

RANGE EXTENSIONS AND BIOGEOGRAPHIC IMPLICATIONS OF CHILEAN NEOGENE MOLLUSKS FOUND IN PERU

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ABSTRACT

Thirty species of marine mollusks once known only from the Lower to Middle Miocene Navidad Group and Pliocene marine terraces of central Chile are reported from forearc basins of south-central Peru. Well preserved microfossils, particularly diatoms and foraminifera, and volcanic ash interbedded with mollusk-bearing sandstones in Peru provide temporal control for the ranges of these species. Few Early Miocene species are found in both Chile and Peru, despite the tropical cast of the more southerly Chilean fauna. A greater proportion of Pliocene species are common to both countries, but with more tropical taxa found in Peruvian deposits. Differences between the Peruvian and Chilean faunas may be explained by latitudinal thermal gradients that changed as coastal upwelling intensity and southern ocean temperatures changed through the Neogene.

Key words: Range extensions, Biogeographic implications, Neogene mollusks, Chile-Peru.

RESUMEN

Ampliación de distribución e implicaciones biogeográficas de moluscos neógenos chilenos registrados en Perú. Treinta especies de moluscos marinos hasta ahora sólo conocidos para el Mioceno Inferior a Medio del Grupo Navidad y terrazas marinas del Plioceno de Chile central son reportadas de cuencas de antearco de Perú sur-central. Microfósiles bien preservados, especialmente diatomeas y foraminíferos, y lava volcánica en estratos intercalados con las areniscas portadoras de moluscos, en Perú, proveen un control temporal para la distribución de estas especies. Pocas especies del Mioceno Inferior se encuentran en Chile y Perú, a pesar del carácter tropical de la fauna chilena ubicada más al Sur. Una proporción más grande de especies pliocenas son comunes en ambos países, pero con más taxones tropicales en los depósitos peruanos. Diferencias entre las faunas peruanas y chilenas pueden ser explicadas por gradientes termales latitudinales que cambiaron la intensidad de las surgencias costeras y también las temperaturas de los océanos del Sur durante el Neógeno.

Palabras clave: Ampliación de distribución, Implicaciones biogeográficas, Moluscos Neógenos, Chile-Perú.

INTRODUCTION

Despite 150 years of exhaustive and expert study of Neogene mollusks from Chile (Darwin, 1846; Hupé, 1854; Philippi, 1887; Möricke, 1896; Tavera, 1979; Frassinetti and Covacevich, 1993), a full realization of their biostratigraphic potential has been hindered by a lack of independent age control. Studies of microfossils (e.g., Martinez and Caro, 1980; Ibaraki, 1992a) have partly rectified this situation, but there remain many stratigraphic sections that contain abundant macrofossils but few and poorly preserved microfossils. Radiometric dating of strata is difficult in Chile due to the scarcity of discrete volcanic ash beds representing single eruptive and depositional events.

For the forearc basins (Pisco, Sacaco, Camaná) of south-central Peru (Figure 1), the situation is reversed. The Neogene molluscan fauna has only been studied for the past fifteen years (Muizon and DeVries, 1985; DeVries, 1985, 1986, 1995, 1997a, 1997b, 1997c, 2000; Macharé *et al.*, 1988; DeVries and Vermeij, 1997; Vermeij and DeVries, 1997). Nevertheless, the geochronologic history of the basin has been fairly well-established and provides a well-constrained temporal framework for molluscan biostratigraphy (Muizon and Bellon, 1980, 1986; Muizon and DeVries, 1985; Dunbar *et al.*, 1990; DeVries, 1998). Sediments of the basin are replete with diatoms and the well-preserved remains of other microfossil groups. Moreover, stratigraphic sections contain numerous discrete ash beds that have generally proved amenable to ^{40}K - ^{40}Ar and ^{40}Ar - ^{39}Ar dating.

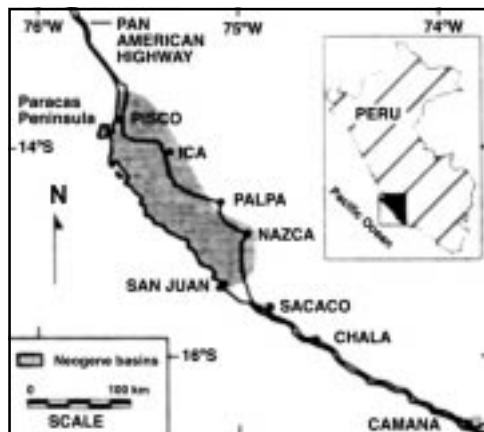


FIGURE 1. Extent of the Pisco Basin in southern Peru. Sacaco and Camaná are at the centers of much smaller sedimentary basins. Deposits associated with upper Pliocene and Pleistocene marine terraces are scattered along the Peruvian margin from the Paracas Peninsula to the border with Chile.

Throughout the Neogene there existed numerous molluscan species common to both Chile and Peru. Radiochronologic and biochronologic ranges for these species can be established for occurrences in Peru. Of course, these ranges may not always apply to the same species found 1000-2000 km south in Chile, either because of significant diachroneity in migration histories or due to the persistence or failure of refugia. Nevertheless, the Peruvian data do provide a basis for evaluating the biostratigraphic and biochronologic importance of molluscan taxa in Neogene deposits of Chile. Furthermore, a comparison of the fossil record from Peru and Chile may reveal patterns of diversity that bear on the evolution of the western South American molluscan fauna and faunal provinces.

Thirty species of mollusks common to both Peru and Chile are considered in this report (Table I). Identifications are based on published descriptions of fossil material, as well as long experience working with the Peruvian fauna (DeVries) and Chilean fauna (Frassinetti). A comparison of specimens from both countries was conducted during a visit by DeVries to the Museo Nacional de Historia Natural in Santiago in 1993. Localities and samples with biostratigraphic or radiometric data from Peru that have not been previously published are listed in the appendix.

Numerical ages for biostratigraphic zonal boundaries and high and low stands of sea level reported by Haq *et al.* (1987) and Barron *et al.* (1985) have been corrected to conform with the magnetostratigraphy of Cande and Kent (1992) and biostratigraphic datums of Curry *et al.* (1995), Shackleton *et al.* (1995), and Mascle *et al.* (1996).

STRATIGRAPHY OF SOUTHERN PERUVIAN BASINS

The Pisco, Sacaco, and Camaná Basins are emergent forearc basins lying between the Peru-Chile Trench and the Andean Cordillera (Thornburg and Kulm, 1981) between latitudes of 13°30'S and 17°S. The stratigraphy of Neogene marine sediments in the Pisco and Sacaco basins (Figure 2) has been described by Muizon and DeVries (1985), Marocco and Muizon (1988), Macharé *et al.* (1988), Dunbar *et al.* (1990), DeVries and Schrader (1996), and DeVries (1997c, 1998). The Neogene section consists of the uppermost Oligocene-Lower to Middle Miocene Chilcatay Formation and Middle Miocene to Pliocene

Pisco Formation. Of the marine terraces in the region, the most elevated were formed during the latest Pliocene (Ortlieb and Macharé, 1990), while those of lesser elevation formed during the Quaternary (Hsu, 1988). Farther south, the Camaná Basin contains latest Oligocene to Middle Miocene fossiliferous sandstones and coquinas assigned to the Camaná Formation (Ruegg, 1952; Stainforth and Ruegg, 1953; Pecho and Morales, 1969; DeVries, 1998). Marine terraces between Sacaco and Camaná yield Pliocene mollusks in the uppermost levels, typically at elevations of about 250 meters above sea level, and Quaternary taxa on lower wave-cut platforms.

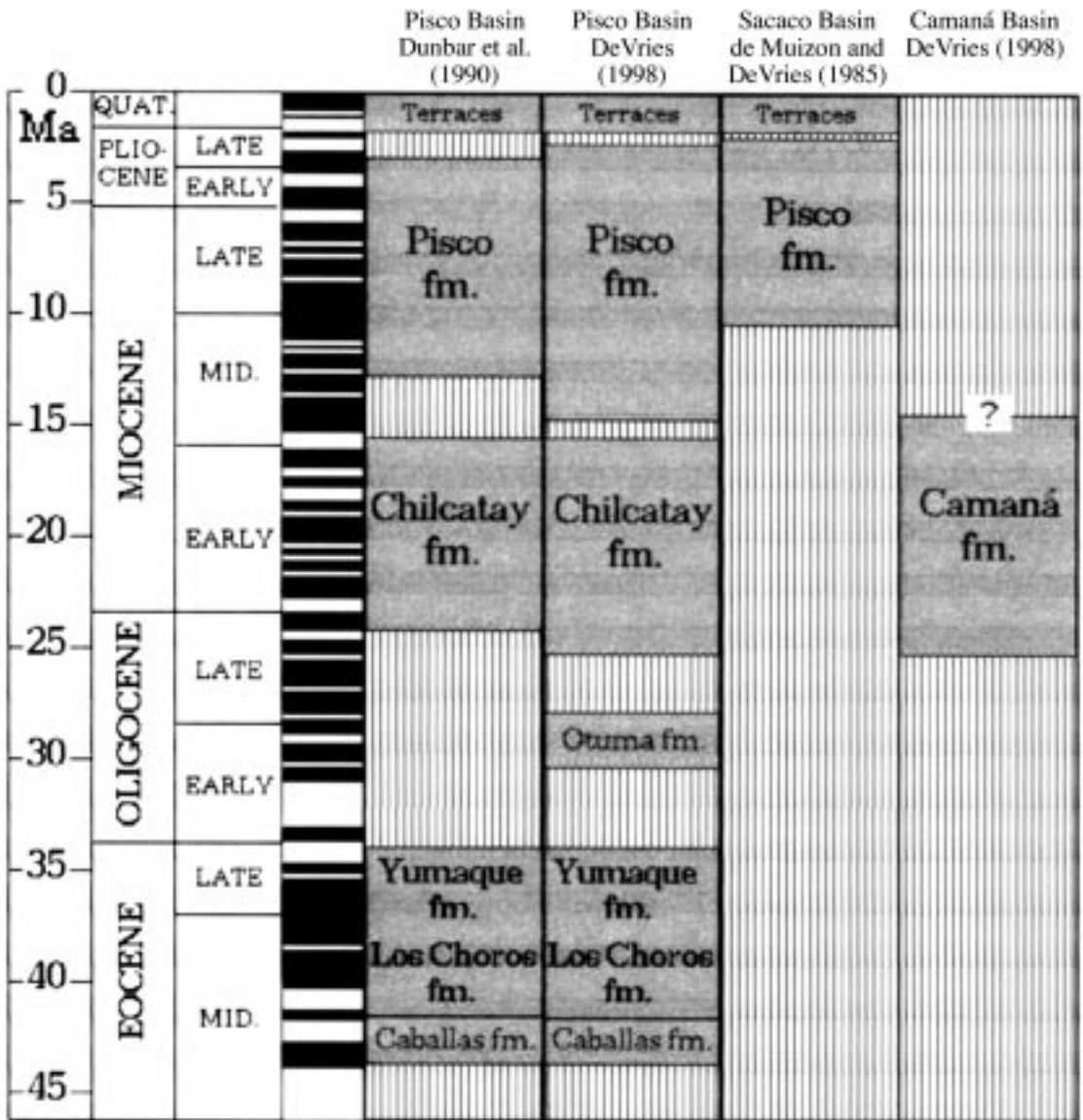


FIGURE 2. Cenozoic stratigraphy of marine sedimentary deposits in the Pisco, Sacaco and Camaná basins.

Radiometric dates and biochronologic ages for samples from the Pisco Basin and outcrops to the south have been published by Newell (1956), Rivera (1957), Muizon and Bellon (1980, 1986), Muizon and DeVries (1985), Macharé and Fourtanier (1987), Macharé *et al.* (1988), Tsuchi *et al.* (1988, 1990, 1992), Marty (1989), Rønning (1990), Dunbar *et al.* (1990), and Ibaraki (1992b, 1992c, 1993). Additional ^{40}Ar - ^{39}Ar age measurements have been provided by L. Snee (United States Geological Survey, Denver, Colorado, USA) and diatom zonal assignments by H. Schrader (University of Bergen, Norway) and P. Tapia (University of Nebraska, USA).

STRATIGRAPHY OF NORTHERN AND CENTRAL CHILEAN BASINS

The outcrops of marine Neogene sedimentary rocks on the central Chilean coast exhibit a discontinuous distribution, limited by the proximity of the Coastal Cordillera and penetration inland of the coastal plain. Their maximum development occurs at the latitude of Navidad (34°S) where fossiliferous deposits are encountered 25 to 30 km from the coast. Most of the remaining deposits are exposed in smaller areas characterized by cliffs, marine terraces, and inland ravines formed during tectonic uplift and subsequent erosion (Covacevich and Frassinetti, 1990).

The Navidad Formation, in its type locality in central Chile, is treated as the reference stratigraphic unit for the study of Chilean Miocene invertebrates. This is especially true for its basal part, the Navidad Member, which contains the greater part of the formation's type fauna.

According to Tavera (1979), the Navidad Formation is divided into three units in its type area (34°S). They are, from oldest to youngest, the Navidad, Lincancheu, and Rapel members. The lowest member is well exposed on coastal cliffs that extend between the Maitenlahue and Pupuya estuaries. In contrast, the Lincancheu and Rapel members crop out farther inland, in the vicinity of the village of Rapel.

Tavera (1979) assigned the entire Navidad Formation to the Burdigalian stage (Early Miocene) based on its macrofossils (Covacevich and Frassinetti, 1986; Frassinetti, 2001). Better defined ages are based on the presence of discoasters in the mudstones of Punta Perro, which are assigned to ages ranging from the late Early Miocene to the middle Middle Miocene (Martínez and Valenzuela, 1979). In a more thorough treatment, Frassinetti and Covacevich (1981) estimated the age of the Navidad Formation as Early to Middle Miocene.

Overlying the Navidad Formation lies the La Cueva Formation (Cecioni, 1978), that, in its type section at Estero El Ganso, includes a fauna typically attributed to the unit (Philippi, 1887; Bruggen, 1950; Herm, 1969) that has traditionally been assigned an Upper Pliocene age.

Deposits of the Coquimbo Formation and correlated units in northern Chile between Mejillones and Tongoy traditionally have been assigned to the Pliocene based on their macrofossil content (Bruggen, 1950; Herm, 1969). Micropaleontological studies of recent years, however, indicate that locally the Neogene sequences assigned to the Coquimbo Formation include beds of Early Middle Miocene and earliest Late Miocene age (Covacevich and Frassinetti, 1990). It is important to note, as well, that Guzmán *et al.* (2000) concluded from studies in the area of Caldera (northern Chile) that Herm (1969) assigned Early Pliocene ages to Upper Miocene deposits, and Late Pliocene ages to Lower Pliocene deposits. Guzmán *et al.* (2000) consequently recommended that Herm's (1969) biostratigraphic interpretations be viewed with caution.

EARLY TO MIDDLE MIOCENE MOLLUSKS IN PERU

The Chilcatay Formation of the Pisco Basin and the basal portion of the more southerly situated Camaná Formation have yielded molluscan assemblages that includes several species heretofore only known from the Navidad Formation of central and southern Chile (Table I).

TABLE I. Molluscan species found in both Chilean and Peruvian deposits. The lower to middle Miocene Navidad Formation is divided into three units. From oldest to youngest, they are the Navidad, Lincanheu, and Rapel members (Tavera, 1979). Unless otherwise noted, the assignment of species to members of the Navidad Formation is according to Tavera (1979).

SPECIES NAME	ROCK UNIT or LOCALITY (CHILE)	ROCK-UNIT (PERÚ)	AGE (PERÚ) (Ma)
<i>Acanthina katzi</i>	Chiloé	Chilcatay	12-25
<i>Acanthina obesa</i>	Lo Abarca	Pisco	3-10
<i>Amiantis domeykoana</i>	Coquimbo Fm.	Pisco	2-12
<i>Chlamys calderensis</i>	Coquimbo Fm.	Pisco	14
<i>Chlamys simpsoni</i>	Coquimbo Fm.	Pisco	4-6
<i>Chlamys vidali</i>	Coquimbo Fm.	Pisco	3-5
<i>Chorus blainvillei</i>	Coquimbo Fm.	Pisco, Talara	3
<i>Chorus frassinettii</i>	Isla Mocha	Pisco	6-10
<i>Chorus grandis</i>	Coquimbo Fm.	Pisco	2-5
<i>Concholepas kieneri</i>	Coquimbo Fm.	Pisco	3-10
<i>Concholepas nodosa</i>	Coquimbo Fm.	Pisco	2-5
<i>Dosinia ponderosa</i>	Coquimbo Fm.	Pisco	3-10
<i>Eucrassatella ponderosa</i>	Navidad, ¿Lincanheu?	Chilcatay	19-25
<i>Eurhomalea fuenzalidai</i>	Coquimbo Fm., La Cueva Fm.	Pisco	2-6
<i>Ficus distans</i>	Navidad	Chilcatay	13-21
<i>Fusinus remondi</i>	Coquimbo Fm.	Pisco	3-6
<i>Glycymeris colchaguensis</i>	Navidad	Chilcatay	19-25
<i>Glycymeris ibariformis</i>	Navidad ¹	Chilcatay	19-25
<i>Herminespina mirabilis</i>	Coquimbo Fm.	Pisco	3-4
<i>Herminespina philippii</i>	Coquimbo Fm.	Pisco	4-10
<i>Macrocallista boliviana</i>	Coquimbo Fm.	Pisco	3
<i>Miltha vidali</i>	Navidad	Chilcatay, Pisco	13-25
<i>Olivancillaria tumorifera</i>	Navidad, ¿Lincanheu?	Chilcatay	17-25
<i>Panopea coquimbensis</i>	Coquimbo Fm.	Pisco	3-14
<i>Testallium cepa</i>	Navidad, Lincanheu, Rapel	Chilcatay	13-25
<i>Trachycardium procerum domeykoanum</i>	Coquimbo Fm.	Pisco	3-4
<i>Turritella affinis</i>	Navidad	Chilcatay	13-14
<i>Turritella breantiana</i>	Navidad, Lo Abarca	Pisco	7-10
<i>Turritella chilensis</i>	Isla Mocha	Pisco	5-7
<i>Turritella cingulatiformis</i>	Coquimbo Fm.	Pisco	2-4

¹ Frassinetti and Covacevich, 1983

Among the most characteristic gastropods of the Early Miocene in Chile are *Ficus distans* Sowerby, 1846 (see Tavera (1979) and Covacevich and Frassinetti (1980)), *Olivancillaria tumorifera* (Hupé, 1854) (Plate 1, figure 6) and *Testallium cepa* (Sowerby, 1846) (= *Gastridium cepa* of authors; see Vermeij and DeVries (1997) (Plate 1, figure 3). These taxa are found, respectively, in the lowest member, lower two members (or only lowest member), and all three members of the Navidad Formation (Tavera, 1979). (Note that Tavera (1979) recorded *O. tumorifera* from the lowest member (Navidad) only in his Table 4). The three species are found together in the northern Pisco basin in the type section of the Chilcatay Formation (Dunbar *et al.*, 1990). They occur in barnacle-rich, fine-grained gravels interbedded with massive medium-grained sandstones with *Ophiomorpha* tubes (e.g., samples DV 443-4 and DV 396-1) suggestive of a shallow nearshore subtidal environment. The sandy interval is underlain and overlain by thick sequences of tuffaceous and diatomaceous siltstones indicative of a low-energy, open-marine setting. The diatom assemblages have been assigned by H. Schrader (written communication, 1987) to the *Rocella gelida*, *Craspedodiscus elegans*, and *Triceratium pileus* zones (24.4-17.8 Ma) of Barron *et al.* (1985) (DeVries, 1997b).

Specimens of *Ficus distans* and *Testallium cepa* occur together on the western side of the Río Ica together with numerous other gastropod species in a 50-cm-thick bioclastic sandstone with barnacle-encrusted igneous boulders that have disarticulated valves of *Ostrea* strewn at their bases. Teeth of *Carcharodon megalodon*, teeth of other species of sharks, and cetacean bones are scattered throughout this strandline deposit (e.g., samples DV 484-6, DV 484-1). Diatoms from underlying siltstones indicate an age of about 14-16 Ma (Rønning, 1990). Both molluscan species are also found along Quebrada Gramonal on the eastern side of the Río Ica in strata of comparable age (sample DV 377-3). In contrast, specimens of *Olivancillaria tumorifera* are found only in lower strata on both sides of the same Río Ica valley (samples DV 575-3; DV 1179-1), which is consistent with the older age of *O. tumorifera* in the Navidad basin of Chile.

Specimens of *O. tumorifera* have also been found in beds near Caravelí, southern Peru, that are tightly correlated with radiometrically dated uppermost Oligocene strata (Noble *et al.*, 1985; DeVries, 2001).

Testallium cepa is one of the most wide-ranging species of the 'Navidad' molluscan fauna in Peru, both geographically and temporally. It is common in coarse-grained sandstones inferred to have been deposited in shallow neritic waters from the northern Pisco Basin to the pampas of Caravelí in southern Peru. Specimens of *T. cepa* found north of Nazca occur in Lower and lower Middle Miocene strata, whereas those from Nazca southward (e.g. samples DV 638-1 and DV 1256-1) are found in Upper Oligocene and lowermost Miocene deposits. The former sample was collected from a transgressive lag of sandstone and conglomerate that blanketed an igneous platform and is overlain by non-marine alluvial deposits with ashes dated at 18-22 Ma (Noble *et al.*, 1979; DeVries, 1998). The latter sample was collected near Caravelí from a 10-15-m thick crossbedded sandy coquina set within a thick section of Tertiary volcanoclastic sediments.

Specimens of *Glycymeris ibariformis* Frassinetti and Covacevich, 1984 and *Eucrassatella ponderosa* (Philippi, 1887) (Plate 2, figures 1 and 3) are well known in the basal Navidad member of the Navidad Formation of central Chile (Tavera, 1979; Frassinetti and Covacevich, 1984). In Peru, these species are often together in sandstone outcrops of the Chilcatay Formation in the northern and central Pisco Basin (e.g., sample DV 377-2) and outcrops of the Camaná Formation in southern Peru (sample DV 1271-1). Associated diatomaceous siltstones (e.g., sample DV 574 180P; see DeVries, 1998) in the Chilcatay region yield ages of Early to early Middle Miocene. Similar ages are provided by diatomaceous deposits associated with sandstones and conglomerates (sample DV 484-1) containing specimens of *Miltha (Matanziella) vidali* (Philippi, 1887), a species of the Navidad Member redescribed by Frassinetti (1978) (Plate 1, figure 7). The stratigraphic range of *M. vidali* in Peru may be significantly longer than the range (Navidad Member of the Navidad Formation) in Chile.

The Middle Miocene fauna of southern Peru is less diverse than either the Early Miocene or Late

Miocene-Pliocene faunas. The most diagnostic species, *Turritella infracarinata* Gryzbowski, 1899, and *Anadara sechurana* Olsson, 1932, range into northern Peruvian waters rather than southwards to Chile (DeVries, 1997c). One of the few distinctive Middle Miocene Peruvian species also found in Chile is *Acanthina katzi* (Fleming, 1972), which was originally described from Isla Chiloé in southern Chile (Watters and Fleming, 1972) and subsequently reported from southern Peru (DeVries and Vermeij, 1997).

LATE MIOCENE TO PLIOCENE FAUNA

Pliocene mollusks from Chile have been extensively described (Hupé, 1854; Philippi, 1887; Herm, 1969), but prior to the studies of D. Frassinetti and V. Covacevich on the central Chilean island of Mocha and central Chilean coast at Lo Abarca (Covacevich and Frassinetti, 1990), Late Miocene mollusks from Chile were not known. Recent studies have also demonstrated the presence of Upper Miocene fossiliferous beds on the northern Chilean coast (Guzmán *et al.*, 2000). Thus, there is now some basis for comparing Chilean material with abundant fossil material from widespread Upper Miocene strata in the Pisco and Sacaco Basins.

One of the oldest Late Miocene species in Peru is *Chorus frassinettii* DeVries, 1997, a species also present on Isla Mocha (DeVries, 1997a). It and several other species also known from Chile, *Herminespina philippii* (Möricke, 1896) (= *Acanthinucella philippi* of Herm, 1969) (Plate 1, figure 4), *H. mirabilis* (Möricke, 1896), *Amiantis domeykoana* (Philippi, 1887) (Plate 2, figure 2), and *Dosinia ponderosa* (Gray, 1838) (Plate 1, figure 8), overlie an ash bed with a ^{40}K - ^{40}Ar age of about 9.5 Ma (Muizon and Bellon, 1986) and underlie ash beds at Aguada de Lomas with ^{40}K - ^{40}Ar age of about 8-9 Ma (Muizon and DeVries, 1985; Muizon and Bellon, 1986). Another Chilean species, *Panopea coquimbensis* d'Orbigny, 1842, is found in Peruvian sandstones (sample DV 420-1) that underlie Middle Miocene diatomaceous siltstones dated at 13.9-13.5 Ma (sample DV 417-3, see DeVries, 1997c), as well as in Upper Miocene sandstones (sample DV 576-6) and uppermost Miocene / Lower Pliocene strata (sample DV 614-10) in southern Peru.

Among the mollusks found in the small Upper Miocene outcrop at Lo Abarca (Covacevich and Frassinetti, 1990) is a small muricid referable to '*Acanthina obesa*', a species informally described by DeVries (1986). '*A. obesa*' is common in Upper Miocene deposits throughout the Pisco and Sacaco Basins.

Some occurrences of Late Miocene molluscan taxa in Peru call into question ranges recently proposed for these species in Chile by Guzmán *et al.* (2000). The genus *Herminespina* appears for the first time in lower Upper Miocene strata in Peru (DeVries and Vermeij, 1997), with some evidence (DeVries, unpublished data) that the genus arose from a late Middle Miocene stock of *Acanthina*. If so, the Middle Miocene age proposed for some specimens of *H. philippii* is doubtful. In another example, the oldest Peruvian specimens of *Concholepas kieneri* Hupé, 1854, occur in lower Upper Miocene beds. They represent an intermediate step in a morphological progression leading from middle Early and Middle Miocene taxa in Peru (*C. unguis* DeVries, 1995, and *C. chirotenensis* DeVries, 2000). Thus, it is unlikely that they also occur in Middle Miocene strata in Chile (Guzmán *et al.*, 2000).

Several species thought by Herm (1969) to have exclusively Pliocene ranges are known to also occur in Upper Miocene strata of the Pisco and Sacaco Basin, including *Concholepas kieneri* Hupé, 1854 (Plate 1, figure 2), which is found in 9-Ma sandstones at Aguada de Lomas. Gastropods in the central Pisco Basin, including *Fusinus* cf. *F. remondi* (Philippi, 1887), *Herminespina philippii*, and *C. kieneri*, are found in coquinas laterally contiguous with diatomaceous deposits dated at 5 to 7 Ma (Rønning, 1990). These ages are in accord with the Late Miocene age determined for this taxa in Chile by Guzmán *et al.* (2000).

Many species from Chile have Peruvian counterparts in the Pisco and Sacaco Basins whose ranges are confined to the Pliocene, including *Chlamys simpsoni* Philippi, 1887, *Trachycardium procerum domeykoanum* (Philippi, 1887) (Plate 1, figure 5), *Macrocallista boliviana* (Philippi, 1887) (Plate 2,

figure 5), and *Eurhomalea fueenzalidai* (Philippi, 1887) (Plate 2, figure 6), all found in Upper Pliocene deposits that cap the Neogene sequence west of Nazca (sample DV 472-1). Chilean species whose ranges in the Sacaco Basin extend upward to sandstones overlying an ash bed dated at 3.9 Ma include *Anadara* aff. *A. chilensis* (Philippi, 1887) (Plate 2, figure 4), *Chlamys vidali* (Philippi, 1887), *Dosinia ponderosa*, *Amiantis domeykoana*, *Turritella cingulatiformis* Möricke, 1896, *Chorus grandis* (Philippi, 1887), *Hermineospina mirabilis* and *Concholepas nodosa* Möricke, 1896 (Muizon and DeVries, 1985; DeVries, 1997a).

Among these species, *Chlamys simpsoni*, *C. vidali*, *Trachycardium procerum domeykoanum*, *Macrocallista boliviana*, and *Turritella cingulatiformis* have no Miocene record in Peru. Thus, their ranges will need to be reconciled with ranges extending into the Late Miocene in Chile (Guzmán *et al.*, 2000). In the case of the venerid *Amiantis*, Peruvian specimens exist in strata as old as Middle and latest Early Miocene, but these belong to an undescribed species different than *A. domeykoana*. The same may be true for Middle Miocene populations from Chile reported by Guzmán *et al.* (2000). A similar situation may also apply to Middle Miocene Chilean specimens of *Dosinia* (Guzmán *et al.*, 2000), since in the case of Peruvian occurrences, specimens older than Late Miocene are not *Dosinia ponderosa*.

A small number of Pliocene species from Chile occur as far north as the Talara Basin of northern Peru. Outcrops of the Taime Formation (DeVries, 1986, 1988a) have yielded specimens of *Chorus blainvillei* (d'Orbigny, 1842) (Plate 1, figure 1), which was first reported from hills West of Piura by Olsson (1932). Other species include 'Acanthina triangularis,' a Late Pliocene taxon informally described by DeVries (1986) that is found in Upper Pliocene/Lower Pleistocene strata of southern Peru and Chile, *Chlamys vidali*, and *Hermineospina mirabilis*.

DISCUSSION

The presence of Early Miocene warm-water or tropical genera (*Cypraea*, *Ficus*, *Murex*, *Cancellaria*, *Oliva*, *Conus*, *Terebra*, *Pinna*, *Eucrassatella*, *Dosinia*) in central and southern Chile and southern Peru reflects the warmer sea-surface temperatures prevalent at that time (Flowers and Kennett, 1993) and parallels the Early Miocene expansion of tropical faunas into higher southern latitudes in New Zealand (Hornibrook, 1992). Many Early Miocene genera from Chile are not found in southern Peru (e.g., *Pleurotoma*, *Distorsio*, *Cassis*, *Surculites*, *Nemocardium*, and *Codakia* (all *sensu* Philippi, 1887). Some absences in Peru (*Pleurotoma* and other genera of the Turridae) might be due to a poor representation of outer-shelf paleoenvironments, which are more commonly encountered in the Navidad Basin of Chile. Other absences in Peru can be attributed to a failure of southern high-latitude genera (e.g., *Struthiolaria*; see Zinsmeister, 1982) and species with South Atlantic affinities (e.g., several species of *Turritella* and *Voluta*; see Ortmann, 1902, and Tavera, 1979) to spread northward into Peruvian waters.

The differences between the Early Miocene faunas of central Chile and southern Peru suggests that a boundary between different environmental regimes lay somewhere between 17°S and 33°S. The presence of Lower Miocene siltstones rich in diatoms and clupeoid fish scales (anchovy, sardine) in southern Peru suggests that the Early Miocene Peruvian coastal zone was highly productive and probably influenced strongly by coastal upwelling. If the upwelled waters off Peru were cooler than the Early Miocene coastal waters of central and southern Chile, the failure of more Chilean species with tropical affinities to occupy Peruvian shores during the Early Miocene might be explained (Figure 3). The faunal dissimilarity might even be maintained despite the existence of Early Miocene eastern boundary currents that would transport high-latitude water towards the equator and could serve as a vector for southern latitude molluscan larvae.

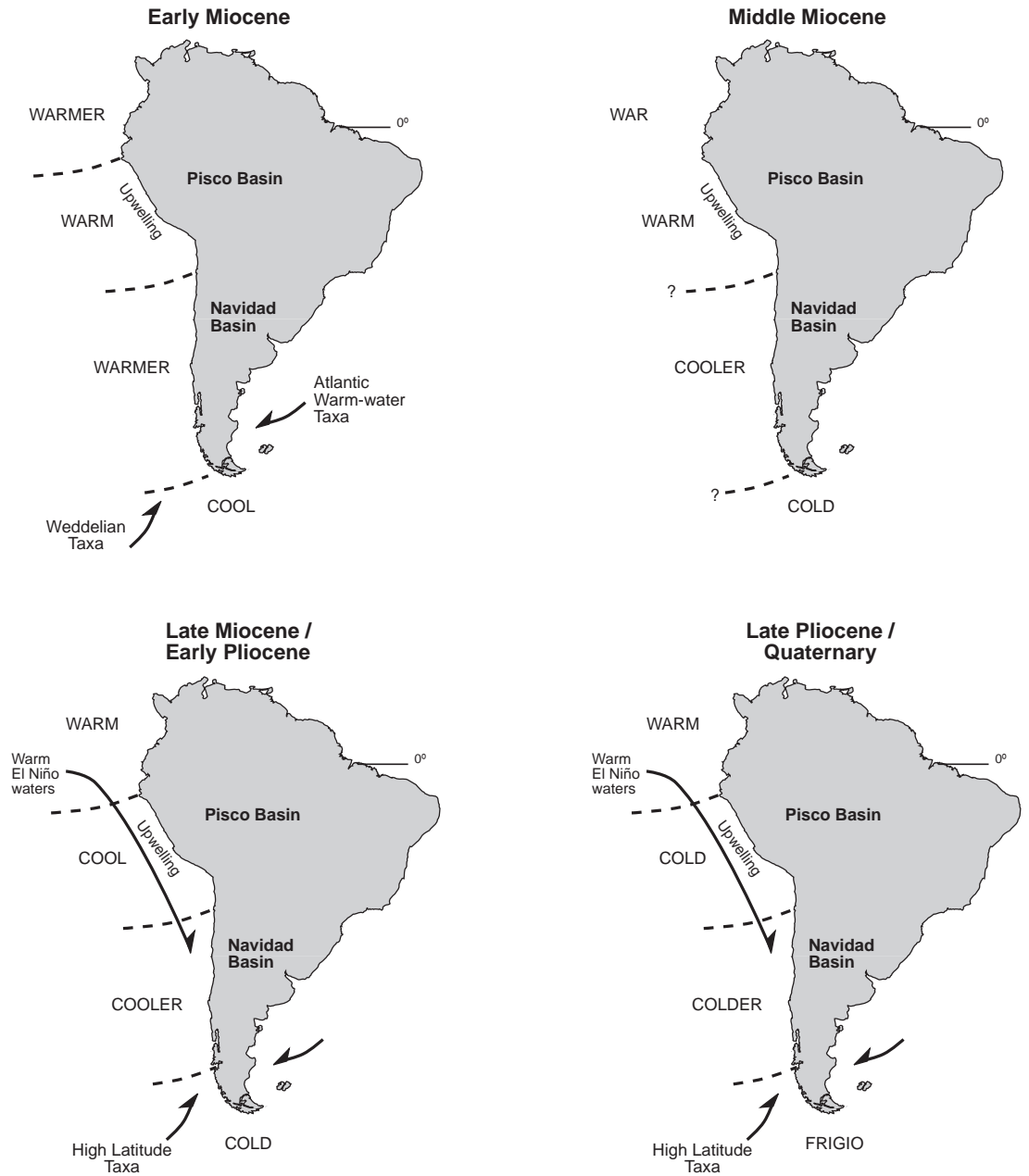


FIGURE 3. Proposed oceanographic regimes along the coast of western South America during the Neogene. Coastal upwelling off Peru might have barred northward and southward migrations of warm-water taxa when global sea surface temperatures were high and permitted a northward expansion of cooler water faunas when global sea surface temperatures were low. Invasions of a select group of warm-water larvae southwards during El Niño events also might have occurred during the late Miocene and Pliocene, as it does today.

The Late Miocene – Pliocene faunas of Peru and Chile have a higher proportion of species in common than do the Early Miocene faunas. The Peruvian fauna is more diverse than the Chilean fauna, largely because it has more taxa associated with the Pliocene counterpart to the equatorial Panamic Faunal Province. Late Miocene Pliocene diatomites and diatomaceous siltstones (Dunbar *et al.*, 1990) containing abundant clupeoid fish remains (DeVries, unpublished data) in the Pisco Basin indicate the existence of high primary and secondary productivity at that time, most likely the consequence of strong and persistent coastal upwelling. El Niño events may have provided the means for tropical larvae to spread southward into the cooler waters of the upwelling zone, as seems to have been the case throughout the Quaternary (DeVries, 1988b; Ortlieb *et al.*, 1990), but a Pliocene thermal barrier to the dispersal of the larvae of many Panamic taxa appears to have existed off southern Peru or northern Chile.

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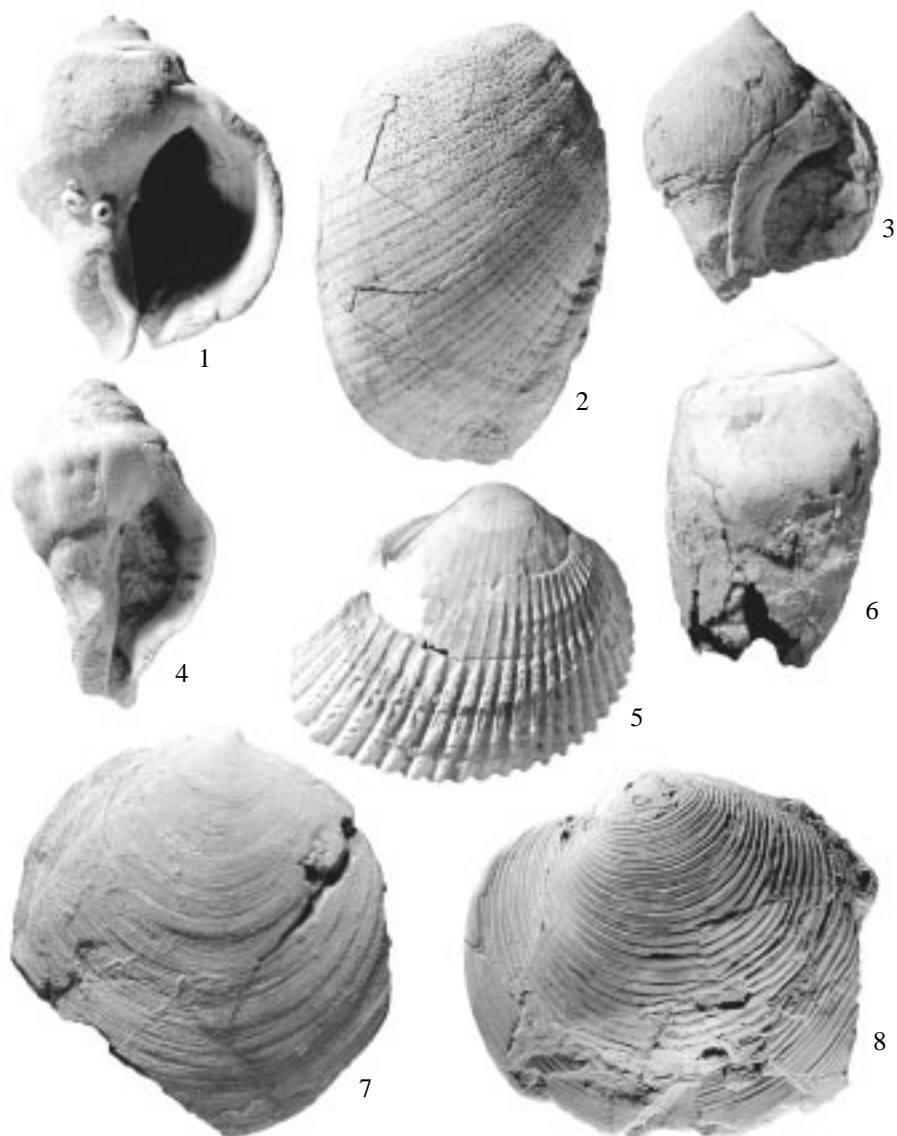
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Appendix

Localities and samples (previously unpublished)

Sample DV 377-2	Southwest wall of Quebrada Gramonal. 14°45'45"S 75°30'27"W (Lomitas 1:100,000 quadrangle).
Sample DV 420-1	South end of Filudo Depression, shell horizons in yellow-orange sandstone beds. 13°53'12"S 76°07'15"W (Pisco 1:100,000 quadrangle).
Sample DV 472-1	Pampa Los Chinos, canyon to village of Santa Clara. Interbedded fine-grained sandstone and siltstone with indurated lenses of mollusks. 14°44'S 75°13'W (Palpa 1:100,000 quadrangle).
Sample DV 484-1	Yesera de Amara. 14°35'38"S 75°40'10"W (Lomitas 1:100,000 quadrangle).
Sample DV 540-2	Cerro Cabeza de Toro. 14°24'47"S 75°35'36"W (Ica 1:100,000 quadrangle). Coquina of balanids and mollusks in apron around basement outcrop.
Sample DV 576-6	Slopes east of Quebrada Gramonal. 14°45'29"S 75°30'15"W (Lomitas 1:100,000 quadrangle).
Sample DV 614-10	South Usaca. 14°54'36"S 75°08'55"W (Palpa 1:100,000 quadrangle).

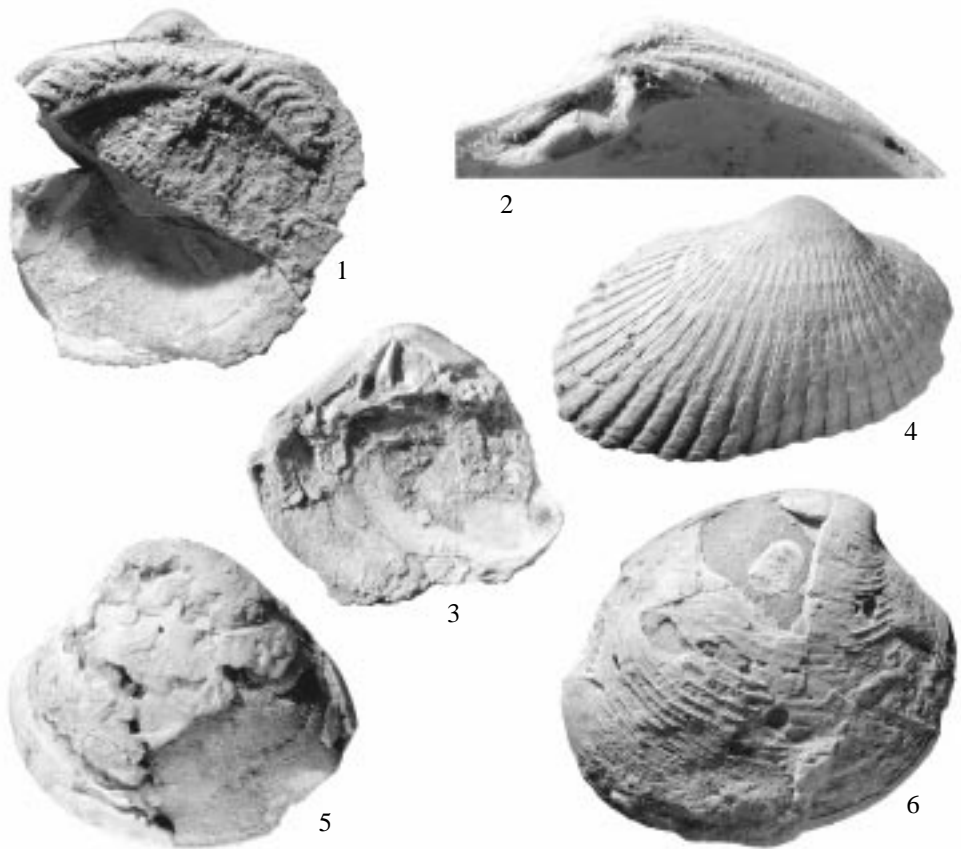
Plate 1



FIGURES 1-8. Miocene and Pliocene mollusks of the Pisco Basin, Peru. (L = length; W = width; measurements in mm).

1. *Chorus blainvillei* (d'Orbigny, 1842). OSU 37355 (topotype), apertural view. L = 75.8; W = 66.8. Quebrada Cardo Grande, near Amotape, Peru. Taime Formation, Upper Pliocene. **2.** *Concholepas kieneri* Hupé, 1854. USNM 447088, abapertural view. L = 102.2; W = 67.6. Locality 83DV 361-6, South Sacaco (15°34'17"S 74°43'26"W), Lower Pliocene. **3.** *Testallium cepa* (Sowerby, 1846). DeVries collection, apertural view. L = 45.7; W = 37.6. Chilcatay Hills, Chilcatay Formation, Lower Miocene. **4.** *Herminespina philippii* (Mörnicke, 1896). DeVries collection, apertural view. L = 38.5; W = 23.4. Locality 87DV 571-1, El Jahuay (15°26'57"S 74°52'06"W), Upper Miocene. **5.** *Trachycardium procerum domeykoanum* (Philippi, 1887). DeVries collection, exterior view. L = 64.2; W = 75.4. Locality 86DV 423-3, north side Quebrada Huaricangana (14°55'33"S 75°17'41"W), uppermost Pliocene / lowermost Pleistocene. **6.** *Olivancillaria tumorifera* (Hupé, 1854). DeVries collection, abapertural view. L = 39.1; W = 24.8. Locality 87DV 396-1, Chilcatay Hills (14°11'42"S 76°06'57"W), Chilcatay Formation, Lower Miocene. **7.** *Miltha (Matanziella) vidali* (Philippi, 1887). DeVries collection. L = 54.0; W = 50.8. Chilcatay Hills, Lower Miocene. **8.** *Dosinia ponderosa* (Gray, 1838). DeVries collection. L = 85.1; W = 92.7. Locality 83DV 368, Aguada de Lomas (15°28'55"S 74°47'39"W), Upper Miocene.

Plate 2



FIGURES 1-6. Miocene and Pliocene mollusks of the Pisco Basin, Peru. (L = length; W = width; measurements in mm).

1. *Glycymeris ibariformis* Frassinetti and Covacevich, 1984. DeVries collection, right valve, interior view. L = 84.7; W = 81.8 (incomplete). Locality 87DV 575-3, Quebrada Gramonal (14°45'40"S 75°30'47"W), Chilcatay Formation, Lower Miocene. **2.** *Amiantis domeykoana* (Philippi, 1887). DeVries collection, hinge, right valve. Corrugated posterior lateral tooth 21.4 mm long. Locality 86DV 423-3, north side Quebrada Huaricangana (14°55'33"S 75°17'41"W), uppermost Pliocene / lowermost Pleistocene. **3.** *Eucrassatella ponderosa* (Philippi, 1887). DeVries collection, portion of right valve, interior. L = 68.9; W = 77.4 (incomplete). Locality 87DV 575-3, Quebrada Gramonal (14°45'40"S 75°30'47"W), Chilcatay Formation, Lower Miocene. **4.** *Anadara* aff. *A. chilensis* (Philippi, 1887). DeVries collection, right valve, exterior view. L = 33.7; W = 48.8. Locality 83DV 380-2 (15°32'29"S 74°43'53"W), Sacaco, Lower Pliocene. **5.** *Macrocallista boliviana* (Philippi, 1887). DeVries collection, left valve, exterior. L = 87.0; W = 98.2. Locality 87DV 538-2, Hacienda Tunga (14°55'39"S 75°08'03"W), Pliocene. **6.** *Eurhomalea fuenzalidai* (Philippi, 1887). DeVries collection, right valve, exterior. L = 71.1; W = 80.6. Locality 83DV 360-2, South Sacaco (15°34'43"S 74°43'17"W), Lower Pliocene.