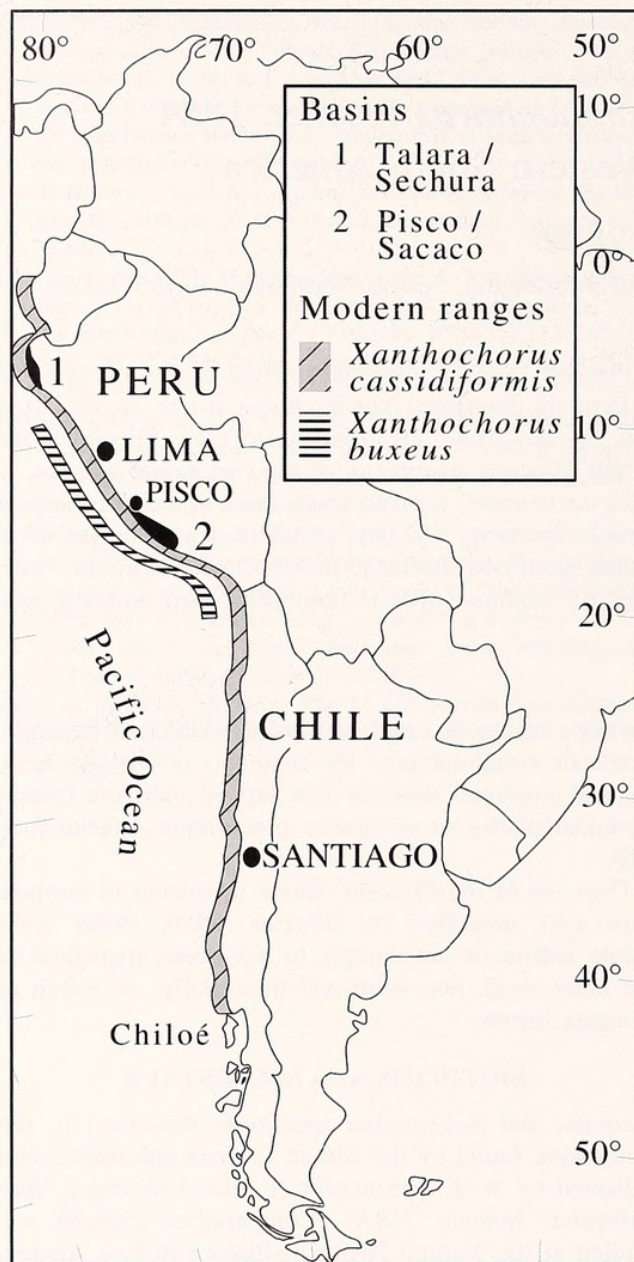


Figure 1. Modern ranges of extant species and location of fore-arc basins with late Cenozoic fossils of *Xanthochorus*.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815

Subfamily TROPHONINAE Cossmann, 1903

Genus *Xanthochorus* Fischer, 1884

Type species (original designation): *Trophon xanthotoma* (Broderip, 1833) (synonym of *Xanthochorus cassidiformis* (Blainville, 1832)).

Original description: "Labre silloné ou plissé, portant un indice de dent comme chez les *Chorus*; opercule typique" (Fischer, 1884, p. 640; as section of *Trophon* Montfort, 1810).

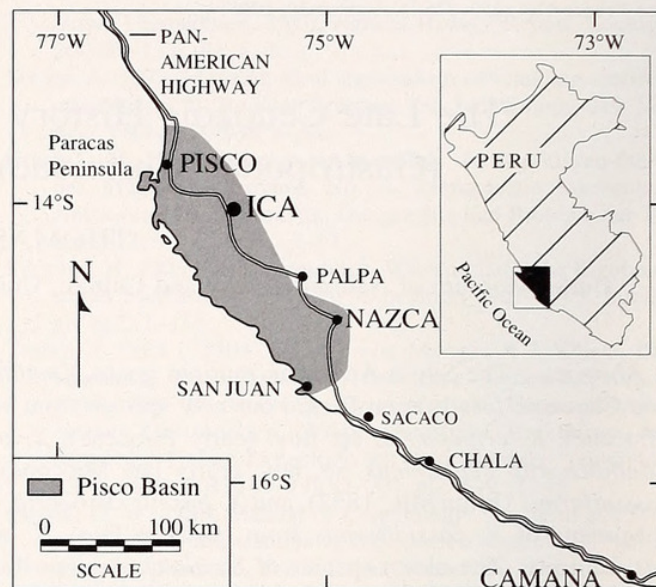


Figure 2. Extent of the Pisco Basin in southern Peru.

Diagnosis: Fusiform, early whorls with regularly spaced rounded or rarely fluted axial ribs; axial sculpture on body whorl variable but lacking regularly spaced full-length lamellar ribs; spiral cords low, flattened, usually present on early spire whorls.

Description: Shell thin to thick, broadly fusiform to pyriform. Spire 25–45 percent of height, protoconch unknown for most species. Teleoconch with 4–6 whorls. Sutures impressed, sutural platform and shoulder variably developed. Periphery near midpoint of aperture, shell sometimes swollen anteriorly. Spire whorls typically with 8–12 bluntly rounded to lamellar axial ribs; ribs becoming irregularly developed or obsolete on penultimate or body whorl. Spiral sculpture with several low, flattened spiral cords on early whorls. Body whorl variably sculptured, smooth or with up to 100 flattened spiral cords, variably differentiated into primary and secondary cords; intersection of colabral growth lines and spiral cords often scabrous but to varying degrees. Aperture ovate to broadly ovate. Outer lip orthocline to slightly prosocline, usually with broad sinus at shoulder. Inside of outer lip sometimes dentate or crenulate. Columella smooth, usually thin, adherent, sometimes slightly excavated. Pseudumbilicus present, variably developed. Siphonal canal one-third to one-half of length of aperture, straight to angled abaperturally; fasciole parallel with siphonal canal or arching abaperturally.

Discussion: There is no consensus on the higher classification of *Xanthochorus* within Muricidae. Radwin and d'Attilio (1976) placed *Xanthochorus* in the subfamily Ocenebrinae Cossmann, 1903. Vokes (1996a, b) assigned the genus to the Eragalaxtinae Kuroda, Habe, & Oyama, 1971, a subfamily characterized by irregular varices, denticulate outer lips, and short siphonal canals. S. Kool

(written communication, 5 December 1989) considered the genus as part of the Trophoninae Cossmann, 1903, as did Fischer (1884) and Cossmann (1903). Kool (1993) later indicated that *Trophon* might be more closely related to the ocenebrine genera *Acanthina* Fischer von Waldheim, 1807, and *Nucella* Röding, 1798, than to other genera traditionally assigned to the Trophoninae. R. Houart (written communication, 11 April 2003) suggested that *Xanthochorus*, with its sublateral opercular nucleus, is part of a clade that includes modern species of *Trophon* s.s. (Figures 3, 60).

Fischer's (1884) diagnosis of *Xanthochorus* does not distinguish it from *Trophon* by means of either character he cited. Crenulations on the outer lip, for example, result mostly from strong spiral sculpture (Figures 17, 59). Smooth specimens of *Trophon geversianus* (Pallas, 1774) and *X. cassidiformis* lack crenulations (Figures 14, 60). The presence of a tooth on the outer lip of *X. cassidiformis* is similarly related to spiral sculpture. The small tooth, when present, is an extension of a strengthened anterior primary spiral cord. The tooth differs from those of ocenebrines *Chorus* Gray, 1847, *Acanthina*, and *Hermespina* DeVries & Vermeij, 1997, which are formed by an infolding of the outer shell, and from the two labral teeth of the Recent rapanine *Concholepas concholepas* (Bruguère, 1789), which are thickened quadrate extensions of spiral cords.

The shell of *Xanthochorus* is best differentiated from that of South American species of *Trophon* by the presence of low, flattened, primary spiral cords, secondary cords, and intervening shallow, narrow, V-shaped grooves. Specimens of *Trophon geversianus* are characterized by sharply rounded or weakly triangular spiral cords, often alternately primary and secondary, and broad, U-shaped, flattened interspaces.

A different character distinguishes species of *Xanthochorus* from western South America and *Trophon* species from the upper Miocene Entrerriense formation of Argentina (Brunet, 1997). Comparison of Brunet's figures and material from W. J. Zinsmeister, in part collected by the author (DeVries et al., 1983), shows a remarkable convergence between Argentinian trophonids of about 10 Ma (Scasso et al., 2001) and late Pliocene-to-Recent Peruvian specimens of *Xanthochorus*. The spiral sculpture of Entrerriense trophonids, however, consists of alternating broad flattened primary and secondary spiral cords or, at most, very few secondary cords, in contrast with the more numerous narrower and less flattened secondary cords in *Xanthochorus*. Some increase in secondary cords is evident in the Entrerriense '*Trophon*' *broggi* Brunet, 1997, but not to the degree seen in *Xanthochorus*. It should be noted as well that late Miocene Argentinian trophonids do not resemble contemporaneous late Miocene *Xanthochorus* from Peru, but only late Pliocene to Recent *Xanthochorus* taxa.

The surface sculpture on specimens of *Stramonita*

homogeneous Brunet, 1997, somewhat resembles that found on specimens of *Xanthochorus cassidiformis* with subdued axial sculpture, but the former possesses a parietal ridge and is only similar in appearance with late Pliocene specimens transitional between *X. xuster* and *X. cassidiformis*, not specimens of contemporaneous late Miocene *X. stephanicus*.

Xanthochorus has been accorded both masculine and feminine status in the naming of species. It can be inferred from Fischer (1884) that *Xanthochorus* is the 'yellow' *Chorus*. Whether Gray (1847) meant *Chorus* to refer to a 'group' (chorus, -i, masculine, Latin) or a membrane (chorion, neuter, Greek), is not known, but his failure to choose the Latin word 'corium' to replace 'chorion' suggests that the masculine 'chorus' was his intent.

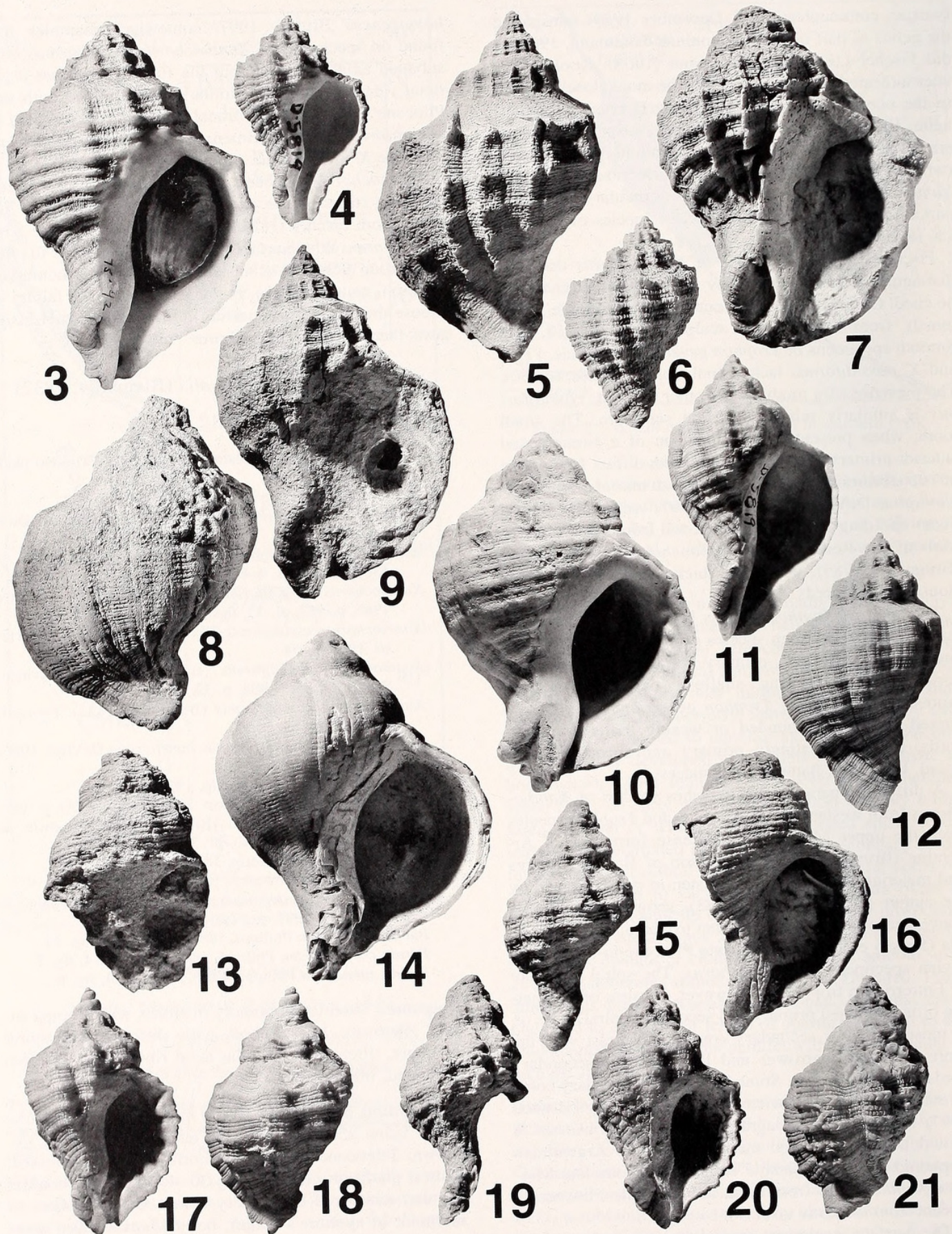
Xanthochorus cassidiformis (Blainville, 1832)

Figures 3–12, 14, 16

- Purpura cassidiformis* Blainville, 1832, p. 230 (also paginated as p. 42).
- Purpura cassidiformis* Hupé in Gay, 1854, p. 188.
- Trophon (Xanthochorus) cassidiformis* Blainville. Dall, 1909, p. 218.
- Xanthochorus cassidiformis* (Blainville). Herm, 1969, p. 136, pl. 16, figs. 6–8.
- Xanthochorus cassidiformis* (Blainville, 1832). DeVries, 1986, p. 587, pl. 37, figs. 5, 7, 8.
- Xanthochorus cassidiformis* (Blainville). Alamo & Valdivieso, 1997, p. 54.
- Xanthochorus cassidiformis* (Blainville, 1832). Guzmán, Saá, & Ortlieb, 1998, p. 32.
- Xanthochorus cassidiformis* (Blainville, 1832). Forcelli, 2000, p. 90, fig. 236.
- Xanthochorus cassidiformis* var. *lamellosa* in DeVries, 1986, p. 589, pl. 37, fig. 9.
- Purpura xanthostoma* Broderip, 1833, p. 8.
- Purpura xanthostoma* Broderip. Hupé in Gay, 1854, p. 189.
- Xanthochorus xanthostoma* (Broderip, 1833). Radwin & d'Attilio, 1976, p. 140, pl. 7, figs. 4, 5.
- Murex squamosus* Broderip, 1833, p. 176.
- Murex squamosus* Sowerby, 1841, pl. 61, fig. 27.
- Coralliophila (Pseudomurex) squamosa* Broderip. Alamo & Valdivieso, 1997, p. 51, fig. 133.
- Buccinum solidum* Philippi, 1887, p. 61, pl. 5, fig. 14.
- Pyrula porphyroidea* Philippi, 1887, p. 52, pl. 4, fig. 7.
- Pyrula subnodosa* Philippi, 1887, p. 55, pl. 4, fig. 6.

Diagnosis: Shell large, broadly fusiform, with sloping sutural platform; body whorl with differentiated spiral sculpture, often with irregular axial ribs. Outer lip often thickened, often dentate.

Description: Shell thick, 40–75 mm long, broadly fusiform. Spire 25–35 percent of length. Protoconch unknown. Teleoconch with 5–6 whorls. Sutures impressed. Sutural platform wide, sloping 30–40 degrees. Shoulder angular, reinforced by primary spiral cord. Periphery at midpoint of aperture's length; body whorl swollen anterior to periphery. Spire whorls with about 12 axial ribs,



bluntly rounded or rarely lamellar. Body whorl with irregular, broadly rounded axial ribs; ribs rarely lamellar or obsolete. Spiral sculpture with 5–7 primary spiral cords: one at shoulder, two straddling periphery, two on anterior portion of body whorl, and 0–2 near base. Interspaces with medial secondary spiral cord and tertiary spiral threads. Sutural platform with 1–2 submedial secondary cords and 8–15 tertiary threads. Intersection of axial and spiral sculpture partially or entirely formed of fine scales. Aperture ovate, about 50 percent of shell length. Outer lip orthocline, tangential to penultimate whorl, with broad, shallow sinus at shoulder in adults, absent in juveniles; inner edge of lip porcellaneous, usually thickened, irregularly beveled, sometimes with 10–12 spirally elongate teeth, sometimes crenulate; rarely with slight extension of next to anteriormost primary spiral cord into small broad tooth. Columella adherent, concave, smooth, porcellaneous. Siphonal canal one-third to one-half length of aperture, somewhat constricted, angled abaperturally 15–30 degrees or rarely straight. Pseudumbilicus wedge shaped. Fasciole prominent, arching parallel to siphonal canal. Operculum with sublateral nucleus.

Type locality: Valparaíso, Chile, gravel and sand bottom, 14–50 m deep.

Discussion: Blainville's (1832) description of *Xanthochorus cassidiformis* and Broderip's (1833) description of *X. xanthostoma* are similar and both species have the same type locality. Axial sculpture, sometimes used to distinguish the two taxa, varies from north to south, with LACM specimens from Chile, the southern end of the modern range, more likely to be strongly sculptured. Some late Pliocene specimens from northern Peru, however, have ribs as strong as those from Chile (Figures 5, 7), whereas some late Pleistocene Chilean specimens have the same muted sculpture as those typical of Peru (Figure 12).

It was suggested by V. Mogollón and R. Houart (2003, personal communications) that *Murex peruvianus* Lamarck, 1816, might be an earlier name for *Xanthochorus cassidiformis*. Lamarck (1822) eventually considered his

taxon from 1816 to be simply "variety b" of *Murex magellanicus* Lamarck, 1822 (= *Trophon geversianus*). Photographs provided by Y. Finet (personal communication, 2003) of two specimens from Lamarck's collection that might be syntypes or holotypes of *M. peruvianus* or *M. magellanicus* 'var. b' are examples of *T. geversianus*. It remains unclear whether these individuals are indeed type specimens, if such specimens were ever collected from Peruvian waters, or if the type locality implicit in the name 'peruvianus' is correct.

Specimens of the Miocene-Pliocene species, *Xanthochorus ochuroma*, sp. nov., typically lack axial ribs on the penultimate and body whorls, lack well differentiated spiral cords, and possess a canaliculate sutural platform and keeled or serrated shoulder. Specimens of two new Pliocene species, *X. xuster* and *X. eripepomis*, lack axial ribs on the penultimate and body whorls and have smoothly rounded shoulders.

The oldest known specimens of *Xanthochorus cassidiformis* (e.g., Figure 16) were found on hillsides overlooking Sacaco (Figure 22). At Sacaco, the shell horizons lie about 8–10 meters above an angular unconformity. A radiometric age of about 3.9 Ma and an early Pliocene diatom flora from lower in the Sacaco section and the position of the oldest marine terrace 100 meters above the occurrences of *X. cassidiformis* (Muizon & DeVries, 1985) suggest an age of about 2–3 Ma for these Sacaco specimens.

Near the northern end of its modern range, specimens of *Xanthochorus cassidiformis* (Figures 5, 7, 9) were found in the Golf Course Member of the upper Pliocene Taime formation of northern Peru (Figure 23) in silty sandstones attributed to lagoonal environments (DeVries, 1986, 1988). Modern specimens in LACM collections come from as far north as Manta, Ecuador (0°55'S).

Material: LACM 75-32 a, W 72.0, L 47.5; LACM 75-32, lot of 5; MUSM INV 023, DV 1418-1, L (59.6), W 43.3; MUSM INV 024, DV 431-1, L 44.0; W (26.1); OSU 37369, DV 244-2, L 54.2, W 41.0; OSU 37371, DV 244-2, L 56.2, W 37.7; UCMP D 5818, L 40.1, W 27.8;

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Figures 3–12, 14, 16. *Xanthochorus cassidiformis*. Figure 3. LACM 75-32 a, apertural view. Length is 72.0 mm. Figure 4. UCMP D 5819 a, apertural view. Length is 30.3 mm. Figure 5. OSU 37371, abapertural view. Length is 56.2 mm. Figure 6. UCMP D 5819 a, abapertural view. Figure 7. OSU 37369, apertural view. Length is 54.2 mm. Figure 8. MUSM INV 023, abapertural view. Length is 59.6 mm. Figure 9. OSU 37371, apertural view. Figure 10. UWBM 97396, apertural view. Length is 61.4 mm. Figure 11. UCMP D-5819 b, apertural view. Length is 47.8 mm. Figure 12. UCMP D-5819 b, abapertural view. Figure 14. UWBM 97397, apertural view. Length is 59.6 mm. Figure 16. UWBM 97398, apertural view. Length is 40.7 mm.

Figures 13, 15, 17–21. *Xanthochorus buxeus*. Figure 13. UWBM 97401, lateral view. Length is 33.8 mm. Note axial ribs extending to penultimate whorl. Broken; anterior missing. Figure 15. UWBM 97400, apertural view. Length is 31.3 mm. Figure 17. MUSM INV 025, apertural view. Length is 35.3 mm. Figure 18. MUSM INV 025, abapertural view. Figure 19. UWBM 97400, lateral view. Figure 20. UWBM 97399, apertural view. Length is 32.6 mm. Figure 21. UWBM 97399, abapertural view.

UCMP 5819, lot of 21; UCMP D 5819 a, L 30.3, W 19.2; UCMP D-5819 b, L 47.8, W 28.4; UCMP D 5819-c, L 30.4, W 19.5; UWBM 97396, WJZ 345, L 61.4, W 43.3; UWBM 97397, DV 732-1, L 59.6, W 46.1; UWBM 97398, DV 431-1, L (40.7), W (28.4); WJZ 345, lot of 17.

Occurrence: Late Pliocene, northern Peru to southern Peru. Pleistocene: Southern Peru to southern Chile. Recent: Ecuador to southern Chile.

Xanthochorus buxeus (Broderip, 1833)

Figures 13, 15, 17–21

- Murex buxeus* Broderip, 1833, p. 194.
Pollia buxea. Sowerby, 1841, pl. 61, fig. 28.
Purpura buxea Broderip. Hupé in Gay, 1854, p. 191.
Tritonalia buxea Broderip. Dall, 1909, p. 219.
Ocenebra buxea (Broderip). Herm, 1969, p. 91.
Ocenebra buxea (Broderip). Keen, 1971, p. 533, fig. 1031.
Xanthochorus buxea (Broderip, 1833). Marincovich, 1973, p. 33, fig. 69.
Xanthochorus buxeus (Broderip, 1833). Radwin & d'Attilio, 1976, p. 139, fig. 87.
Xanthochorus buxea (Broderip, 1833). DeVries, 1986, p. 590, pl. 37, figs. 3, 4.
Ocenebra buxea (Broderip). Alamo & Valdivieso, 1997, p. 50, fig. 130.
Murex horridus Broderip, 1833, p. 176. [Not Brocchi, 1814].
Murex horridus Broderip. Potiez & Michaud, 1838, p. 417, pl. 33, figs. 12, 13.
Fusus horridus. Sowerby, 1841, pl. 61, fig. 29.
Trophon (*Xanthochorus*) *horridus* Broderip. Dall, 1909, p. 218.
Murex broderipii Michelotti, 1841, p. 41.
Xanthochorus broderipii (Michelotti). Keen, 1971, p. 556, fig. 1097.
Xanthochorus broderipii (Michelotti). Alamo & Valdivieso, 1997, p. 54.
Murex boivini Kiener, 1842, v. 7, p. 81, pl. 43, fig. 2.

Diagnosis: Shell small, high-spired, with strong axial and spiral sculpture on all whorls; shoulder rounded; outer lip thickened, crenulate or dentate.

Description: Shell thick, up to 35 mm long, stoutly fusiform. Spire 35–45 percent of height. Protoconch unknown. Teleoconch with 4 whorls. Sutures slightly impressed. Sutural platform planar to slightly convex, inclined 30–50 degrees. Shoulder rounded to intermittently angular, reinforced by a primary spiral cord. Periphery at or posterior to midpoint of aperture's length; body whorl weakly swollen near base of aperture. Whorls with 8–12 evenly spaced axial ribs, becoming more irregular on body whorl and extending to base. Spiral sculpture with 5–6 evenly spaced primary spiral cords between shoulder and base, with 2–3 secondary cords in interspaces. Sutural platform with 5–8 secondary spiral cords. Tiny scales present at intersection of spiral cords and growth lines. Aperture ovate, about 30–40 percent of shell length. Outer lip slightly prosocline, nearly tangential to

penultimate whorl, without broad sulcus at shoulder; thickened, beveled, with 7–8 circular or spirally elongate teeth along inner edge. Columella adherent, smooth, porcellaneous, concave. Siphonal canal short, about one-quarter to one-third length of aperture; constricted by swollen and thickened outer lip; angled about 20 degrees abaperturally. Pseudumbilicus wedge shaped. Fasciole strong, arched.

Type locality: Iquique, Chile, "sandy bottom at the depth of eighteen fathoms" (Broderip, 1833, p. 194) (18 fm = ~35 m).

Discussion: The oldest known specimens of *Xanthochorus buxeus* (e.g., Figures 15, 19) are found at Sacaco (Figure 22) with specimens of *X. xuster* near the foot of the Sacaco hills in bioclastic sandstone 18 meters above an angular unconformity and 10 meters above the first known occurrence of *X. cassidiformis*. A single specimen of *Xanthochorus* (Figure 13) from a nearby horizon (DV 739-1) has a rounded shoulder and strong axial ribs on the spire whorls, like *X. buxeus*, but no axial ribs on the body whorl, nor well differentiated primary spiral cords, both characters of *X. xuster*, with which the morphologically intermediate specimen also occurs.

Adult specimens of *Xanthochorus buxeus* differ from comparably sized juvenile specimens of *X. cassidiformis* (Figures 4, 6, 11, 12) in possessing a rounded shoulder and stronger, more regular axial ribs. The persistence of regular rounded ribs onto the body whorl of *X. buxeus* represents a paedomorphic expression of patterns of axial sculpture seen in older fossil species of the genus.

Specimens of *Xanthochorus buxeus* at 18 and 34 m in the Sacaco section occur with the gastropods *Polinices*, *Nassarius*, *Mitrella*, and *Cancellaria buccinoides* Sowerby, 1832, and with single valves reworked from beds above and below containing paired valves of *Pitar* and *Mulinia*. Such bivalve associations in northern Peru were attributed to nearshore shelf environments (DeVries, 1986), consistent with settings observed for modern populations of *X. buxeus* off Chile (Guzmán et al., 1998).

Material: MUSM INV 025, DV 465a-1, L 35.3, W 22.3; MUSM INV 026, DV 1422-2, L 29.4, W (15.5); OSU 37569, DV 136, L 29.8, W 16.9; UWBM 97399, DV 465a-1, L 32.6, W 20.7; UWBM 97400, DV 1422-2, L 31.3, W (16.2); UWBM 97401, DV 739-1, L (33.8), W (22.2).

Occurrence: Late Pliocene: southern Peru. Pleistocene: Southern Peru to central Chile. Recent: North-central Peru to central Chile.

Xanthochorus xuster, sp. nov.

Figures 24–30, 32–34

Diagnosis: Shell with rounded shoulder; axial sculpture absent or nearly so on penultimate and body whorls; spi-

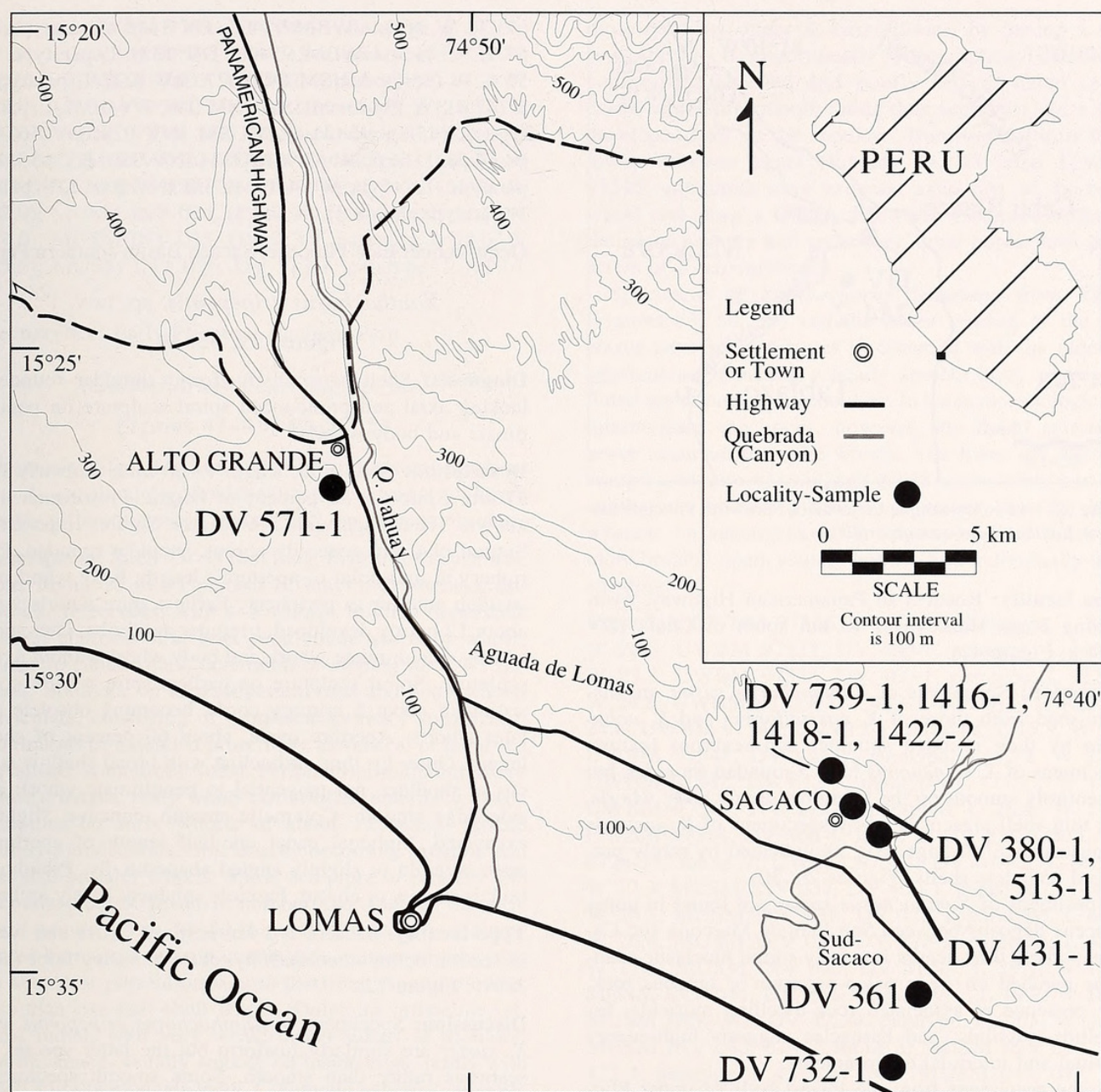


Figure 22. Sacaco and vicinity with (a) type locality of *Xanthochorus eripepomis*, sp. nov. (DV 380), (b) type locality of *Xanthochorus stephanicus*, sp. nov. (DV 571), and other locality-samples referred to in text.

ral sculpture of barely differentiated cords and threads entirely covered with rasplike scales.

Description: Shell thin to moderately thick, length to 70 mm, fusiform. Spire 25 percent of shell length. Protoconch unknown. Teleoconch with 5–6 whorls. Sutures impressed. Sutural platform absent or weakly developed; shoulder broadly, evenly rounded. Periphery just posterior to midpoint of aperture's length; body whorl slightly swollen near base of aperture. Earliest whorls with about 12 closely spaced axial ribs; axial sculpture usually ab-

sent on penultimate and body whorls. Spiral sculpture of up to 100 spiral cords and threads; every fourth cord somewhat strengthened; rasplike scales produced at intersection of colabral growth lines and spiral cords. Outer lip orthocline, nearly tangential to penultimate whorl, with broad, shallow sinus between suture and periphery; inside edge weakly crenulate. Columella smooth, concave, slightly excavated. Siphonal canal one-half length of aperture, open, usually straight. Pseudumbilicus small, narrow; fasciole barely arched.

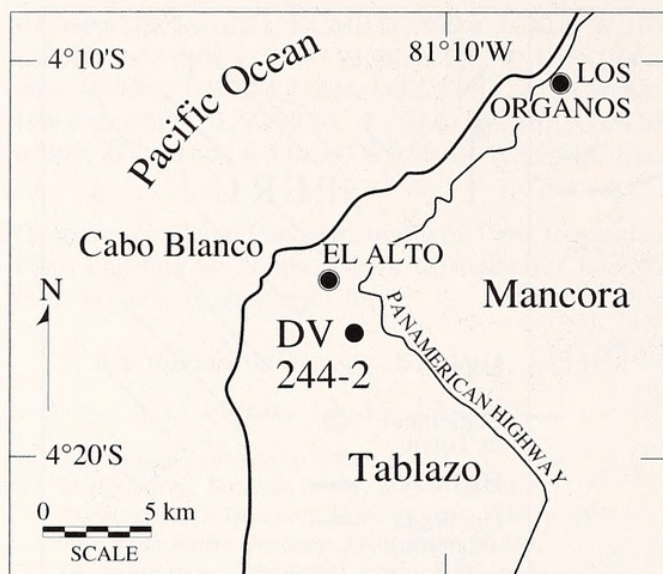


Figure 23. Locality-sample in northern Peru with Pliocene fossils of *Xanthochorus cassidiformis*.

Type locality: Roadcut in Panamerican Highway, overlooking Playa Huaccyaco, 10 km south of Chala (DV 1254-8; Figure 40).

Discussion: Specimens of *Xanthochorus xuster* are distinguished from those of *X. cassidiformis* and *X. ochuroma* by their rounded shoulder and scabrous texture. Specimens of *X. eripepomis* have a rounded shoulder, but are entirely smooth on the penultimate and body whorls. The thin shell present in many specimens of *X. xuster* is a consequence of diagenesis, as indicated by rarely preserved complete shells (Figures 26, 30).

Specimens of *Xanthochorus xuster* are found in upper Pliocene deposits between San Juan de Marcona and Camaná, where they occur in poorly sorted bioclastic sandstone perched on steep paleo-outcrops of igneous rock. The presence of associated rock-dwelling muricids, fissurellids, mytilids, and barnacles suggests high-energy subtidal and intertidal environments.

Some specimens from the lowest beds of upper Pliocene sequences at Sacaco and near Acarí are morphologically intermediate between *Xanthochorus xuster* and *X. cassidiformis* (Figures 28, 29). They have a broad aperture and primary spiral cord on a weakly angled shoulder, as do specimens of *X. cassidiformis* (e.g., Figure 14) and scabrous, poorly differentiated spiral cords, as do specimens of *X. xuster*. One of the specimens (Figure 29) was found together with fossils of *X. cassidiformis* and *X. buxeus*.

Etymology: 'xuster,' Greek noun for 'rasp,' referring to scabrous texture of shell.

Material: UWBM 97402, DV 1254-8, holotype, L (52.8), W 35.8; UWBM 97403, DV 739-1, paratype, L 56.0, W 37.9; UWBM 97404, DV 1331-1, paratype, L

(43.2), W 36.2; UWBM 97405, DV 1418-1, paratype, L 67.9, W 44.9; UWBM 97406, DV 1331-1, paratype, L 55.6, W (35.6); MUSM INV 027, DV 1032-1, paratype, L (47.0), W (34.0); MUSM INV 028, DV 1031-1, paratype, L (45.8), W (31.4); MUSM INV 029, DV 567-2, paratype, L 66.6, W 43.9; MUSM INV 030, DV 1331-1, paratype, L (45.5), W 34.7; MUSM INV 031, DV 1416-1, paratype, L (48.3), W (44.3).

Occurrence: Late Pliocene, Sacaco Basin, southern Peru.

Xanthochorus eripepomis, sp. nov.

Figures 31, 35–39

Diagnosis: Shell narrowly fusiform; shoulder rounded; lacking axial and pronounced spiral sculpture on penultimate and body whorls.

Description: Shell thin, length to 60 mm, narrowly fusiform. Spire 25–35 percent of height. Protoconch unknown. Teleoconch with 5–6 whorls. Sutures impressed. Sutural platform generally absent; shoulder rounded. Periphery at mid-point of aperture's length; body whorl not swollen anterior to periphery. Earliest spire whorls with about 12 poorly developed, irregular axial ribs; later spire whorls, penultimate whorl, and body whorl without axial sculpture. Spiral sculpture on earliest spire whorls consisting of about 8 primary cords, becoming obsolete on later whorls. Aperture ovate, about 60 percent of shell length. Outer lip thin, orthocline with broad shallow sulcus at shoulder, not tangential to penultimate whorl; inside edge smooth. Columella smooth, concave, slightly excavated. Siphonal canal one-half length of aperture, open, straight or slightly angled abaperturally. Pseudumbilicus narrow or absent. Fasciole subdued, barely arched.

Type locality: Sacaco, 1–2 km north of house and well, in section below unconformity, close to valley floor (DV 380-1; Figure 22).

Discussion: Specimens of *Xanthochorus eripepomis* and *X. xuster* are similarly fusiform but the latter species is scabrous rather than smooth. Some smooth specimens (Figures 31, 36) with a weakly canaliculate sutural platform and shoulder keel are morphologically intermediate between *X. ochuroma* and *X. eripepomis*.

Typical examples of *Xanthochorus eripepomis* from Sacaco occur in deposits of cross-bedded sandstone with thick lenticular accumulations of well-preserved bivalves (*Anadara*, *Amiantis*, *Dosinia*, and *Eurhomalea*), numerous small gastropods (*Nassarius*, *Polinices*), and several entire skeletons of large cetaceans, suggesting a nearshore environment with shallow sandbars and strong currents (Muizon & DeVries, 1985).

Etymology: 'eripepomis,' from 'eripenti,' Greek adjective for 'fallen,' and 'epomis,' Greek noun for 'shoulder'; describing the steeply sloped shoulders of these specimens.

Material: UWBM 97531, DV 380-1, holotype, L (47.1), W 31.7; UWBM 97532, DV 513-1, paratype, L (32.4), W 22.4; UWBM 97533, DV 513-1, paratype, L 41.2, W (22.7); UWBM 97534, DV 513-1, paratype, L (27.9), W 23.4; UWBM 97535, DV 513-1, paratype, L (20.8), W 16.9; MUSM INV 032, DV 513-1, paratype, L (42.2), W 28.3; MUSM INV 033, DV 513-1, paratype, L (31.5), W (18.9); MUSM INV 034, DV 513-1, paratype, L 31.6, W (17.0); MUSM INV 035, DV 513-1, paratype, L 28.0, W (15.6); MUSM INV 036, DV 513-1, paratype, L (29.0), W 20.9.

Occurrence: Early Pliocene, southern Peru.

Xanthochorus ochuroma, sp. nov.

Figures 41–45, 47–50, 53

Diagnosis: Shell fusiform to pyriform; sutural platform usually canaliculate; shoulder turriculate; spiral sculpture poorly differentiated on body whorl, sometimes obsolete.

Description: Shell 45–55 mm long, fusiform to pyriform. Spire about 25 to 35 percent of length. Protoconch unknown. Teleoconch with 4–5 whorls. Sutures impressed. Sutural platform of at least penultimate and body whorls planar to canaliculate, horizontal or sloping up to 45 degrees. Shoulder on at least penultimate and body whorls turriculate, consisting of prominent primary spiral cord, continuous or extended posteriorly as vertical or incurved serrations, sometimes fluted. Periphery at midpoint of aperture's length; body whorl not swollen anteriorly. Axial sculpture on early whorls of about 12 evenly spaced bluntly rounded axial ribs, usually becoming irregular and obsolete on later whorls. Spiral sculpture of primary and secondary cords, fewer in number and rounded on early spire whorls, up to 30–40 in number, flattened, and separated by narrow incised interspaces on later whorls; may be absent or present on sutural platform. Aperture ovate, less than one-half shell length. Outer lip orthocline, almost radial, with very weak, broad sulcus at shoulder; not thickened, usually smooth on inside edge, rarely with 8–10 spirally elongate teeth. Columella adherent, smooth, concave. Siphonal canal just over half of aperture's length, open to slightly constricted, angled 5–20 degrees abaperturally. Pseudumbilicus narrow to absent. Fasciole weak, not strongly arched.

Type locality: DV 472-1, Pampa de Los Chinos, 7 km south of Changuillo (Figure 61).

Discussion: Specimens of *Xanthochorus ochuroma* are common in an upper Miocene-lower Pliocene tidal deltaic sequence that occupies the distal reaches of the Rio Grande and Rio Nazca valleys. Rocks at the type locality near Yauca, 120 km south of Nazca, include cobble conglomerates and sandstones deposited at the mouth of the ancestral Río Yauca.

Specimens of *Xanthochorus ochuroma* differ from

those of the younger *X. cassidiformis* by having a narrower profile; a proportionally longer siphonal canal; exceptionally flattened and poorly differentiated spiral cords, which are smooth rather than scabrous; and a well developed keel on the shoulder. Transitional forms from lower Pliocene strata (Figures 45, 48; also UWBM 97545, unfigured) have irregular axial ribs on the body whorl and show a tendency towards increased differentiation of primary and secondary spiral cords, both characters of *X. cassidiformis*.

Specimens of *Xanthochorus ochuroma* from Yauca (Figures 43, 50, 53) and the lower reaches of the Rio Nazca have some features in common with the older *X. stephanicus*, including a nearly smooth body whorl and fluted serrations on the shoulder. In these morphologically intermediate specimens, however, the fluted serrations never occur on the spire whorls. The flutes are laterally compressed, almost solid, and grade successively into one another to produce a nearly continuous shoulder keel, whereas on specimens of *X. stephanicus* the flutes are more broadly open, usually hollow, and individually free-standing.

Material: UWBM 97536, DV 614-3, holotype, L 46.0, W 28.6; UWBM 97537, DV 460-1, paratype, L (43.7), W 27.3; UWBM 97538, DV 460-1, paratype, L (27.8), W 24.8; UWBM 97539, DV 472-1, paratype, L 36.0, W 21.8; UWBM 97540, DV 613-1, paratype, L 15.9, W 9.5; UWBM 97541, DV 472-1, paratype, L 32.2, W 21.6; UWBM 97542, DV 613-3, paratype, L (27.7), W 17.9; UWBM 97543, DV 613-1, paratype, L 28.4, W 17.6; UWBM 97544, DV 460-1, lot of 2; UWBM 97545, DV 472a-13, lot of 2; UWBM 97551, DV 614-3, L (40.3), W 30.3; MUSM INV 037, DV 460-1, paratype, L (44.6), W 26.3; MUSM INV 038, DV 472-1, paratype, L 40.3, W 26.6; MUSM INV 039, DV 472-1, paratype, L 31.0, W 17.5; MUSM INV 040, DV 513-1, L 29.1, W 15.0; MUSM INV 041, DV 361-10, paratype, L 19.2, W 10.5; MUSM INV 042, DV 472-4, paratype, L 38.5, W 26.3; MUSM INV 043, 614-3, lot of 3; MUSM INV 044, DV 472-4, paratype, L 41.3, W 24.8; MUSM INV 047, DV 614-3, lot of 3; MUSM INV 049, DV 613-1, lot of 2.

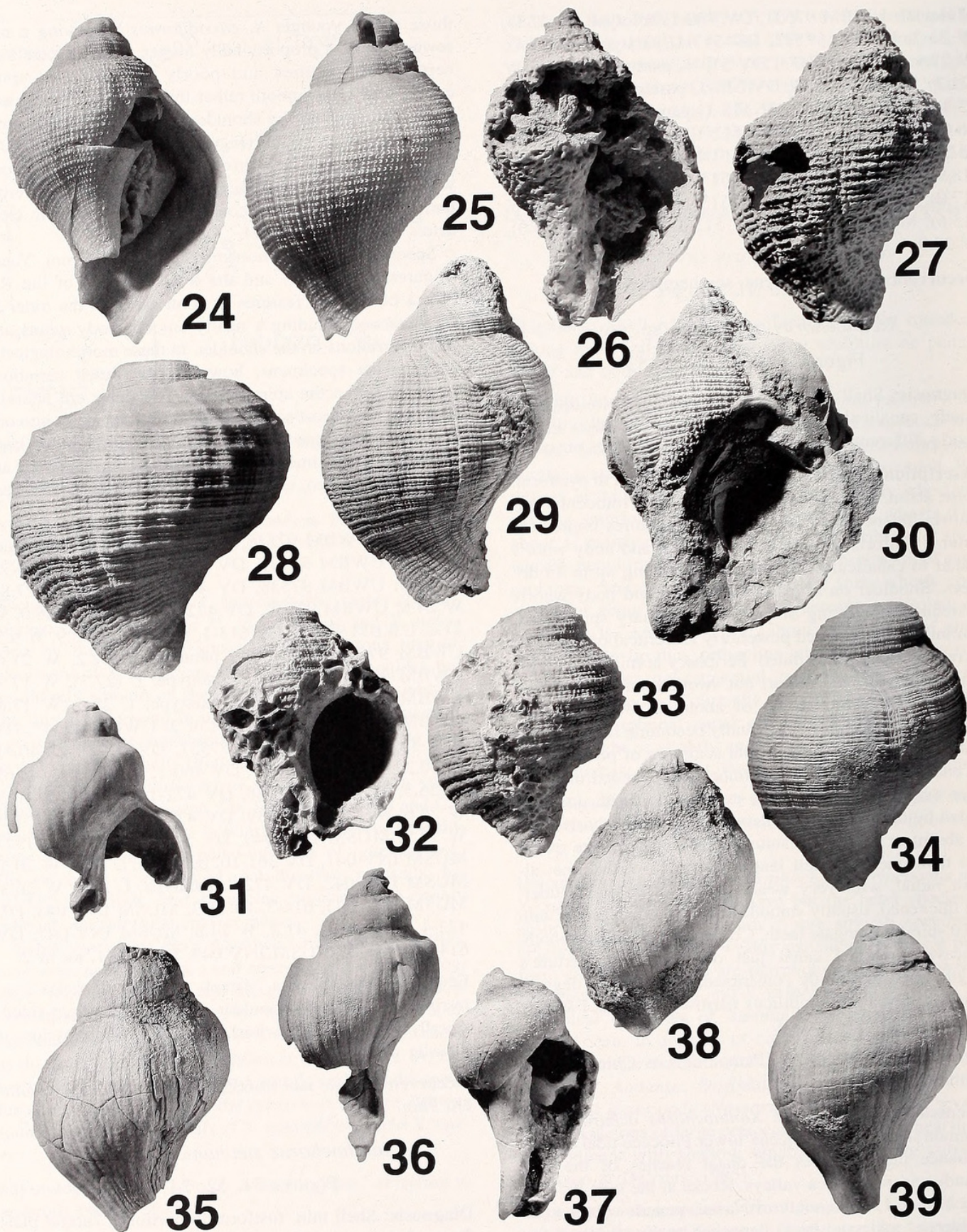
Etymology: 'ochuroma,' Greek noun for 'fortress', referring to the keeled shoulder and nearly straight-sided, spirally grooved body whorl that give the impression of a castle wall.

Occurrence: Late late Miocene to early Pliocene, southern Peru.

Xanthochorus stephanicus sp. nov.

Figures 51, 52, 54–58

Diagnosis: Shell thin, fusiform to pyriform; sutural platform of most whorls typically canaliculate, shoulder of most whorls typically turriculate with numerous fluted serrations.



Description: Shell 40–45 mm long, fusiform to pyriform, length-to-width proportion about 1.6 to 1.7. Spire 35–45 percent of height. Protoconch unknown. Teleoconch with 4–5 whorls. Sutures deeply impressed. Sutural platform of all but first whorl typically canaliculate, horizontally planar. Shoulder on all but first spire whorl typically with 9–12 bluntly solid or fluted serrations; serrations upright or incurved. Periphery posterior to mid-point of aperture's length; body whorl not swollen anteriorly. Axial sculpture on early spire whorls of lamellar or bluntly rounded ribs extending partly or entirely to base from fluted shoulder serrations. Ribs on later whorls irregular, typically extending anteriorly less than half the whorl's length. Spiral sculpture on early spire whorls of about 7–8 subdued cords; body whorl with 20–40 flattened, subdued to obsolete cords and threads. Aperture ovate to quadrate, less than one-half length of shell. Outer lip orthocline, almost radial, with broad weak sulcus at shoulder; very thin, smooth on inside edge. Columella thin, adherent, smooth, weakly concave. Siphonal canal about half of aperture's length, open, somewhat constricted by anterior constriction of outer lip; straight or angled up to 10 degrees abaperturally. Pseudumbilicus very narrow. Fasciole weakly to moderately developed, straight or slightly arched.

Type locality: Alto Grande, south of intersection of Pan-american Highway with abandoned paved road to San Juan de Marcona (DV 571-1; Figure 22).

Discussion: Lamellar ribs with hollow fluted serrations on the shoulder, including discrete flutes on spire whorls, distinguish specimens of *Xanthochorus stephanicus* from those of all younger species of *Xanthochorus*. Specimens with well developed lamellar ribs resemble South American examples of *Trophon*, except that the lamellar ribs of *X. stephanicus* rarely extend across the midpoint of the body whorl and flare radially much less (Figure 57) than axial ribs in such species of *Trophon* as *T. geversianus* (Figures 59, 60).

Etymology: 'stephanicus,' from 'stephanis,' Greek noun

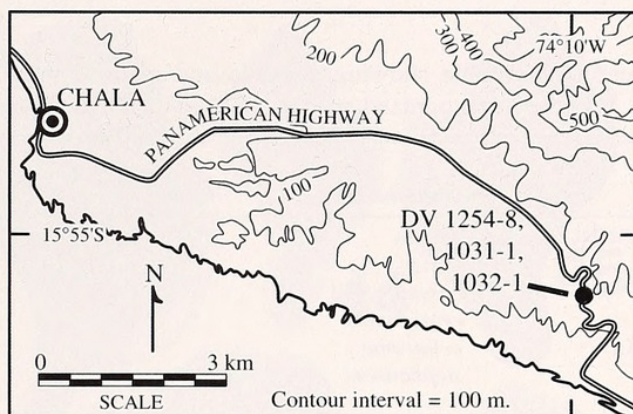


Figure 40. Type locality (DV 1254) and other locality-samples for *Xanthochorus xuster*, sp. nov.

for 'parapet,' Latinized adjective referring to the serrated wall ascending along the shoulder of the whorls.

Material: UWBM 97546, DV 571-1, holotype, L (36.1), W 24.1; UWBM 97547, DV 571-1, paratype, L (9.6), W 9.9; UWBM 97548, DV 571-1, paratype, L (35.0), W 20.7; UWBM 97549, DV 571-1, lot of 2; UWBM 97550, DV 571-1, paratype, L (33.1), W 20.0; MUSM INV 045, DV 571-1, paratype, L (35.2), W 22.4; MUSM INV 046, DV 571-1, paratype, L (10.7), W 9.4; MUSM INV 048, DV 571-1, paratype, L (29.6), W 17.3.

Occurrence: Early late Miocene, southern Peru.

DISCUSSION

Morphological variability within collections of *Xanthochorus* from the same locality and from correlative stratigraphic horizons is so great that a cladistic analysis of characters would require comparing means and standard deviations for characters measured on a large number of individuals. The scarcity of large numbers for some species presently precludes such a statistical treatment.

What remains are two lines of evidence for delineating phylogenetic relationships: stratigraphic occurrence and

Figures 24–30, 32–34. *Xanthochorus xuster*, sp. nov. Figure 24. UWBM 97402, holotype, apertural view. Length is 52.8 mm. Figure 25. UWBM 97402, abapertural view. Figure 26. UWBM 97403, paratype, apertural view. Length is 56.0 mm. Figure 27. UWBM 97403, abapertural view. Figure 28. MUSM INV 031, paratype, abapertural view. Length is 48.3 mm. Figure 29. UWBM 97405, paratype, abapertural view. Length is 67.9 mm. Figure 30. MUSM INV 029, paratype, apertural view. Length is 66.6 mm. Figure 32. MUSM INV 030, paratype, apertural view. Length is 45.5 mm. Figure 33. MUSM INV 030, abapertural view. Figure 34. MUSM INV 027, paratype, abapertural view. Length is 47.0 mm.

Figures 31, 35–39. *Xanthochorus eripepomis*, sp. nov. Figure 31. UWBM 97534, paratype, apertural view. Length is 27.9 mm. Figure 35. MUSM INV 032, paratype, abapertural view. Length is 42.2 mm. Figure 36. MUSM INV 034, paratype, abapertural view. Length is 31.6 mm. Figure 37. UWBM 97532, paratype, apertural view. Length is 32.4 mm. Figure 38. UWBM 97531, holotype, abapertural view. Length is 47.1 mm. Figure 39. MUSM INV 033, paratype, abapertural view. Length is 31.5 mm.

Table 1

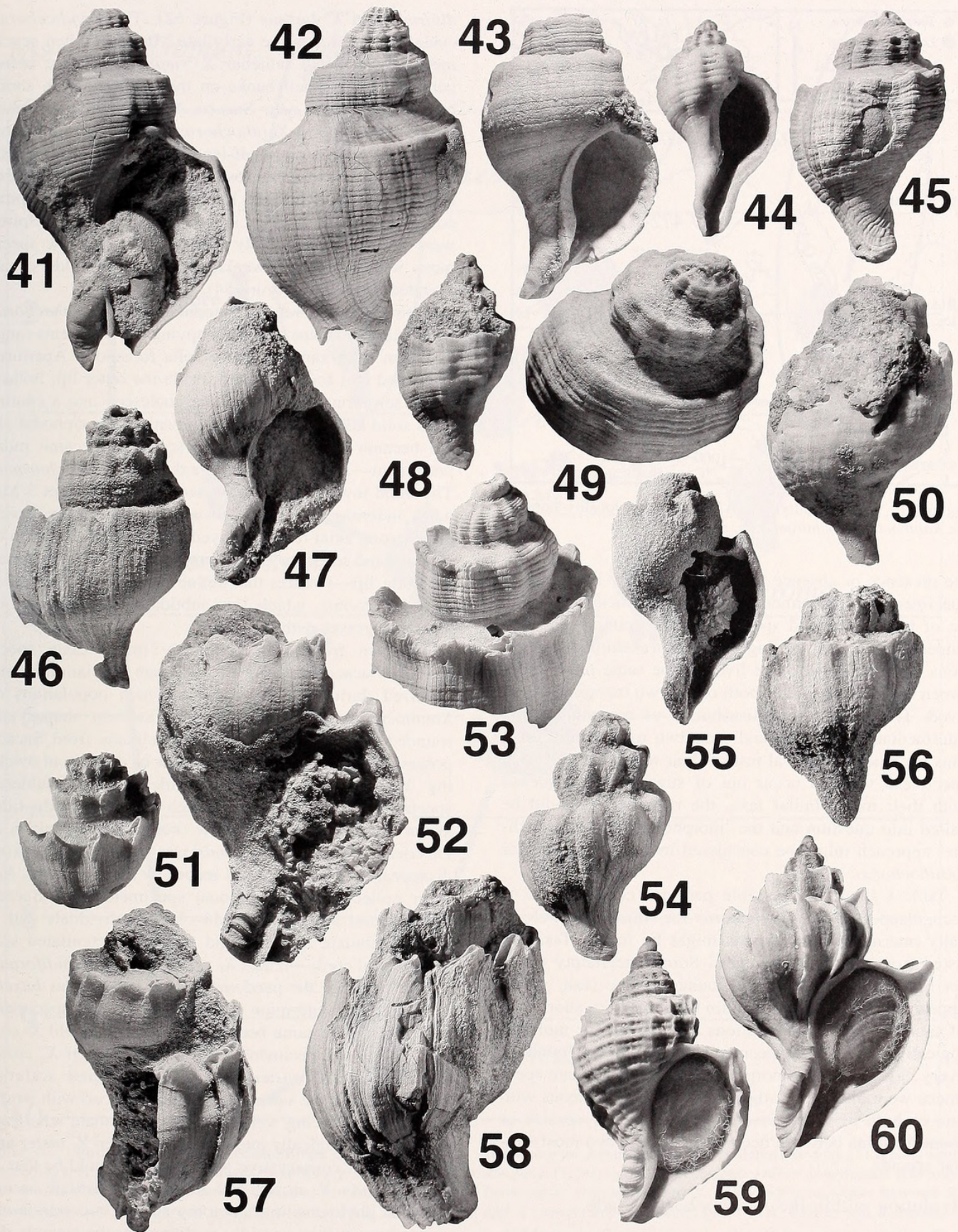
Contingency table showing possible and realized intermediate morphologies in specimens inferred to be transitional between recognized species of *Xanthochorus*. Specific characters for transitional specimens are listed below.

		YOUNG ← OLD					
	<i>Xanthochorus</i>	<i>buxeus</i>	<i>xuster</i>	<i>cassidiformis</i>	<i>eripepomus</i>	<i>ochuroma</i>	<i>stephanicus</i>
YOUNG	<i>buxeus</i>	—	✓				
	<i>xuster</i>		—	✓		✓	
↑	<i>cassidiformis</i>			—		✓	
	<i>eripepomus</i>				—	✓	
OLD	<i>ochuroma</i>					—	✓
	<i>stephanicus</i>						—
<i>buxeus/xuster</i>							
rounded axial ribs on penultimate whorl - <i>buxeus</i>							
rounded shoulder - <i>buxeus</i>							
poorly differentiated spiral sculpture - <i>xuster</i>							
scaley surface - <i>xuster</i>							
<i>cassidiformis/ochuroma</i>							
some degree of differentiation of spiral sculpture - <i>cassidiformis</i>							
keeled shoulder - <i>ochuroma</i>							
narrow aperture and body whorl - <i>ochuroma</i>							
<i>xuster/cassidiformis</i>							
angular, non-keeled shoulder - <i>cassidiformis</i>							
broad aperture and body whorl - <i>cassidiformis</i>							
scaley surface - <i>xuster</i>							
poorly differentiated spiral sculpture - <i>xuster</i>							
<i>eripepomus/ochuroma</i>							
smooth surface - <i>eripepomus</i>							
weakly keeled shoulder - <i>ochuroma</i>							
<i>ochuroma/stephanicus</i>							
spiral sculpture on all whorls - <i>ochuroma</i>							
absence of fluted keel on early whorls - <i>ochuroma</i>							
high keel on shoulder - <i>stephanicus</i>							
incipient fluting on keel - <i>stephanicus</i>							

Figures 41–45, 47–50, 53. *Xanthochorus ochuroma*, sp. nov. Figure 41. UWBm 97536, holotype, apertural view. Length is 46.0 mm. Figure 42. UWBm 97536, paratype, abapertural view. Figure 43. UWBm 97537, apertural view. Length is 43.7 mm. Figure 44. MUSM INV 040, paratype, apertural view. Length is 29.1 mm. Figure 45. UWBm 97539, paratype, abapertural view. Length is 36.0 mm. Figure 47. MUSM INV 037, paratype, apertural view. Length is 44.6 mm. Figure 48. MUSM INV 041, paratype, abapertural view. Length is 19.2 mm. Figure 49. MUSM INV 039, paratype, oblique spire view. Length (not visible) is 31.0 mm. Figure 50. UWBm 97537, abapertural view. Figure 53. UWBm 97538, oblique spire view. Length (not visible) is 27.8 mm.

Figures 46, 51, 52, 54–58. *Xanthochorus stephanicus*, sp. nov. Figure 46. MUSM INV 045, paratype, abapertural view. Length is 35.2 mm. Figure 51. UWBm 97547, paratype, oblique spire view. Length (not visible) is 9.6 mm. Figure 52. UWBm 97546, holotype, apertural view. Length is 36.1 mm. Figure 54. MUSM INV 048, paratype, abapertural view. Length is 29.6 mm. Figure 55. UWBm 97548, paratype, apertural view. Length is 35.0 mm. Figure 56. UWBm 97548, abapertural view. Figure 57. UWBm 97546, oblique lateral view. Figure 58. UWBm 97546, abapertural view.

Figures 59, 60. *Trophon geversianus*. Figure 59. DeVries private collection, Punta Villarino, Golfo San José, Chubut Province, Argentina, apertural view. Length is 37.6 mm. Figure 60. DeVries private collection, Punta Villarino, Golfo San José, Chubut Province, Argentina, apertural view. Length is 44.9 mm.



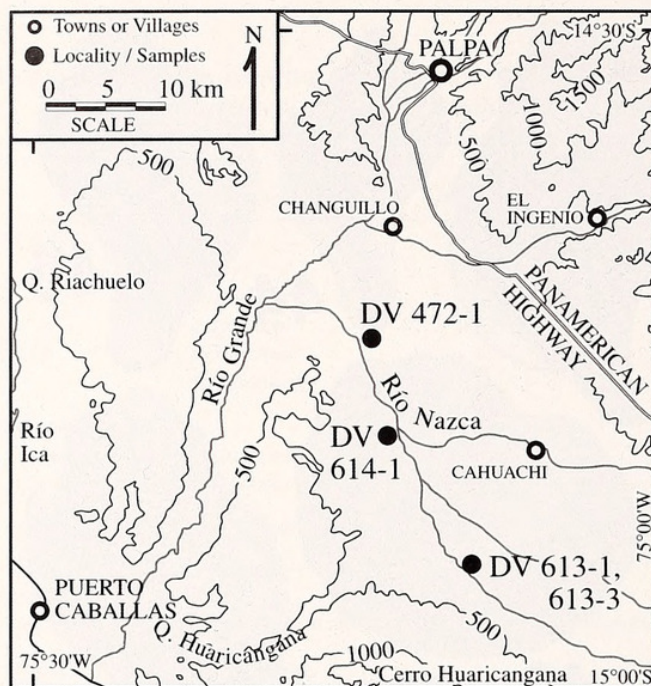


Figure 61. Type locality (DV 472) and other locality-samples for *Xanthochorus ochuroma*, sp. nov.

the presence or absence of morphologically intermediate specimens, i.e., specimens exhibiting characters diagnostic of two recognized species. Such specimens are presumed to represent phylogenetically transitional populations and inferred to have lived at the same time or between times when one or both of the two recognized taxa lived. The stratigraphic distribution of morphologically intermediate specimens and their two most similar taxa thus becomes a minimal test of their relatedness. If such specimens were to occur out of stratigraphic sequence with their most similar taxa, the relatedness should be called into question and the 'morphologically intermediate' approach might be considered invalid altogether for *Xanthochorus*.

Table I shows all possible pairwise combinations of recognized taxa of *Xanthochorus* for which morphologically intermediate specimens might be found. Taxa are listed from oldest to youngest. Some uncertainty exists for the relative ages of the youngest three taxa, which appear to have originated within the same very short span of time. Checked combinations are marked for morphologically intermediate specimens that have been found. In every case for which morphologically intermediate specimens were discovered, they were contemporaneous with one or both of their associated most similar species or found in strata between occurrences of the two most similar species.

Evolution within the *Xanthochorus* Clade

Fossil specimens of *Xanthochorus* from Peru establish a probable origin for the two modern species, *X. cassi-*

diformis and *X. buxeus* (Figure 62). The *Xanthochorus* clade has its root in the early late Miocene, when specimens of the small lamellar *X. stephanicus* were being concentrated in shell banks on the exposed north shore of an embayment near Sacaco. Within-population phenotypic variation in *Xanthochorus* was already the norm. Most individuals had half-length fluted axial ribs, but some had rounded axial ribs on the earliest whorls. Spiral cords were usually absent, but on some shells weak spiral cords were present, especially on earlier whorls. Spires were generally moderately high, except in a few specimens with tall spires, weakly turruculate shoulders, and rounded axial ribs (Figure 54).

Between 9 Ma and 3 Ma populations of *Xanthochorus* became more robust while occupying environments ranging from open sandy shelf to delta foreshore. Apertures thickened and acquired teeth inside the outer lip; hollow fluted serrations on the shoulder coalesced into a continuous solid keel of diminishing elevation; the siphonal canal became shorter; and spiral sculpture became more prominent—a suite of characters that define *X. ochuroma*. The trend towards robustness accelerated at about 3 Ma, when individuals of *X. ochuroma* became larger; developed strong axial ribs; displayed greater differentiation of primary and secondary spiral cords; and greatly thickened the outer lip—features that define modern populations of *X. cassidiformis*, which live subtidally on substrates of sand and gravel with *X. buxeus*.

Evidence from morphologically intermediate specimens at Sacaco indicates two separate speciation events occurred during the Pliocene in which populations of *Xanthochorus* arose with narrow fusiform shapes and rounded shoulders. Transitional specimens from Sacaco possess features of keeled specimens of delta-front dwelling *X. ochuroma* and smooth-sided, slope-shouldered specimens of *X. eripepomis*, which inhabited sandy, tide-swept shoals fronting a narrow coastal plain (Muizon & DeVries, 1985). *X. eripepomis* was a short-lived taxon, disappearing from the fossil record by about 2.5 Ma. Another collection of transitional specimens from Sacaco from around 3 Ma to 2.5 Ma—large individuals with a weakly tabulate shoulder and poorly differentiated scabrous spiral cords—unites *X. xuster* with *X. cassidiformis*.

The origin of the paedomorphic *Xanthochorus buxeus* is difficult to determine because the earliest specimens are found in the same beds at Sacaco as very old *X. cassidiformis* and specimens transitional between *X. cassidiformis* and *X. xuster*. A round-shouldered scabrous specimen from the same stratigraphic interval with strong axial ribs advancing well onto the penultimate whorl appears morphologically intermediate between *X. xuster* and *X. buxeus*. A conservative interpretation would be that *X. cassidiformis*, *X. xuster*, and *X. buxeus* constitute an unresolved phylogenetic trichotomy sharing a common ancestor from within a rapidly evolving lineage recently descended from *X. ochuroma*.

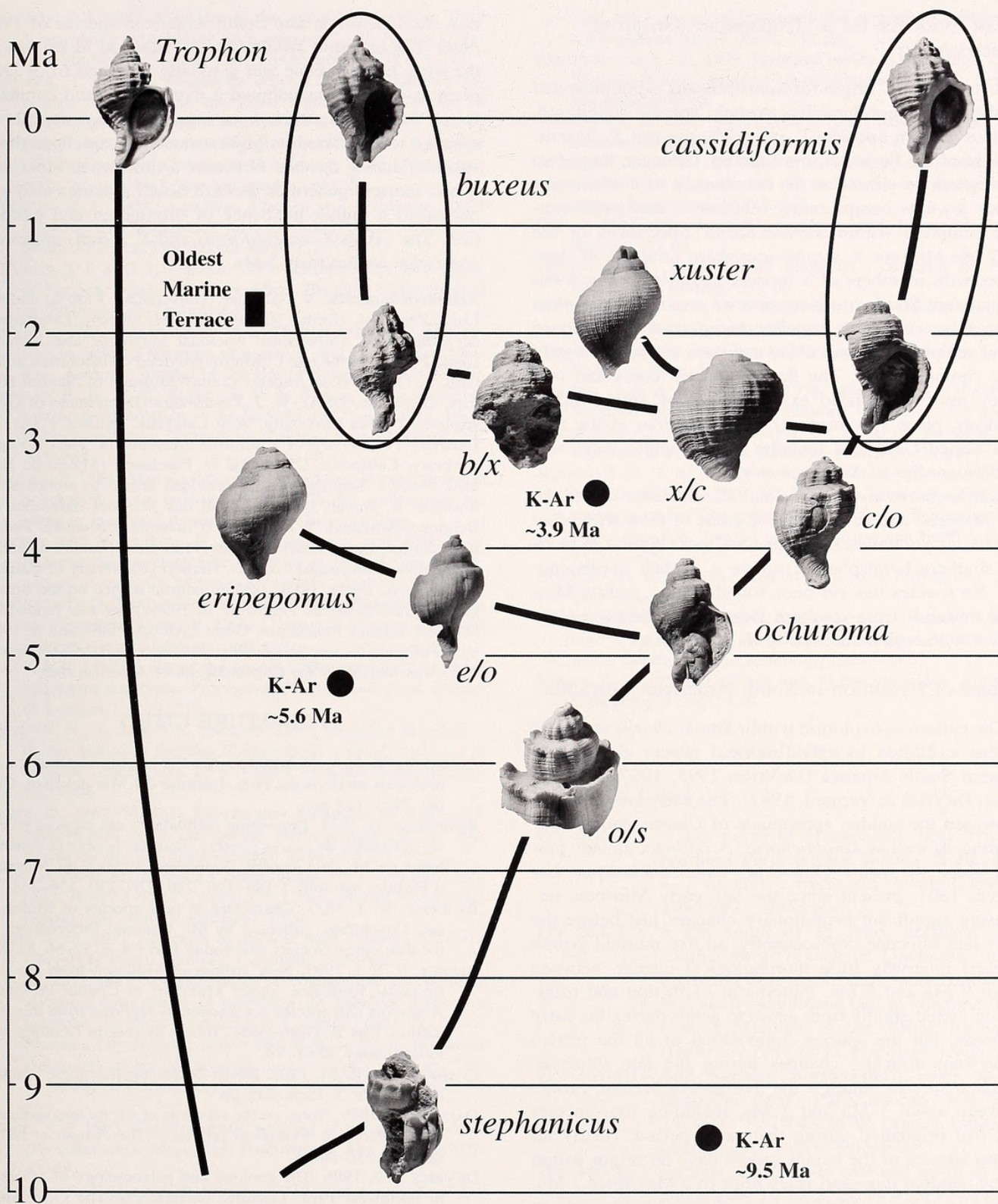


Figure 62. Inferred evolutionary relationships between species of *Xanthochorus*. Arrangement of tree determined by (1) typical shell morphology of taxa, (2) intermediate morphology of atypical specimens, and (3) stratigraphic occurrence. o/s = transitional specimen between *Xanthochorus ochuroma* and *X. stephanicus*; e/o = same, between *X. eripepomus* and *X. ochuroma*; c/o, same, between *X. cassidiformis* and *X. ochuroma*; x/c, same, between *X. cassidiformis* and *X. xuster*; and b/x, same, between *X. buxeus* and *X. xuster*.

Fossil Evidence for a 'Trophonine' Origin of *Xanthochorus*

A 'trophonine' origin for *Xanthochorus* is not indicated by the robust, non-lamellar, strongly spirally sculptured, dentate modern species, *X. cassidiformis* and *X. buxeus*. In light of the Peruvian fossil record, however, these two species can be viewed as the culmination of evolutionary trends towards compactness, robustness, and paedomorphic sculpture within *Xanthochorus*. Specimens of the early late Miocene *X. stephanicus* share a number of characters with members of a broader clade including fossil and modern South American species resembling *Trophon geversianus*, including lamellar, fluted axial ribs; reduced spiral sculpture; a small ovate aperture; and a moderately long siphonal canal. The flattened spiral cords and tendency towards rounded axial ribs on the spire whorls, however, place specimens of *X. stephanicus* at the root of a nested clade that includes only younger fossil and modern species of *Xanthochorus*.

Xanthochorus stephanicus and *X. ochuroma* shared the late Miocene and early Pliocene coast of Peru with other species, as yet undescribed, that are more similar to modern southern hemisphere *Trophon* s. s. than *Xanthochorus*. No species has yet been found among middle Miocene muricids from southern Peru that could be a plausible *Trophon*-like ancestor to *X. stephanicus*.

Pattern of Evolution in South American Muricids

The pattern of evolution within *Xanthochorus* is similar to that exhibited by other muricid genera endemic to western South America (DeVries, 1995, 1997, 2000, in press; DeVries & Vermeij, 1997). The early late Miocene witnessed the sudden appearance of *Chorus* and *Hermispina*, as well as *Xanthochorus*. *Acanthina*, already present since the latest Oligocene, and *Concholepas* Lamarck, 1801, present since the late early Miocene, underwent significant evolutionary changes just before the early late Miocene. Subsequently, all five muricid genera showed relatively little morphological change between about 9 Ma and 5 Ma. Patterns of extinction and origination varied greatly from genus to genus during the early Pliocene, but the species composition of all the genera underwent dramatic changes during the late Pliocene. Thirteen species amongst the five genera became extinct between about 3 Ma and 2 Ma, including four species that had originated during that same period. Nearly all extant species of the extant genera have an origin within a few hundred thousand years prior to 2 Ma. Since 2 Ma, only *Acanthina* populations have diverged sufficiently to readily justify the recognition of separate species.

CONCLUSION

Late Cenozoic fossils from southern Peru provide evidence for a shared common ancestor for the muricid ge-

nus, *Xanthochorus*, and South American species of *Trophon*. The endemic *Xanthochorus* clade had its origins in the early late Miocene and gradually diverged from *Trophon* as populations adopted a more robust and compact form. The genus attained its maximum diversity (three species) and suffered its highest rates of extinction (three species) during the late Pliocene, a time when other endemic muricid genera of western South America also experienced a higher incidence of origination and extinction. The extant *X. cassidiformis* and *X. buxeus* appeared somewhat earlier than 2 Ma.

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APPENDIX

Localities Cited

- DV 136 1 km north of Huanchaco, near Trujillo, northern Peru; terrace surface at elevation 4–7 m above mean sea level. (DeVries, 1986:842). Holocene.
- DV 244-2 5 km south of El Alto, northern Peru, southernmost branch of Quebrada Taime, dissected hills above cliff face; continuous thin shelly sandstone bed in siltstone; Golf Course Member of the Taime formation (DeVries, 1986:849). Upper Pliocene.
- DV 361-10 Sud Sacaco, northeastern edge of depression near Panamerican Highway, 15°34'17"S, 74°43'26"W (Yauca 1:100,000 quadrangle). Lower Pliocene.
- DV 380-1 Sacaco, shelly beds east and north of well and house, 15°32'29"S, 74°43'53"W (Yauca 1:100,000 quadrangle). Upper lower Pliocene.
- DV 431-1 Sacaco, south-southeast of well and house, *Xanthochorus* in ledges above concentrations of *Dosinia* (Yauca 1:100,000 quadrangle). Upper lower Pliocene.

- DV 460-1 Roadcut in Panamerican Highway, northwest of Yauca, north face, 15°39'49"S, 74°31'50"W (Yauca 1:100,000 quadrangle). Lower Pliocene.
- DV 465a-1 San Juan de Marcona—San Nicholas bridge, roadcut in terrace (San Juan 1:100,000 quadrangle). Upper Pleistocene.
- DV 472-1 Pampa Los Chinos, 90 m up section from floor of valley, interbedded siltstone and sandstone with lenses of mollusks, 14°43'50"S, 75°13'27"W (Palpa 1:100,000 quadrangle). Lower Pliocene.
- DV 472-4 Pampa Los Chinos, shelly interval lower than 90 m elevation in section, 14°43'50"S, 75°13'27"W (Palpa 1:100,000 quadrangle). Lower Pliocene.
- DV 472a-13 Pampa Los Chinos, mollusks from uppermost marine beds, 1.3 km east of measured section, 14°43'50"S, 75°13'27"W (Palpa 1:100,000 quadrangle). Upper lower Pliocene.
- DV 513-1 Sacaco, 1.5 km north of well and house, east side of Quebrada Sacaco, shell beds over crossbedded sandstones, 15°31'42"S, 74°43'02"W (Yauca 1:100,000 quadrangle). Lower upper Pliocene.
- DV 567-2 Sacaco, hillside east of house and well, 15°32'06"S, 74°43'30"W (Yauca 1:100,000 quadrangle). Lower upper Pliocene.
- DV 571-1 Alto Grande, designated "El Jahuay" in Muizon & DeVries (1985), top of hill, 15°26'57"S, 74°52'06"W (Acarí 1:100,000 quadrangle). Lower upper Miocene.
- DV 613-1 5 km downstream from Hacienda Tunga, upper fossiliferous beds above gypsum and ash (Palpa 1:100,000 quadrangle). Lower Pliocene.
- DV 613-3 5 km downstream from Hacienda Tunga, thin fossiliferous sandstone above lingulid sandstone (Palpa 1:100,000 quadrangle). Lower Pliocene.
- DV 614-3 Usaca, near locality DV 613, shell beds at 23 m in section, 14°54'36"S, 75°08'55"W (Palpa 1:100,000 quadrangle). Lower Pliocene.
- DV 732-1 Sud Sacaco, south end of Quaternary terrace (Yauca 1:100,000 quadrangle). Pleistocene.
- DV 739-1 Sacaco, hillside east of house and well (Yauca 1:100,000 quadrangle). Lower upper Pliocene.
- DV 1031-1 Morro Abra de los Chaparrinos, half way up section, 15°48'41"S, 74°21'18"W (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 1032-1 Morro Abra de los Chaparrinos, descending from highest terrace level, south side of first curve, 15°52'59"S, 74°10'05"W (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 1254-8 Morro Abra de los Chaparrinos, pebbly bioclastic indurated sandstone, 46.5 m in section, 15°53'25"S, 74°09'52"W (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 1331-1 1–2 km north of mouth of Quebrada Caracoles, base of two yellow-green knolls in valley, 15°30'13"S, 74°44'32"W (Yauca 1:100,000 quadrangle). Lower upper Pliocene.
- DV 1416-1 'Rosetta' knoll, Acarí Depression, 15°36'37"S, 74°38'02"W (Yauca 1:100,000 quadrangle). Lower Pliocene to Upper Pliocene.
- DV 1418-1 East side of Acarí Depression, 15°34'50"S, 74°36'59"W (Yauca 1:100,000 quadrangle). Upper Pliocene.
- DV 1422-2 Sacaco, hillside east of Quebrada Sacaco, between 200-m knoll and house with well, 15°31'43"S, 74°44'38"W (Yauca 1:100,000 quadrangle). Lower upper Pliocene.
- LACM 75-42 Chile. Recent.
- UCMP-D
5818 Southern outskirts of Coquimbo, just south of road intersection to village of La Herradura. Fossiliferous beds resting on older sands. Chilean coordinates 6680.45 km N, 272.75 km E. Collected 1970 by J. W. Durham.
- UCMP D
5819-2 Outcrops in roadcut along road leading to village of Guanaquero, about 2 km northeast from village, from terrace beds in top of roadcut. Chilean coordinates 6657.75 km N, 268.5 km E. Collected 1970 by J. W. Durham.
- WJZ 345 Coquimbo, Chile. Marine terrace. Upper Pleistocene.



Devries, T J. 2005. "The late Cenozoic history of Xanthochorus Fischer, 1884 (Gastropoda : Muricidae) in western South America." *The veliger* 47, 259–276.

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