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A REVIEW OF THE GENUS *CHORUS* GRAY, 1847 (GASTROPODA:MURICIDAE) FROM WESTERN SOUTH AMERICA

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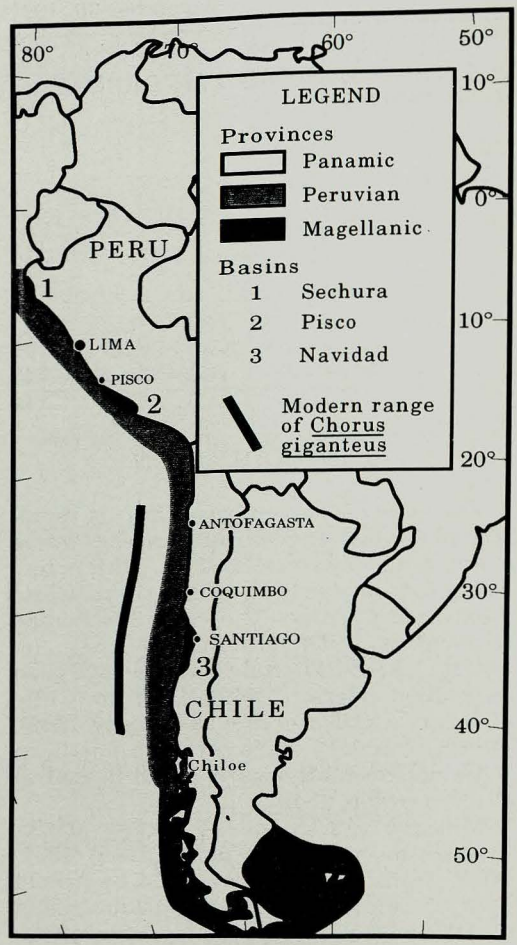
I. ABSTRACT

The muricid genus *Chorus* Gray, 1847, is represented by a single extant species, *C. giganteus* (Lesson, 1830), which lives along the coast of central and southern Chile. New fossils from southern Peru extend the temporal range of *Chorus* from the Pliocene to the Late Miocene (*C. frassinettii*, n. sp.) and the geographic range of three Chilean species [(*C. doliaris* (Philippi, 1887), *C. grandis* (Philippi, 1887), and *C. giganteus*)] into Peru. *Chorus covacevichi*, n. sp., is described from the Pliocene of Chile. Consistent morphological criteria are established for distinguishing all known species of *Chorus*. The genus has been endemic to the Peruvian Province and/or Pacific portion of the Magellanic Province since at least 9 Ma. Extinctions and range contractions of *Chorus* species near the end of the Pliocene may be due to a loss of habitat related to contemporaneous tectonic and oceanographic events.

II. INTRODUCTION

The genus *Chorus* Gray, 1847, is represented by just one living species, *Chorus giganteus* (Lesson, 1830), which has ranged from central to southern Chile (Text-figure 1) since the early Pleistocene (Carcelles, 1954; Herm, 1969; Osorio, 1979). Several Pliocene species have been described (Herm, 1969), all from Chile except one, *C. blainvillei* (d'Orbigny, 1842), which was first discovered in northern Peru and soon afterward found in central Chile (Darwin, 1846).

Miocene and Oligocene species attributed to the genus *Chorus* by Olsson (1931, 1932) from northern Peru and by Arnold (1903) and Anderson (1905) from California are incorrectly identified. Examination of type and figured specimens shows that *Acanthina (Chorus) meroensis* Olsson, 1931, *A. (Chorus) sula* Olsson, 1931, and *A. (Chorus) sula cruziana* Olsson, 1932, are buccinids of



Text-figure 1. The modern range of *Chorus giganteus* Gray, 1847, Quaternary molluscan provinces, and selected Cenozoic sedimentary basins of western South America.

undetermined genera and that *Acanthina (Chorus) voluta* Olsson, 1932, is a pseudolivid (Vermeij and DeVries, 1997). Californian specimens are properly referred to the ocenebrine genus *Forreria* Jousseaume, 1880 (Grant and Gale, 1931).

The classification of *Chorus* within the Muricidae remains uncertain. Gray (1847) created the name for a single species previously assigned to *Monoceros* Lamarck, 1809. He noted similarities with two other muricid genera from the same region, *Nucella* Röding, 1798 (= *Acanthina* Fischer von Waldheim, 1807) and *Concholepas* Lamarck, 1801. *Acanthina* has been assigned to Thaididae Jousseaume, 1888 (*e.g.* Keen, 1971; Abbott, 1974), and more recently, Ocenebrinae Cossmann, 1903 (Kool, 1993; Vermeij and Kool, 1994). *Concholepas* was assigned to Thaididae (or Thaidinae) by Cooke (1919) and Stuardo (1979), but Kool (1993) places it with Rapaninae Gray, 1853. Vermeij and Vokes (1997) consider *Chorus* to belong to a "*Thais*-like" clade of ocenebrines because it has a broadly rounded aperture and no subsutural cord or parietal ridge. *Chorus* differs from most ocenebrines, however, in lacking varices or any other colabral sculpture.

Between 1983 and 1997, field work in the Pisco Basin, an emergent forearc basin on the coast of south-central Peru (Text-figure 1), has yielded an abundance of Late Miocene and Pliocene specimens of *Chorus*. These specimens have been compared with material from the Museo de Historia Natural, Universidad Ricardo Palma (Lima, Peru); examples of *C. blainvillei* collected in northern Peru by the author in 1981 (DeVries, 1986, 1988); and specimens of *Chorus* collected in southern Peru by J. Macharé (formerly with the Instituto Geofísico del Perú) between 1980 and 1984; as well as Chilean specimens in the collections of W. J. Zinsmeister (Purdue University, West Lafayette, Indiana); the California Academy of Sciences (San Francisco); the Museum of Paleontology, University of California (Berkeley); the Museo Nacional de Historia Natural (Santiago, Chile); and the Tavera collection at the Departamento de Geología, Universidad de Chile (Santiago, Chile). The many localities from which these specimens were collected are listed in Part VII and shown in Text-figure 2. Unpublished ^{39}Ar-^{40}Ar dates were provided by L. Snee (United States Geological Survey, Boulder, Colorado).

Study of this material has resulted in the first comprehensive generic diagnosis and description of shell morphology of *Chorus* (see Text-figure 3 for a schematic picture of a *Chorus* specimen); a consistent diagnosis of all known species of

Chorus, including juvenile specimens; and the identification of two new fossil species of *Chorus*.

III. DISCUSSION

Biogeography: The discovery of *Chorus doliaris, C. giganteus,* and *C. grandis* in southern Peru and *C. frassinettii,* n. sp., in both southern Peru and central Chile establishes a minimum range of about 15°S to 36°S for most species of the genus for the Late Miocene and Pliocene. Specimens of *C. blainvillei* from uppermost Pliocene deposits in northern Peru (4°30'S) and *C. doliaris* and *C. giganteus* from Pliocene deposits as far south as 47°S and 45°S, respectively, hint at a wider range for *Chorus*. In contrast, the modern range of *C. giganteus* (23°S to 42°S) is more restricted.

The disappearance of *Chorus* species from low latitudes after the Pliocene is notable for the area affected (1200 km of coastline) and taxonomic breadth (four of four species affected, three of which became extinct), but reflective of biogeographic changes for other muricid genera from western South America. At least one species each of *Acanthina, Concholepas, Herminespina* DeVries and Vermeij, 1997, and *Xanthochorus* Fischer, 1884, lived as far north as 4°30'S near the end of the Pliocene or during the Early Pleistocene (DeVries, 1986, 1988). At present, species of three of those genera do not range so far north, and all species of one genus, *Herminespina,* are extinct.

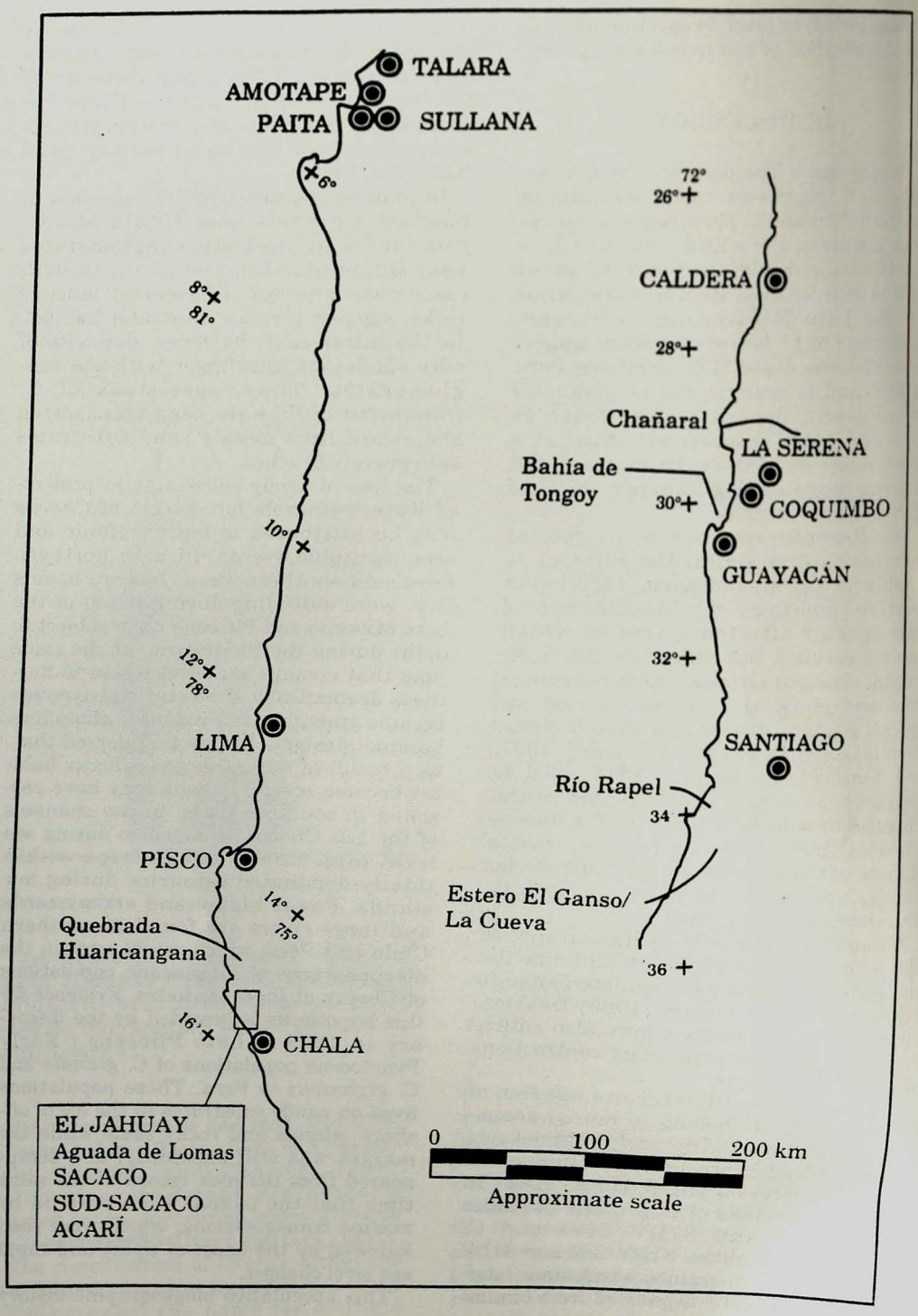
An accelerated loss of molluscan species along the coast of Peru and Chile at the end of the Pliocene has been attributed to a loss of habitat (Herm, 1969; DeVries, 1985). This explanation may also suffice for the extinction and range contractions of species of *Chorus*.

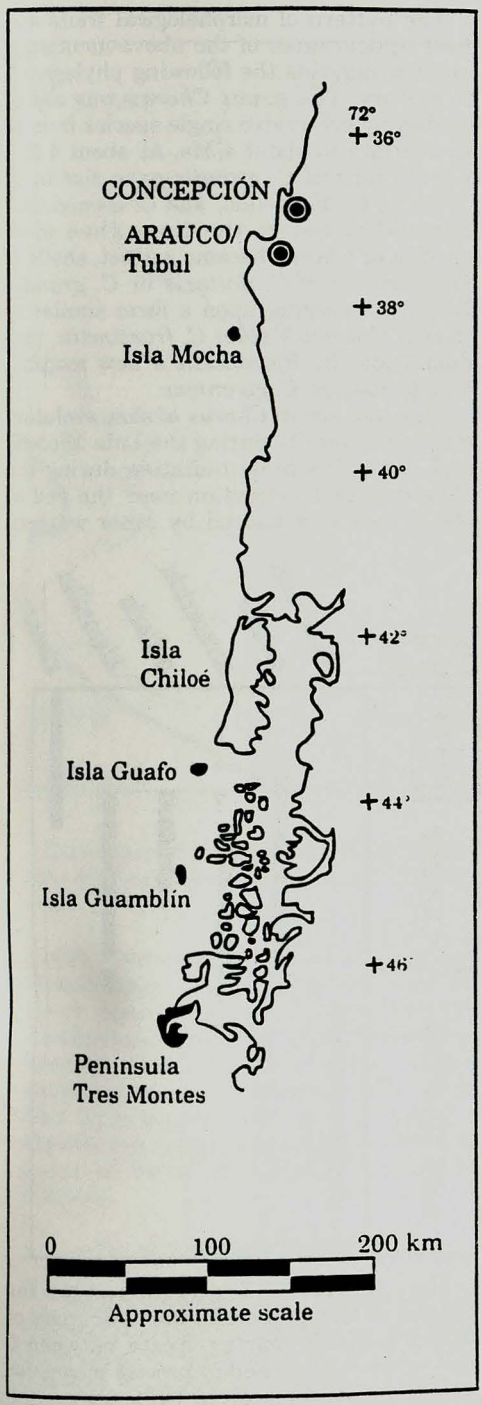
Pliocene and Pleistocene species of *Chorus* in Chile belong to faunal assemblages associated with sandy subtidal substrates along protected and unprotected shores (biotopes 3 and 5; Herm, 1969). In Peru, occurrences of *C. grandis* (localities 87DV 517 and 87DV 569) and *C. blainvillei* (localities 81DV 272 and 81DV 273) in medium-grained sandstones laterally and vertically separated from bioclastic gravels and outcrops of basement igneous rock are consistent with Herm's interpretation. Living populations of *Chorus giganteus* in southern Chile are observed to live subtidally within protected waters, half-buried in muddy sand (Gallardo, 1981).

In contrast, occurrences of *C. grandis* in bioclastic gravels near Chala and *C. frassinettii* in bioclastic conglomerates near Quebrada Huaricangana, in both cases near outcrops of basement igneous rocks, suggest a rocky intertidal habitat. In the latter case, however, deposits of silty sandstone interfinger with the conglomerates. Thus, specimens of *C. frassinettii* could have been transported shoreward from muddy sand substrates onto gravely beaches.

The loss of sandy substrates in protected waters suitable for species of *Chorus* may be attributed to both tectonic and oceanographic events. In both northern Peru and southern Peru, forearc basins that were subsiding during much of the Late Miocene and Pliocene were subject to uplift during the Pleistocene, at the same time that eustatic sea level began to fluctuate dramatically. Protected embayments became emergent and indented shorelines became straight. It may be inferred that, as a result of these changes, *Chorus* habitat became scarce. Refugia may have persisted in southern Chile, in the channels of the Los Chonos Archipelago during sea level high-stands and perhaps within tidally-dominated estuaries during low stands. Fewer high-stand embayments and large rivers are found in northern Chile and Peru, which might explain the disappearance of Pleistocene populations of *Chorus* at those latitudes. Evidence for this hypothesis is provided by the discovery in 1996 of Late Pliocene / Early Pleistocene populations of *C. grandis* and *C. giganteus* in Peru. These populations lived on sandy substrates in the lee of offshore islands and rocky reefs while the margin was still subsiding, and disappeared from the rock record at the same time that the islands were overrun by marine transgressions, which were soon followed by the onset of uplift and rapid sea level changes.

This speculative biogeographic history


TALARA
AMOTAPE
PAITA
SULLANA
6°
8°
81°
10°
12°
78°
LIMA
PISCO
14°
75°
Quebrada
Huaricangana
16°
CHALA
EL JAHUAY
Aguada de Lomas
SACACO
SUD-SACACO
ACARÍ
72°
26°
CALDERA
28°
Chañaral
LA SERENA
Bahía de
Tongoy
30°
COQUIMBO
GUAYACÁN
32°
SANTIAGO
Río Rapel
34
Estero El Ganso/
La Cueva
36
0
100
200 km
Approximate scale



Text-figure 2. Localities from Peru and Chile mentioned in the text.

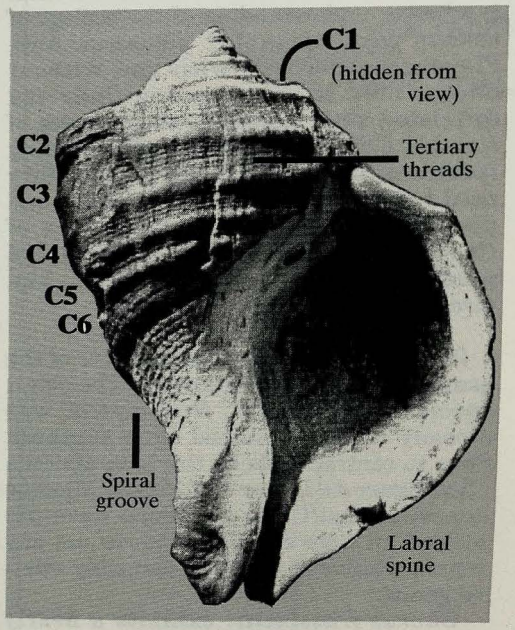
of *Chorus* needs to be tested. Most critical is a better understanding of the ecology of modern populations of *C. giganteus*. Also, Pleistocene deposits with and without *Chorus* need to be mapped in Chile and correlated with independent measures of suitable *Chorus* habitat. Finally, limiting factors other than habitat availability need to be examined for *C. giganteus*, and possibly by proxy, extinct species of *Chorus*: temperature, salinity, prey and predator interactions, competition, and disease.

Phylogeny: The direct predecessor of the genus *Chorus* is not yet known. The oldest species of *Chorus, C. frassinettii*, was already well established from southern Peru to central Chile by the Late Miocene (Text-figure 4). Lower and Middle Miocene deposits from Chile and Peru have not yielded an older species of *Chorus* nor any representative of an older, plausibly related genus.

Chorus frassinettii exhibits a nearly complete suite of *Chorus* characters. The prevalence of well differentiated spiral chords and inflated body whorls in most younger species suggests that uniform spiral sculpture and pyriform shape may be ancestral features. These features reappear in a somewhat different manner in the extant *C. giganteus*. The Pliocene record of intervening extinct species suggests, however, that the superficial similarity of *C. frassinettii* and *C. giganteus* represent convergence.

Chorus grandis is the second oldest species of *Chorus*. It shares with most younger species an anterior inflation of the body whorl, but is distinguished from all younger species by a preponderance of tertiary threads on the body whorl of adult specimens, a trait it shares with the older *C. frassinettii*. The species appears to have lived from about 6 Ma to 2 Ma. It remains unclear whether Late Pliocene populations of this species or *C. doliaris* gave rise to the modern *C. giganteus*.

Chorus doliaris is a Late Pliocene species that shares with *C. grandis* and *C. frassinettii* the presence of numerous tertiary threads. Unlike those older species, however, the threads never overwhelm the strong primary cords that characterize



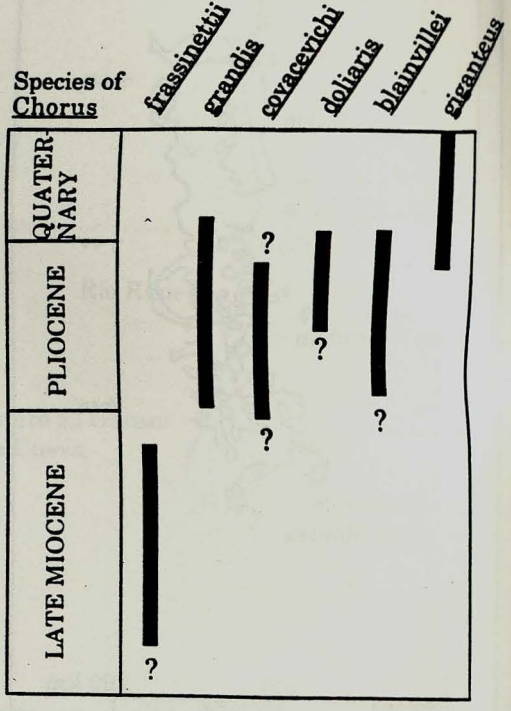
Text-figure 3. Illustration of a *Chorus* specimen to show the numbering scheme (C1, C2, C3, C4, C5, C6) of the primary spiral cords. Primary cord, C1, would be hidden from view in any case, but in this specimen of *Chorus doliaris,* it is absent. Tertiary spiral threads are numerous, whereas secondary spiral cords are absent.

both juveniles and adults. In one Chilean collection, a specimen of *C. doliaris* with greatly reduced anterior inflation and more prominent anterior primary spiral cords is found together with two similar specimens on which the anterior primary spiral cords are even more prominent and the tertiary spiral threads absent, *i.e.,* specimens of *C. giganteus.*

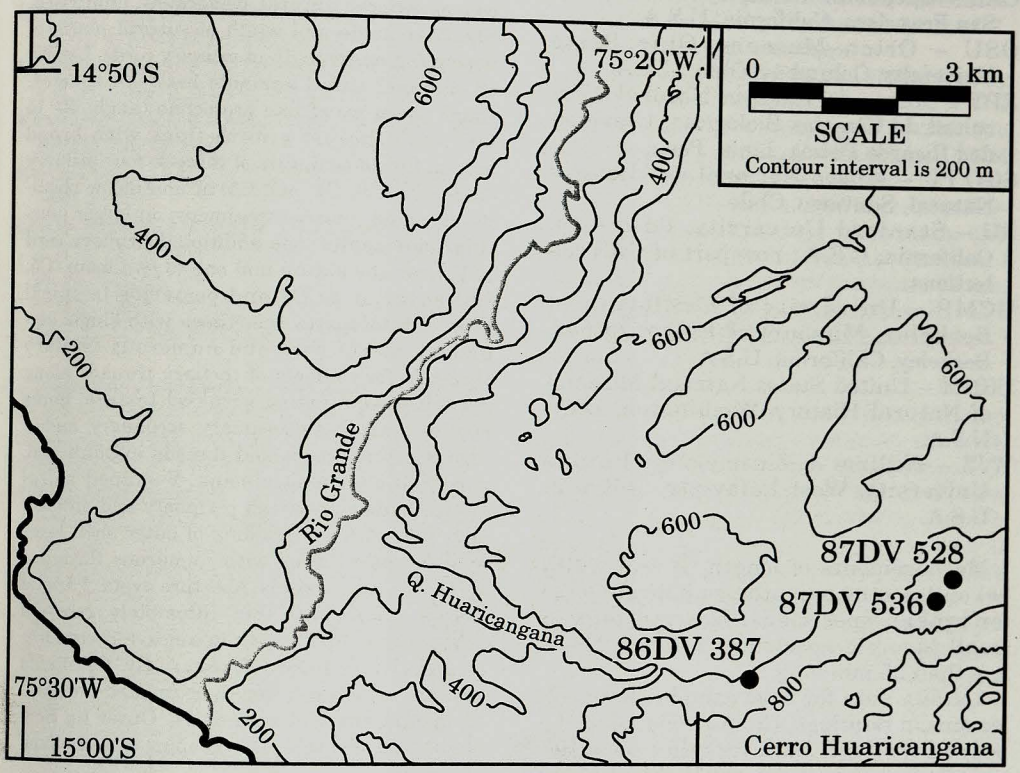
Chorus blainvillei and *C. covacevichi* have only a Pliocene record. Both are characterized by a marked reduction in primary spiral cords in both juvenile specimens (three cords, instead of four) and adult specimens, as well as partial or complete reduction in secondary cords and tertiary threads.

The pattern of morphological traits and first appearances of the above-mentioned species suggests the following phylogenetic history. The genus *Chorus* was represented by successive single species from at least 9 Ma to about 4 Ma. At about 4 Ma, populations of *C. grandis* gave rise to *C. doliaris, C. blainvillei,* and *C. covacevichi.* Somewhat before the time when most species of *Chorus* became extinct, shells of populations of *C. doliaris* or *C. grandis* began converging upon a form similar to that of the much older *C. frassinettii,* producing by the Pleistocene a new morphological species, *C. giganteus.*

This pattern in *Chorus* of slow evolution and low diversity during the Late Miocene and Early Pliocene, radiation during the Pliocene, and extinction near the end of the Pliocene is shared by other western



Text-figure 4. Temporal ranges for species of the genus *Chorus.* A scarcity of dated mollusk-bearing strata between 5 and 4 Ma in Peru and imprecise means for dating bioclastic beds in Chile leaves the earliest appearance of Pliocene species uncertain.



Text-figure 5. Quebrada Huaricangana, south-central Peru, the type locality (87DV 528) of *Chorus frassinettii,* n. sp. Other localities mentioned in the text are shown on the map.

South American muricid genera: *Concholepas, Herminespina,* and to a much lesser extent, *Acanthina* and *Xanthochorus* (DeVries, 1995; DeVries and Vermeij, 1997). Further study of other molluscan genera is needed before persuasive arguments can be advanced to explain the tempo of evolution along the coast of Peru and Chile during the Neogene.

IV. ACKNOWLEDGMENTS

I would like to thank D. Frassinetti (Museo Nacional de Historia Natural, Santiago, Chile) and V. Covacevich (Servicio Nacional de Geología y Minería, Chile) for making collections available for study in Chile and for their helpful critique of the manuscript, and W. Zinsmeister (Purdue University, West Lafayette, Indiana) and G. Vermeij (University of California-Davis) for their reviews of the manuscript. V. Alleman (Universidad Ricardo Palma, Lima, Peru) kindly lent her assistance during a field season in Peru in 1995. R. Martinez-Pardo and E. Valenzuela (Departamento de Geología, Universidad de Chile) arranged access to the Tavera collection. I am grateful to W. Zinsmeister and the several institutions that loaned specimens for this study. Research was funded in part by National Science Foundation Grant EAR-85-03886 and the Conchologists of America, Inc.

Abbreviations for repositories of fossil specimens and localities are as follows:

CAS – California Academy of Sciences, San Francisco, California, U.S.A.
OSU – Orton Museum, Ohio State University, Columbus, Ohio, U.S.A.
RPT – Museo de Historia Natural, Facultad de Ciencias Biológicas, Universidad Ricardo Palma, Lima, Peru.
SGO.PI. – Museo Nacional de Historia Natural, Santiago, Chile.
SU – Stanford University, Palo Alto, California, U.S.A.; now part of CAS collections.
UCMP – University of California at Berkeley, Museum of Paleontology, Berkeley, California, U.S.A.
USNM – United States National Museum of Natural History, Washington, D.C., U.S.A.
WJZ – William J. Zinsmeister, Purdue University, West Lafayette, Indiana, U.S.A.

Measurements of length (l) and width (w) enclosed by parentheses indicate sizes for broken specimens. Descriptions of small juvenile specimens refer to those less than 25 mm long.

Locality data for most samples from collections in Santiago, Chile are listed in the body of the text. Data for other localities are presented in section VII. Most place names are shown on the map in Text-figure 2.

Pagination for Philippi (1887) refers to the Spanish edition.

V. SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815
Genus CHORUS Gray, 1847

Chorus GRAY, 1847, Proceedings of the Zoological Society of London, v. 15, p. 136.
Type Species: (Original designation) *Monoceros giganteus* Lesson, 1830.

Genus Diagnosis: Fusiform, often inflated anteriorly. Axial sculpture of opisthocyrt growth lines; spiral sculpture of six primary cords, wrinkled secondary and tertiary cords, and a V-shaped groove. Some spiral sculpture secondarily lost. Groove ending with labral spine on inside of outer lip, half way between periphery and anterior end.

Genus Description: Length 50 to 100 mm, rarely to 130 mm; fusiform, often inflated anteriorly. Spire low to moderate with five to seven convex whorls; sutures moderately impressed. Shoulder angle and width of sutural platform depending on strength of primary cords. Length of siphonal canal variable between species. Axial sculpture of fine prosocline (angle 40° to 60°), opisthocyrt growth lines with broad apices. Spiral sculpture of three to four primary cords (C2, C3, C4, and C5) at and below shoulder in small juvenile specimens; on larger juveniles and adults, one additional primary cord (C1) near the suture and one to two more (C5, C6) anterior to C4 and posterior to spiral groove. Interspaces sometimes with single secondary spiral cord and numerous tertiary threads. Tiny offsets of tertiary threads along growth lines creating wrinkled texture. Some species with loss of primary, secondary, and/or tertiary spiral cords and threads in adult and, rarely, juvenile specimens. V-shaped spiral groove midway between periphery and anterior end, formed from infolding of outer shell layer at interspace. Neck with numerous flattened spiral threads or cords. Aperture ovate. Parietal area in adults with thin, incomplete, recessed callus. Inner lip straight to concave posteriorly, straight or inclined left anteriorly. Columella smooth, sometimes weakly excavated anteriorly. Pseudumbilical area short. Outer lip nonplanar, non-dentate. Labral spine at end of spiral groove.

Discussion: One of the notable features on specimens of *Chorus* is the labral spine. Other spine-bearing Neogene genera from western South America include *Acanthina* Fischer von Waldheim, 1807; *Testallium* Vermeij and DeVries, 1997; *Herminespina* DeVries and Vermeij, 1997; and *Concholepas* Lamarck, 1801. Individuals of *Acanthina* and *Testallium* are not constricted or only weakly constricted at the base and lack the numerous well-developed primary spiral cords present on specimens of *Chorus*. Specimens of *Herminespina* and *Testallium* have axial sculpture. Specimens of *Concholepas* lack a spiral groove and most species lack labral spines (DeVries, 1995). The pair of labral spines on *Concholepas concholepas* Lamarck, 1801, extend from interspaces, rather than a spiral groove.

CHORUS GIGANTEUS (Lesson, 1830)
Plate 1, figures 1-4; Plate 2, figure 4

Monoceros giganteus LESSON, 1830, p. 405, pl. 11, fig. 4; PHILIPPI, 1887, p. 59.
Monoceros giganteum Lesson. REEVE, 1846, v. 3, pl. 1, fig. 3; HUPÉ, 1854, v. 8, p. 198.
Monoceros fusoides KING, 1832, *in* KING and BRODERIP, p. 348.
Monoceros giganteus ? Lesson. MÖRICKE, 1896, p. 564.
Chorus giganteus (Lesson). CARCELLES, 1954, p. 272, pl. 5, figs. 1-11; HERM, 1969, p. 135, pl. 15, figs. 4a, 4b.
Chorus grandis (Philippi). HERM, 1969, pl. 15, figs. 3a, 3b (not of Philippi).

Diagnosis: No anterior inflation, with rounded shoulder and elongate siphonal canal; strongest primary cords towards anterior, including one or two anterior to spiral groove; tertiary threads absent.

Description: Shell to 130 mm long, fusiform to pyriform; spire about 20 percent of shell length; siphonal canal about 30 percent of shell length. Shoulder rounded, no sutural ramp on large juveniles and adults; periphery just anterior to midpoint between suture and spiral groove. Spiral sculpture of six cords posterior to spiral groove, posteriormost (C1) weak or absent; the next three (C2, C3, C4) moderately strong, with posteriormost (C2) at shoulder; C5 and C6 anterior to C4, more closely spaced and usually stronger than posterior cords. A single secondary cord between C2 and C3, sometimes as strong as adjacent primary cords. Spiral groove situated between two moderately strong flattened cords. Neck of body whorl with one to three moderately strong primary cords and several secondary cords. Tertiary cords rarely developed anywhere on whorl. Pseudumbilical area and excavated anterior end of columella narrow; inner lip concave posteriorly, inclined to left anteriorly. Small juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), secondary spiral cords between some but not all primary cords.

Type specimen: Unknown.

Type locality: Chile.

Occurrence: (Late Pliocene) southern Peru to central Chile. (Quaternary) central to southern Chile, 23°-42°S (Osorio, 1979; Gallardo, 1981). Late Pliocene ages are assigned on the basis of associated mollusks (Isla Guamblín: Frassinetti and Covacevich, 1995) and position below Pleistocene marine terraces with a modern fauna (Chile specimens: Herm, 1969; Acarí specimens: this report). The two specimens from Acarí constitute the first records of *C. giganteus* of any age from Peru.

Material examined: USNM 447062, locality WJZ 281, Tubul, Pleistocene, l 64.6 mm, w 41.7 mm; USNM 447063, locality WJZ 285, Río Rapel, Recent, l 49.7 mm, w 31.5 mm; USNM 447064, WJZ 659, Isla Guamblín, Late Pliocene, l (38.5) mm, w 26.6 mm; UCMP D-3733c, La Serena, Pliocene, l 127.0 mm, w 82.9 mm; UCMP D-3735a, La Serena, Pliocene, l 38.4 mm, w 24.9 mm; UCMP D-3735b, l 23 mm, w 14.3 mm; RPT 26, Acarí, Late Pliocene, l 41.3 mm, w 29.0 mm; RPT 27, Acarí, Late Pliocene, l (67) mm, w 70.5 mm.

Discussion: A well-formed sutural ramp and absence of primary cords on the neck characterize two Pliocene specimens of *C. giganteus* from Chile (UCMP D-3735a, plate 1, figure 2; UCMP D-3735b, plate 2, figure 4). Additionally, primary spiral cords near the periphery are stronger than the anterior cords. These features are typical of *C. doliaris*. Thus, these specimens of *C. giganteus* may represent populations transitional between *C. doliaris* and Quaternary *C. giganteus*, a hypothesis supported by the occurrence in the same Chilean collection of a specimen of *C. doliaris* (UCMP D-3735c; plate 2, figure 5). On the other hand, undescribed specimens from Upper Pliocene / Lower Pleistocene deposits near Acarí exhibit traits of both *C. giganteus* (produced siphonal canal, differentiated primary and secondary spiral cords) and nearly contemporaneous *C. grandis* from 100 km farther south (numerous tertiary spiral threads, sutural platform; unfigured specimens USNM 447081, USNM 447111), resulting in a morphology convergent with that of *C. doliaris*. Further study is needed to determine the Pliocene species most closely related to the extant *C. giganteus*.

CHORUS DOLIARIS (Philippi, 1887)
Plate 1, figures 5-8; Plate 2, figure 2

Monoceros doliaris PHILIPPI, 1887, p. 57, pl. 6, fig. 11.
Monoceros pyrulatus PHILIPPI, 1887, p. 57, pl. 5, fig. 7.
Monoceros costatus Sowerby. PHILIPPI, 1887, p. 56, pl. 5, fig. 9 (not of Sowerby).

Monoceros cf. *M. pyrulatus* Philippi. MÖRICKE, 1896, p. 566.

Chorus doliaris (Philippi). HERM, 1969, p. 134, pl. 15, fig. 6; pl. 16, fig. 3; pl. 17, fig. 1.

Diagnosis: Moderate anterior inflation and pronounced sutural platform; three strong spiral cords at and below shoulder; tertiary spiral threads filling all interspaces.

Description: Length to 60 mm; fusiform, somewhat inflated anteriorly. Spire, neck each about 20 percent of shell length. Spiral sculpture of large juveniles with six primary cords: three very strong cords at (C2) and anterior to (C3, C4) shoulder; one weak primary cord (C1) on sutural ramp; two moderately strong spiral cords (C5, C6) between C4 and spiral groove; secondary cords and tertiary threads between central or all primary cords. C2, C3, and C4 remaining very strong on adult specimens; C1 and C6 weakening considerably; secondary and tertiary threads becoming stronger, more numerous on adult specimens. Neck with seven to ten tertiary spiral threads, in some cases with one primary spiral cord. Pseudumbilicus and excavated anterior portion of columella wide; posterior inner lip concave; anterior inner lip straight or twisted left. Labral spine inside of outer lip. Small juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), tertiary spiral threads between all primary cords.

Type specimen: Holotype, SGO.PI.500.

Type locality: La Cueva, Chile.

Occurrence: (Late Pliocene) Southern Peru to southern Chile. Late Pliocene ages are based on associated molluscan fauna and stratigraphic position of specimens (Herm, 1969; Frassinetti and Covacevich, 1995). UCMP and WJZ samples do not specify "early" or "late" for their Pliocene designations.

Material examined: (all samples Pliocene). USNM 447069, locality WJZ 266, La Cueva, l 56.7 mm, w 46.7 mm; USNM 447070, locality WJZ 266, l 28.9 mm, w 22.3 mm; USNM 447071, locality WJZ 848, Isla Guafo, l 58.4 mm, w (40.2) mm; USNM 447072, locality WJZ 848, l (45.9) mm, w (30.0) mm; USNM 447073, locality WJZ 859, Isla Guamblín, Late Pliocene, l 58.3 mm, w (42.0) mm; USNM 447077, locality 82JM 82024, Quebrada Carrizal, l (40.2) mm, w 35.9 mm; USNM 447113, locality WJZ 266, l 18.4 mm, w 13.4 mm; UCMP D-3735C, Coquimbo, l 46.2 mm, w (31.9) mm; UCMP D-5826a, Estero El Ganso, l 24.3 mm, w 18.4 mm; UCMP D-5826b, l 20.9 mm, w 16.1 mm; SGO.PI.1217, Quebrada Salinas, Tongoy, two juvenile specimens; SGO.PI.1303, Estero El Ganso, La Cueva, four adult specimens; SGO.PI.5698, Isla Guafo, two specimens; SGO.PI.5699, Isla Guafo, five adults; SGO.PI.5700, Isla Guafo, one adult. *"Monoceros costatus,"* SGO.PI.517, Guayacán; SGO.PI.841, La Cueva, three specimens; SGO.PI.501, Guayacán, two specimens.

Discussion: The wrinkled tertiary spiral threads and anterior inflation present in

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PLATE 1

Figures — Page

1-4. *Chorus giganteus* (Lesson, 1830) 132

1. (x 1) USNM 447062; length 64.6 mm, width 41.7 mm. Locality: WJZ 281, Tubul, Chile; Pleistocene.
2. (x 1) UCMP D-3735a; length 38.4 mm, width 24.9 mm. Locality: Coquimbo, Chile; Pliocene.
3. (x 1) USNM 447063; length 49.7 mm, width 31.5 mm. Locality: WJZ 285, Concepción, Chile; Recent.
4. (x 1) USNM 447064; length (38.5) mm, width 26.6 mm. Locality: WJZ 659, Isla Guamblín, Chile; Late Pliocene.

5-8. *Chorus doliaris* (Philippi, 1887) 133

5. (x 1) UCMP D-3735c; length 46.2 mm, width (31.9) mm. Lateral view; encrusted with barnacles. Locality: Coquimbo, Chile; Pliocene.
6. (x 1) USNM 447071; length 58.4 mm, width (40.2) mm. Locality: WJZ 848, Península Tres Montes, Chile; Pliocene.
7. (x 1.5) UCMP D-5826a; length 24.3 mm, width 18.4 mm. Locality: Estero El Ganso, Chile; Pliocene.
8. (x 1.5) USNM 447070; length 28.9 mm, width 22.3 mm. Locality: WJZ 266, Estero El Ganso, Chile; Pliocene.

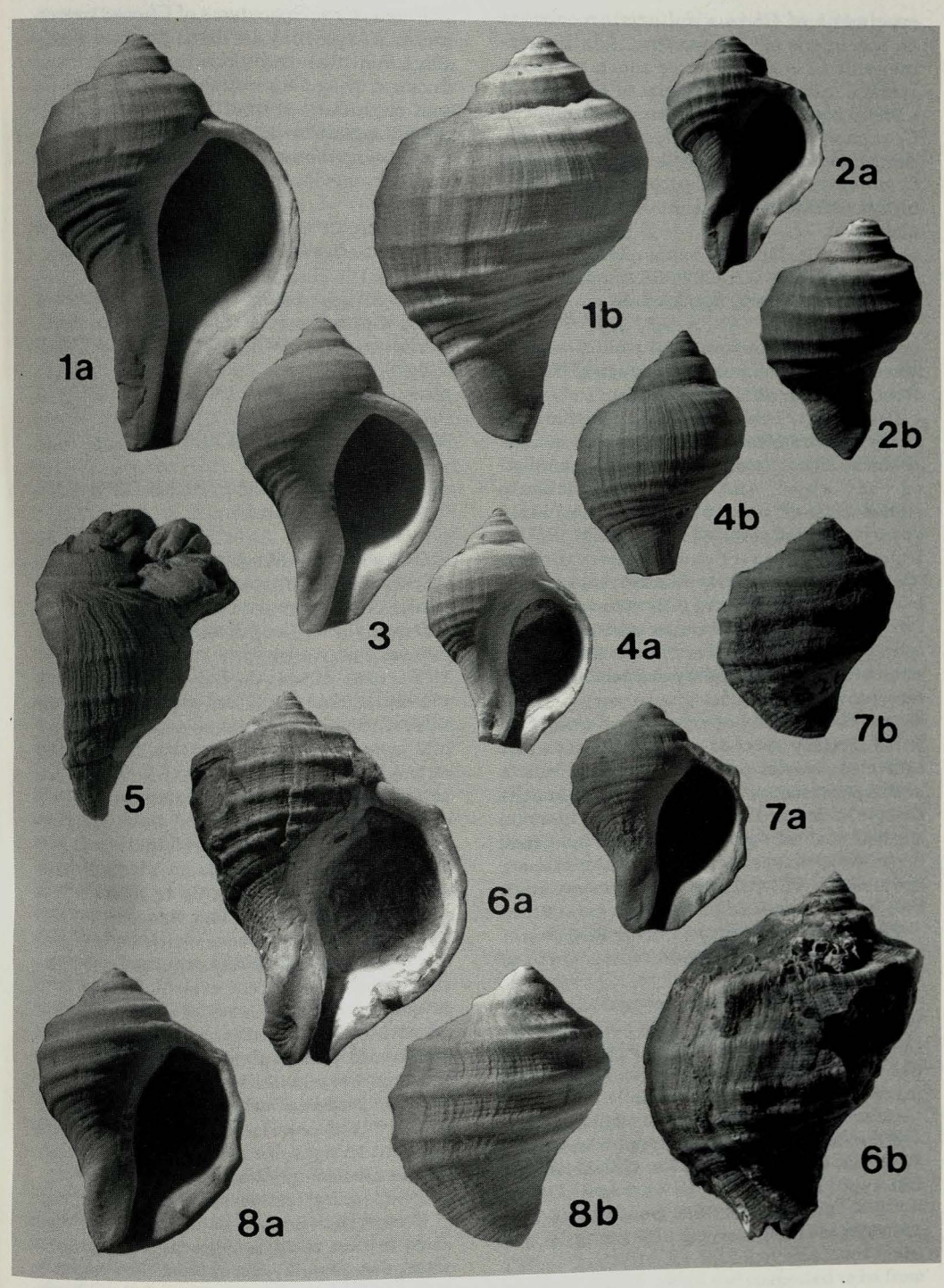

PLATE 1

near Paita; Olsson (1932, p. 6) rediscovered the species near Amotape.

Occurrence: (Pliocene) northern to southern Chile. Chilean localities include both lower and upper Pliocene strata; no distinction is made on SGO.PI. sample labels or in Herm (1969). (Latest Pliocene) northern Peru. The occurrence of specimens of *Chorus blainvillei* at the base of the Taime Formation (DeVries, 1988), together with specimens of typically Pleistocene species (DeVries, 1986), suggests a very late Pliocene or early Pleistocene age in the Sechura Basin (Text-figure 1).

Material examined: All OSU specimens are topotypes from upper Pliocene localities 81DV 272 (Quebrada Sogrona) and 81DV 273 (Quebrada Cardo Grande). All other Peruvian and Chilean material of undifferentiated Pliocene. OSU 37351, l 17.5 mm, w 12 mm; OSU 37352, l 32.9 mm, w 23.2 mm; OSU 37353, l 45.4 mm, w 33.2 mm; OSU 37354, l 59.4 mm, w 46.6 mm; OSU 37355, l 75.8 mm, w 66.8 mm; OSU 37357, l 68.9 mm, w 55.3 mm; SGO.PI.513, Coquimbo; SGO.PI.504, Isla Chiloé; SGO.PI.1102, Caldera; SGO.PI.1096, Caldera; CAS 61701.01, Quebrada Culebrón, Coquimbo, 12 specimens; UCMP D-5790a, Caldera, l (52.2) mm, w 41.2 mm; UCMP D-5790b, l (36.3) mm, w 27.7 mm; UCMP D-5790c, l (32.9) mm, w 25.4 mm.

Discussion: Specimens of *Chorus blainvillei* collected from the type locality in northern Peru, as well as specimens found close at Coquimbo, Chile, the type locality of *C. blainvillei nodosus*, show a wide range in the development of nodular primary spiral cords, suggesting that *C. blainvillei nodosus* should be considered a synonym of *C. blainvillei*. Specimens of *C. covacevichi*, n. sp., may be distinguished from nodulose specimens of *C. blainvillei* by their pyriform outline and absence of secondary cords and tertiary threads on even small juvenile specimens.

CHORUS FRASSINETTII, n. sp.
Plate 2, figure 1; Plate 3, figures 1-4

Diagnosis: Rounded shoulder, minimal anterior inflation. Spiral sculpture in juveniles of nearly equally strong primary and secondary cords, in adults, nearly equally strong primary and secondary cords and tertiary threads.

PLATE 2

Figures — Page

1. *Chorus frassinettii*, n. sp.. 138
   (a, x 1.5; b, x 1.6) USNM 447066; length 19.6 mm, width 14.0 mm.
   Locality: 87DV 571-1, El Jahuay, Peru; Late Miocene.
2. *Chorus doliaris* (Philippi, 1887) 133
   (a, x 1.5; b, x 1.6) USNM 447113; length 18.4 mm, width 13.4 mm.
   Locality: WJZ 266, La Cueva, Chile; Pliocene.

3,6,7. *Chorus grandis* (Philippi, 1887) 136

3. (a, x 1.5; b, x 1.6) USNM 447119; length (18) mm, width 13.4 mm.
   Locality: WJZ 385, Chile, Pliocene.
6. (x 1) USNM 447074; length 57.6 mm, width 42.0 mm.
   Locality: 87DV 517, Sud-Sacaco, Peru; late Early Pliocene.
7. (x 1.5) CAS 61701.02; length (30.5) mm, width 22.4 mm.
   Locality: SU 103, Quebrada Culebrón, Coquimbo, Chile; Pliocene.

4. *Chorus giganteus* (Lesson, 1830) 132
   (x 1.5) UCMP D-3735b; length 23 mm, width 14.3 mm.
   Locality: Coquimbo, Chile; Pliocene.

5, 10. *Chorus blainvillei* (d'Orbigny, 1842) 137

5. (a, x 1.5; b, x 1.6) OSU 37351; length 17.5 mm, width 12 mm.
   Locality: 81DV 273, near Amotape, Peru; Late Pliocene.
10. (x 0.75) OSU 37357; length 68.9 mm, width 55.3 mm.
    Locality: 81DV 273, near Amotape, Peru; Late Pliocene.

8, 9. *Chorus covacevichi*, n. sp. 136

8. (x 1.5) USNM 447076 (paratype); length 26.8 mm, width 19.6 mm.
   Locality: WJZ 253, Coquimbo, Chile; Pliocene.
9. (x 1) USNM 447068 (holotype); length (50.1) mm, width 41.9 mm.
   Locality: WJZ 253, Coquimbo, Chile; Pliocene.

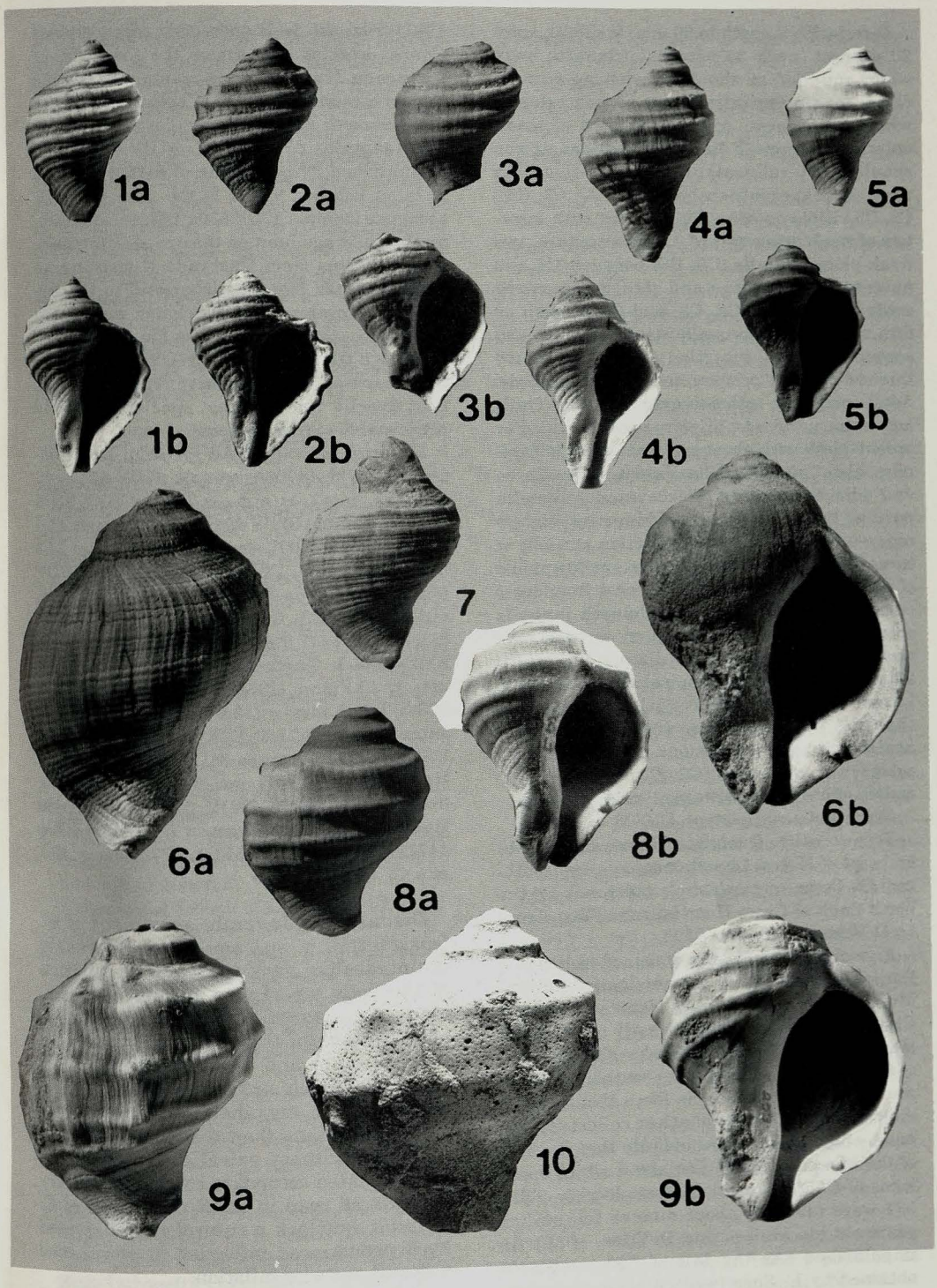

PLATE 2

Description: Length to 90 mm; fusiform; spire 20 percent, neck 35 percent of length; body whorl rounded at shoulder, with no sutural ramp; maximum inflation at or posterior to whorl's midpoint. Axial sculpture of weak opisthocyrt growth lines with apices at the shoulder. Spiral sculpture of juveniles with three, strong, evenly-spaced cords (C2, C3, C4); C2, C3 visible on spire. Third whorl with insertion of weak primary cord (C1) near suture, two weak primary cords (C5, C6) between C4 and nascent spiral groove and strong secondary cords between C1, C2, C3, and C4. Fourth or fifth whorl with subequally strong primary and secondary cords, insertion of single tertiary threads between primary and secondary cords. Adult specimens with subequal secondary cords and tertiary threads; primary cords subdued or absent. Neck with about six spiral cords in juveniles, about nine in adults. Pseudumbilical area and adjacent portion of excavated columella narrow. Posterior portion of inner lip slightly concave to straight; anterior portion straight or turned slightly left. Labral spine shallow infold of outer lip in small juveniles, inset from outer edge of outer lip in adults. Smooth juvenile specimens with weak C1 cord on early whorls, nascent spiral groove, no discernible labral spine, and three weak spiral cords on neck. Larger smooth juveniles with faint tertiary threads, spiral groove, and labral spine. Sculpted juvenile specimens with four strong primary spiral cords (C2, C3, C4, C5), secondary spiral cords between all primary cords.

Type specimen: Holotype, USNM 447116.

Type locality: Quebrada Huaricangana, 40 km west of Nazca, Departamento de Ica, south-central Peru, in bioclastic sandstones on the north flank of Cerro Huaricangana (Text-figure 5); DeVries locality 86DV 528.

Etymology: This species is named in honor of Daniel Frassinetti C., paleontologist with the Museo Nacional de Historia Natural, Santiago, Chile, who has contributed greatly to an understanding of the Tertiary mollusks of Chile.

Occurrence: (Late Miocene) southern Peru to south-central Chile. In the Pisco Basin, radiometric dates of volcanic ashes collected from nearby Aguada de Lomas indicate that the base of the Miocene section, just above which specimens of *Chorus frassinettii* from locality 87DV 531 were taken, is about nine or ten million years old (de Muizon and DeVries, 1985). An unpublished ^{39}Ar-^{40}Ar date of 7.51 ± 0.05 Ma obtained by L. Snee (written communication, 1991) from ash beds underlying coarse-grained *Chorus*-bearing deposits on the south side of Quebrada Huaricangana (sample 87DV 528 1Snee) establishes an age of about eight Ma for *C. frassinettii* specimens from lower in the section (samples 87DV 528-1, 87DV 536-1). An unpublished ^{39}Ar-^{40}Ar date of 6.45 ± 0.03 Ma from an ash bed higher in the same bioclastic sequence (sample 87DV 530a 12Snee) establishes an upper age limit on the age of *C. frassinettii* specimens from Quebrada Huaricangana (sample 87DV 528-3). Higher still in the section, at a level roughly correlative with uppermost Miocene ash beds three km farther east (5.62 ± 0.01 Ma; sample 87DV 532a 1Snee; Snee, written communication, 1990), are beds that overlie the youngest specimens clearly attributable to *C. frassinettii*.

Material examined: All material Late Miocene. USNM 447065, sample 87DV 571-1, El Jahuay, l (47.4) mm, w 34.1 mm; USNM 447066, sample 87DV 571-1, l 19.6 mm, w 14.0 mm; USNM 447067, sample 87DV 571-1, l 37.3 mm, w 27.2 mm; USNM 447082, sample 87DV 536-1, Quebrada Huaricangana, l (48) mm; USNM 447083, Quebrada Huaricangana l (23.4) mm, w 17.9 mm; USNM 447084, sample 87DV 528-3, Quebrada Huaricangana, l 25.5 mm, w 17.2 mm; USNM 447085, sample 87DV 528-3, l 50.5 mm, w (35.4) mm; USNM 447112, sample 87DV 571-1, l 16.0 mm, w 10.6 mm; USNM 447115, sample 86DV 387-3, Quebrada Huaricangana, l (47) mm, w 37.7 mm; 447116, holotype, sample 87DV 528-1, Quebrada Huaricangana, l 83.0 mm, w (56) mm; USNM 447117, locality 87DV 571-1, l 27.3 mm, w 19.1 mm.

Discussion: Juvenile specimens of *C. frassinettii*, n. sp., smooth and strongly sculpted alike, lack the anterior inflation of the body whorl seen in juvenile specimens of *C. grandis*. Those larger juveniles of *C. frassinettii* that are strongly sculpted have primary and secondary spiral cords, which are much stronger and more nearly equal than in any other species of *Chorus*. Adult specimens show the same pattern of subdued primary spiral cords and subequal crinkled secondary cords and tertiary threads as seen in adult specimens of *C. grandis*, but lack a sutural ramp (created by a pronounced inflection at spiral cord C2) and anterior inflation.

Collections made by D. Frassinetti and

V. Covacevich in 1993 from Isla Mocha (about 38°S, central Chile) include large juvenile specimens of *Chorus frassinettii* identical with those from the Pisco Basin and adult specimens that exhibit a range of unusual morphologies, including keeled spiral cords C2, C3, and C4 reminiscent of those seen on some Chilean specimens of *C. doliaris*; elevated spires constituting 30 percent of the shell length; and typically sculpted specimens without any anterior constriction. Pending the acquisition of more specimens from central Chile, including juveniles, the specimens from Isla Mocha will be considered normal and aberrant forms of *C. frassinettii*.

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PLATE 3

Figures

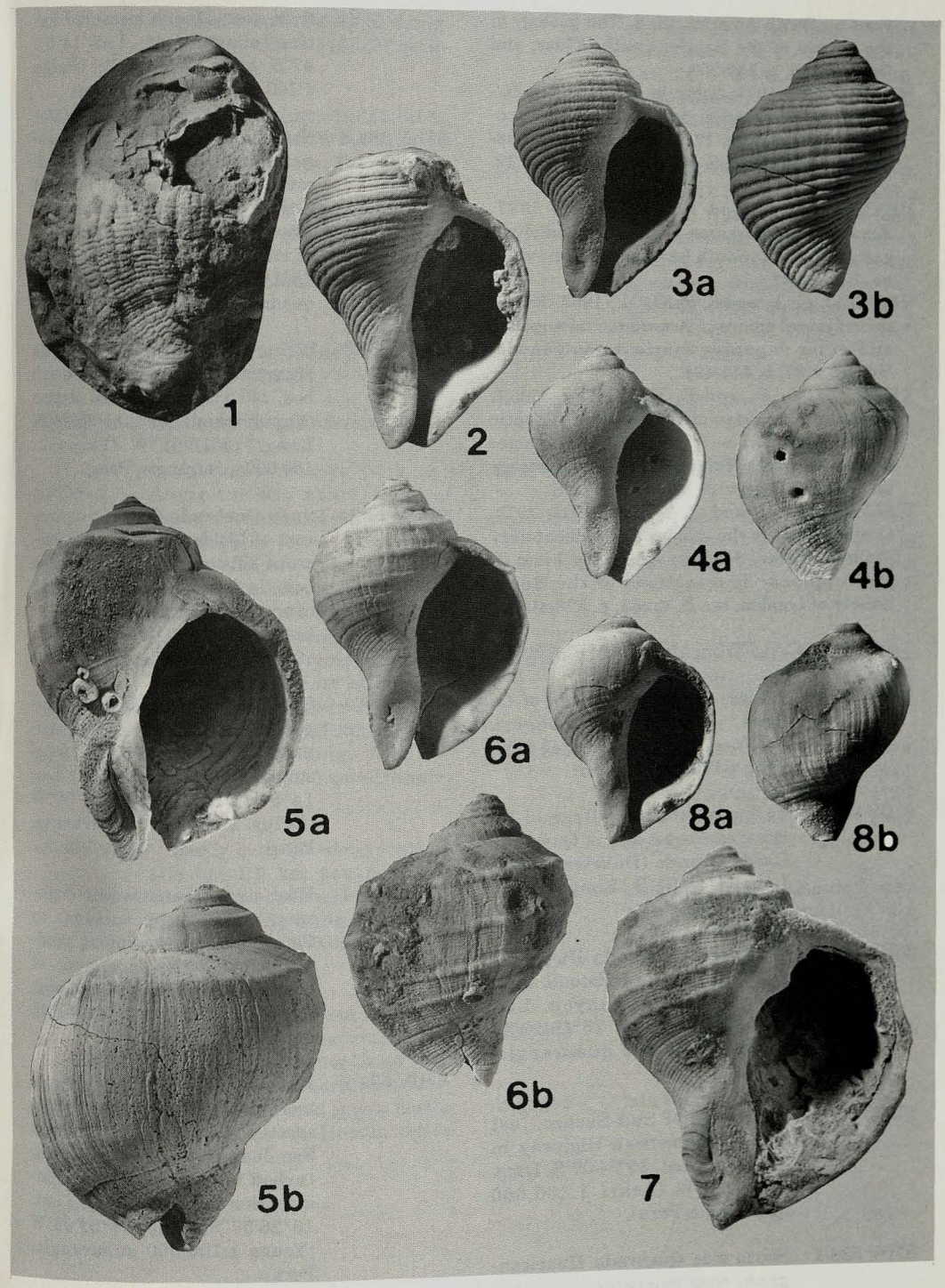

PLATE 3

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VII. LOCALITIES AND SAMPLES

81DV 272 2.5 km southwest village of La Brea, Quebrada Songora (DeVries, 1986). Lat. 04°42'49"S, Long. 81°05'35"W (Peru).

81DV 273 14 km southeast village of La Brea; northwest arm of Quebrada Cardo Grande (DeVries, 1986). Lat. 04°48'21"S, Long. 81°01' 49"W (Peru).

86DV 387-1 South side Quebrada Huaricangana; in yellow sandstone, fault slice on side of canyon. Lat. 14°58'44"S, Long. 75°19'23"W (Palpa 1:100,000 quadrangle, Peru).

87DV 517-1 North end of Sud-Sacaco, just below Panamerican Highway, in sandstone. Lat. 15°34'02"S, Long. 74°43'23"W (Acarí 1:100,000 quadrangle, Peru).

87DV 528-1 South side Quebrada Huaricangana, conglomerates and sandstones descending from flank of Cerro Huaricangana, third gulch from west; 17 m in measured section (unpublished). Lat. 14°57' 47"S, Long. 75°16'58"W (Palpa 1:100,000 quadrangle, Peru).

87DV 528-3 South side Quebrada Huaricangana, conglomerates and sandstones descending from flank of Cerro Huaricangana, east of third gulch from west, along crest of ridge. Lat. 14°57'47"S, Long. 75°16'58"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 530a 12Snee North side Quebrada Huaricangana, 15-cm thick ash bed, 140.9 m in measured section (unpublished). Lat. 14°55'34"S, Long. 75°15'08"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 532a 1Snee Quebrada Huaricangana, east of Molde de Queso diatomaceous siltstones, 30-cm thick ash bed, 74.4 m in measured section (unpublished). Lat. 14°55'06"S, Long. 75°15'33"W (Palpa 1: 100,000 quadrangle, Peru).

87DV 536-1 South side Quebrada Huaricangana, bluff flanking valley, mollusks from lower 25 m of measured section (unpublished). Lat. 14°57'11"S, Long. 75°17'08"W (Palpa 1:100,000 quadrangle, Peru).

87DV 569-1 West side of Panamerican Highway, across from entrance to Sacaco. southeast-dipping sandstone bed with specimens of *Chorus*. Lat. 15°33'16"S, Long. 74°44'08"W (Yauca 1:100,000 quadrangle, Peru).

87DV 571-1 El Jahuay, hillside west of Panamerican Highway, south of intersection with road northwest to San Juan de Marcona. (Area disturbed following highway construction in early 1990's.) Lat. 15°26'57"S, Long. 74°52'06"W (Yauca 1:100,000 quadrangle, Peru).

95DV 812-1 South side of Quebrada Huacllaco, roadcut along Panamerican

Highway. Lat. 15°52'S, Long. 74°11'W (Chala 1:100,000 quadrangle, Peru).

82JM 82024 Río Grande. Lat. 14°55'00"S, Long. 75°07'00"W (Palpa 1: 100,000 quadrangle, Peru).

CAS 61701.01 Quebrada Culebrón, Coquimbo, Chile, near bottom of section.

CAS 61701.02 Quebrada Culebrón, Coquimbo, Chile.

CAS 61702.01 Railroad cut 3/4 miles east of Guayacán, Chile.

CAS 61703.01 Upper ten feet of terrace east of Coquimbo, Chile.

RPT 26, 27 Along the Río Acarí, edge of Pampa Totoral, southeast of Sacaco, Peru.

UCMP D-5790 Quebrada Blanca, about 750-1250 m east of Panamerican Highway at Caldera, soft, poorly consolidated, flat-lying beds, with most samples from cliff exposures. [Same as Quebrada Blanca section of Herm (1969, p. 25)]. Lat. 27°03'S, Long. 70°47'W (Caldera 1:50,000 quadrangle, Chile).

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

UCMP D-3733 Along Panamerican Highway, 10 km north of La Serena, in first deep road cuts north of flat marshland, 1 km northwest junction with side road going northeast to Quebrada Honda; series of thin lenses of fossiliferous sands between beds of gravel. Lat. 29°48'30"S, Long. 71°16' 30"W (Coquimbo 1:50,000 quadrangle, Chile).

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. Lat. 29°48'30"S, Long. 71°16' 30"W (Coquimbo 1:50,000 quadrangle, Chile).

WJZ 253 Roadcut north of Coquimbo, Chile.

WJZ 266 La Cueva, Chile.

WJZ 281 North shore of Río Tubul, mouth of canyon at southern end of Cerro Rari, near Arauco, Chile. Lat. 37°13'41"S, Long. 73°27' 09"W.

WJZ 285 Recent beach, north side of Río Rapel, Chile. Lat. 33°53'36"S, Long. 71°51'W.

WJZ 385 One km east of La Herradura, southwest of village of Miramar. Lat. 29°59'01"S, Long. 71°20' 42"W (Coquimbo 1:50,000 quadrangle, Chile).

WJZ 659 Cove on southeast side Punta Middleton, Isla Guamblín, Chile. Lat. 44°51'31"S, Long. 75°09' 37"W (Isla Guamblin 1:50,000 quadrangle, Chile).

WJZ 848 Caleta Samuel, Isla Guafo, Chile. Lat. 43°35'32"S.

WJZ 859 Isla Guamblín, Chile.