

Cretaceous bivalves from Ecuador and northern Peru

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Abstract

New collections of bivalves from Cretaceous sections (Albian-Maastrichtian) in the central Andean Basin, a forearc basin in northern Peru/Ecuador, and the Paita Basins illustrate how paleobiogeographical affinities changed through geological time. During the middle Albian (at Chinimbini), the taxa are cosmopolitan. Upper Albian and Cenomanian faunas (Chinimbini, along Río Misahuallí in Ecuador, and at Pongo de Rentema in Peru) contain mainly Tethyan faunas (known from northern Africa, Texas, and southern Europe). The early Turonian faunas (mainly inoceramids) are Tethyan and have very wide extension. The Coniacian-Santonian faunas (Celendin Formation) are comparable to those from northwest and west Africa, but oysters have a somewhat younger age in Africa than in Ecuador and Peru. Most important, toward the Campanian-Maastrichtian, the faunas from the Paita Basins became largely endemic. For a few taxa of stratigraphical or systematic importance, a more detailed taxonomy is provided.

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Resumen

Hemos estudiado nuevas colecciones de bivalvos del Cretácico (Albiano a Maastrichtiano) de la Cuenca andina y de estrechas cuencas de ante-arco del Ecuador y del Norte del Perú (cuencas Celica-Lancones y Paita-Yunguilla). Comentamos la evolución paleobiogeográfica revelada por estas faunas. Hacia el Campaniano-Maastrichtiano, las faunas de las cuencas de ante-arco se vuelven netamente endémicas. Algunas especies están descritas en detalle.

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1. Introduction

Cretaceous sections in northern Peru, previously studied by Benavides-Cáceres (1956) and Olsson (1944), have been resampled and studied along with new sections in Ecuador (in scientific cooperation between IRD [France] and Petroecuador). For a detailed study of these sections, see Jaillard et al. (2006); herein, we focus on the bivalve fauna whose ages range from Albian to Maastrichtian. Their preservation varies from steinkern to fully preserved shells, especially in the Campanian-Maastrichtian strata of northern Peru.

Bivalves from this area previously have been studied, listed, or illustrated by Gabb (1877), Gerhardt (1898a,b), Neumann (1907), Brüggén (1910), Benavides-Cáceres (1956), Schlagintweit (1912), Reeside in Wasson and Sinclair (1927), Steinmann (1929), Olsson (1934, 1944), Richards in Knechtel et al. (1947), Wilson (1963), and Willard (1966). Although we have studied the original material of some of these authors (i.e., Benavides-Cáceres, Olsson, Reeside, Richards, and Willard) for comparison, this article is based on new material collected during several field seasons since 1994.

The Chinimbini, Río Misahuallí (Ecuador), and Rentema (northern Peru) sections belong to the central Andean Basin (Fig. 1), a Cretaceous, backarc, pericratonic shallow-marine basin on the Peruvian-Ecuadorian active margin. During the latest Cretaceous-Paleogene, the basin evolved progressively toward a continental retroarc basin (Jaillard et al., 1997). Sedimentation in the region was dominated by a shallow marine, low-energy regime that induced environments that occasionally were restricted to dysaerobic.

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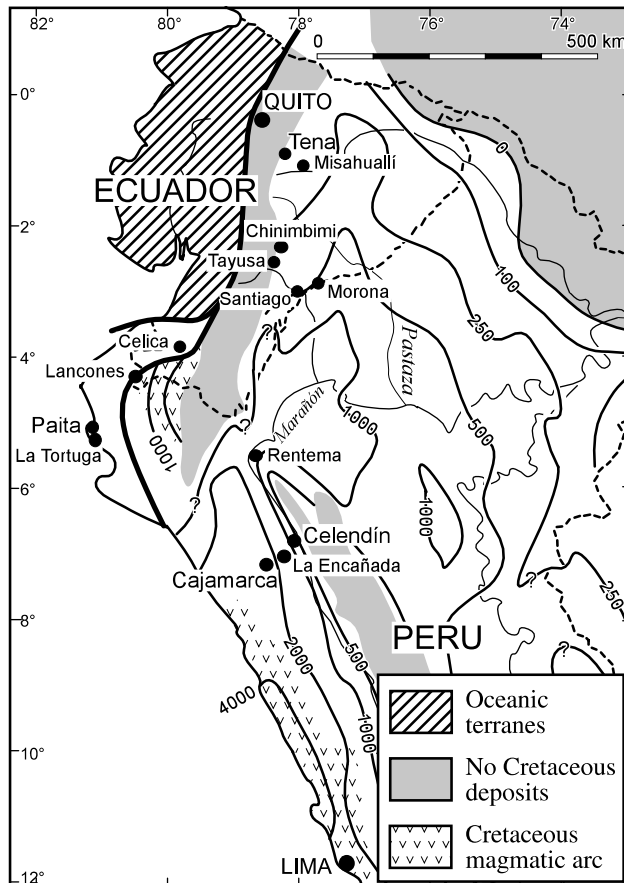


Fig. 1. Paleogeographic sketch of northern Peru and Ecuador during the Cretaceous, with isopach map for the Albian-Turonian interval and location of the main sections cited in the text.

The La Mesa and La Tortuga sections, south of Paita, belong to a narrow forearc basin of latest Cretaceous age, with exposures in northwesternmost Peru and western Ecuador (Jaillard et al., 1998, 1999; Fig. 1). This basin, informally designated the Celica-Lancones Basin, is marked by high-energy, open marine environments and predominantly detrital sedimentation.

2. Bivalve fauna

2.1. Backarc basins

2.1.1. Ecuador

The Chinimbimi section in the Oriente Basin of Ecuador is located in the southern part of the subandean zone, northeast of Méndez on the Upano River, and the Río Misahuallí section occurs in the northern part of the subandean zone, east of Tena (Fig. 1). These sections yield numerous Albian bivalves from the lower part of the Basal Napo Formation.

At Chinimbimi (Fig. 2), the middle Albian is characterized by the common occurrence of *Actinoceramus con-*

centricus (Parkinson, 1819), associated with *Inoceramus* cf. *anglicus* Woods, 1911, and ‘*Pycnodonte*’ *navia* (Hall, 1856). The upper Albian beds contain abundant epifaunal bivalve fauna dominated by *Oscillolopha syphax* (Coquand, 1862a) and *Ceratostreon boussingaulti* (Orbigny, 1842) associated with less common *Modiolus* sp., *Merklinia* cf. *chihuahuensis* (Boese, 1910), *Neithea* sp., and spondylids. The infaunal bivalve fauna comprises mainly *Pleuromya* sp., associated with less frequent *Nuculana* sp., *Pterotrigonina* sp., lucinids, *Venericardia* aff. *bisculpta* (Gerhardt, 1898a, b), *Crassatella maroimensis* White, 1887, and cardiids (Fig. 2).

Along Río Misahuallí (Figs. 1 and 3), the epifaunal upper Albian bivalve faunas (basal Napo Formation) represent shallow marine environments. In the basal Napo shales, we collected *Aucellina* sp. and *Actinoceramus concentricus* (Parkinson, 1819), the latter of which indicates a late Albian age.

The overlying ‘T’ limestones yield *Oscillolopha syphax* (Coquand, 1862a), *Ceratostreon boussingaulti* (Orbigny, 1842), *Pseudolimea blancensis* (Stanton, 1947), *Neithea syriaca* (Conrad, 1852), *N. texana* (Roemer, 1852), and *Nucula* sp. (internal mould). Higher in the section, the ‘U’ limestones and sandstones (lower Napo Formation) yield ?*Neithea* sp. aff. *roemeri* (Hill, 1889) and *Aucellina* sp., which suggest a late Albian-early Cenomanian age.

The Turonian middle Napo Formation yields *Astarte* sp. and ?*Mytiloides* sp., which also occurs at the base of the overlying upper Napo Formation, thereby suggesting an age not younger than earliest Coniacian.

There are several additional localities in the backarc basins of Ecuador. The Tayusa section of the basal Napo Formation is located along the Upano River, approximately 5 km southwest of Chinimbimi, in the southwestern part of the Oriente Basin of Ecuador (Fig. 1). Albian strata of this section yield *Oscillolopha syphax* (Coquand, 1862a) (sample 94.T) and *Ceratostreon* sp. (sample 94.72).

Specimen 94.80, a *Plicatula* sp., was collected from the lower Napo Formation (chiefly Cenomanian) of the southern Oriente Basin (Ecuador) along the Santiago-Morona road (Fig. 1), approximately 8 km west of the Yaupi River. Along the Pastaza River (central Oriente Basin, between Tena and Chinimbimi, Fig. 1), the Turonian middle Napo Formation yields *Inoceramus* sp. and *Corbis* sp. (sample 94.89).

Sample 94.76 comes from an isolated outcrop of the upper Napo Formation (probably Santonian) located along the Santiago-Morona road, 3.5 km west of the Yaupi River (southern Oriente Basin, Ecuador). This sample contains *Pycnodonte flicki* Pervinquière, 1912, *Plicatula ferryi* Coquand, 1862a, and an unidentified inoceramid.

2.1.2. Peru

In northern Peru, the section at Pongo de Rentema, located along the Río Marañón (Fig. 1; Dept. Amazonas), yields abundant bivalve faunas of Albian-Santonian age (Fig. 4). The Albian of the Pongo de Rentema section (Robert, 2002) does not contain age-diagnostic bivalves.

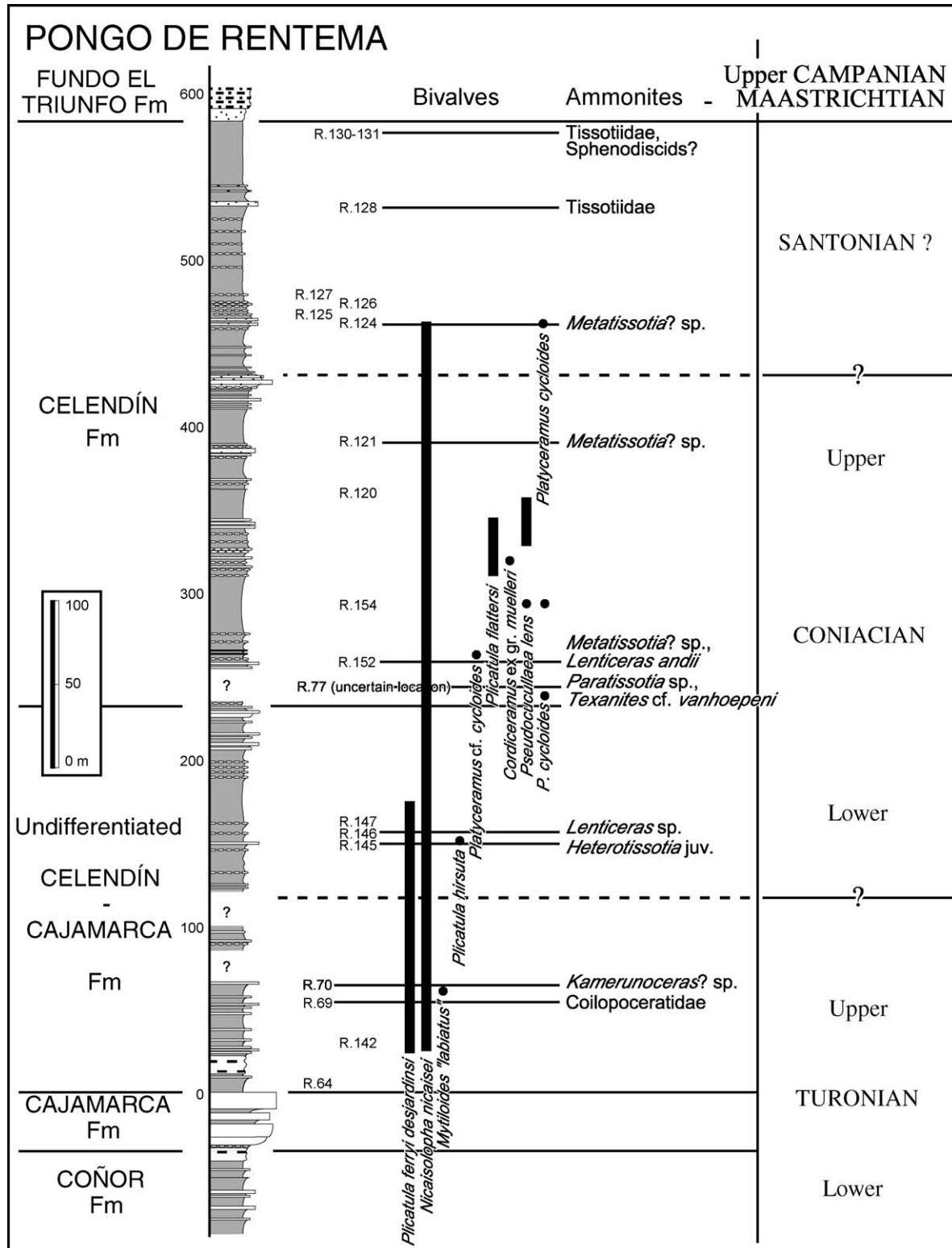


Fig. 2. Lithology of the Chinimbimi section (Ecuador) and distribution of the bivalves. Age indications from Bulot (in Jaillard et al., 1997). Filled circles and lines, in situ samples; open circles, loose samples.

The Pariatambo Formation yields *Pollex?* sp. and *Pholadomya* sp., whereas the Mujarrún Formation contains '*Ostrea soleniscus?* Meek, 1872, *Panopea* sp., and *Opis* cf. *elevata* Stephenson, 1952.

The overlying Romirón Formation contains an epifauna of oysters and pectinids (Tables 1 and 2) and a few infaunal taxa, such as taxodonts, trigoniids, some heterodonts, and pholadomyids. The Romirón assemblage is typically

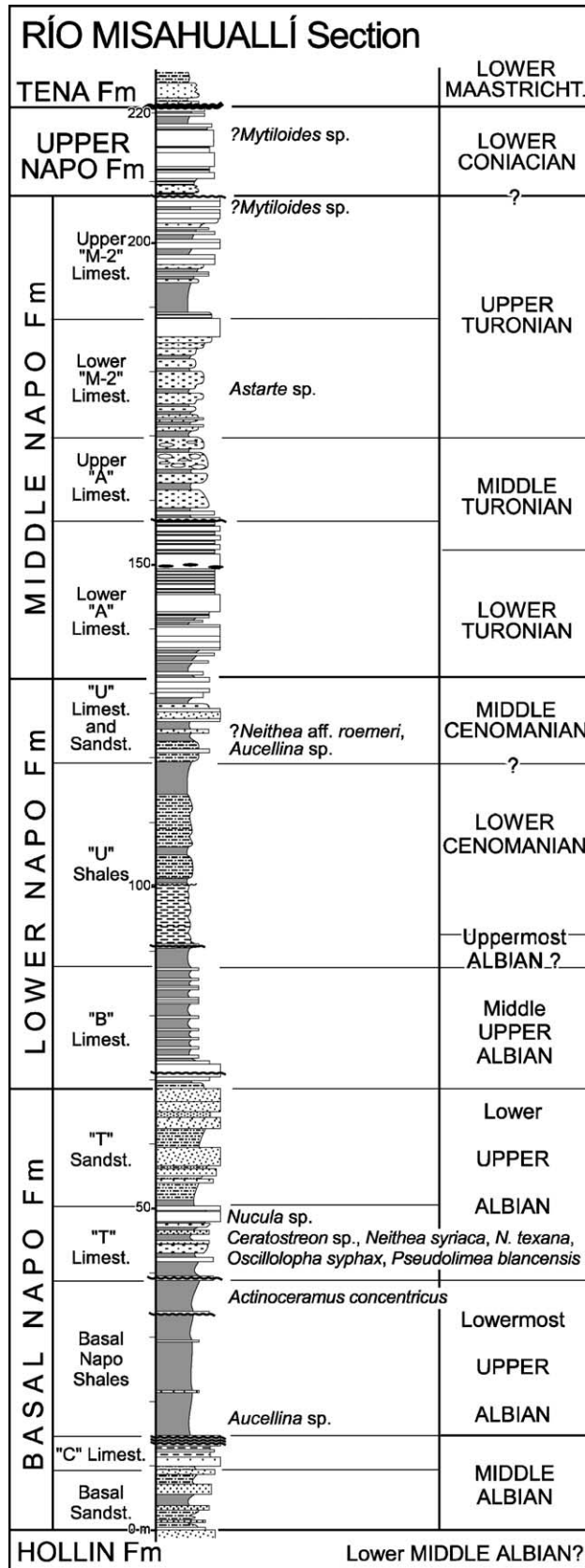


Fig. 3. Lithology of Río Misahuallí section (Ecuador) and distribution of the bivalves. Age indications after Jaillard et al. (1997).

middle-late Cenomanian in age and includes numerous oysters such as *Costagrya olisiponensis* (Sharpe, 1850), *Exogyra trigeri* (Coquand, 1869), *Ilymatogyra africana* (Lamarck, 1801), and *Rhynchostreon mermeti* (Coquand, 1862b), as well as pectinids such as *Chlamys stantoni* (Hill, 1893), *Neithea hispanica* (Orbigny, 1850), and *N. dutruegi* (Coquand, 1862a).

The transitional strata between the Romirón and Coñor Formations (samples R 33-41) contain the oyster *Ilymatogyra africana* (Lamarck, 1801) and the infaunal bivalve *Homomya* sp.

The Coñor Formation of early Turonian age yields a less abundant fauna with typical Turonian inoceramids (*Mytiloides* spp. and *Sergipia* sp.). It is dominated by an epifaunal assemblage, among which the following taxa are recognized from base to top (Fig. 4): *Pteria* sp., *Mytiloides mytiloides* (Mantell, 1822), *M. opalensis* (Boese, 1923), *Sergipia* sp., *Plicatula ferryi desjardinsi* Coquand, 1862a, an arcid, *Plagiostoma grenieri* (Coquand, 1862a), and *Pseudoptera* cf. *viana* Stephenson, 1952. Infaunal bivalves are represented by scarce *Aphrodina* sp. (two steinkern specimens). In addition, the lower part of the lower Turonian Coñor Formation yields the inoceramid *Sergipia* sp. (sample 214I of Petroperú).

The Cajamarca Formation is of middle Turonian age, but the bivalves collected are not age diagnostic.

The overlying Celendín Formation contains a fairly homogeneous fauna. At Pongo de Rentema, the lower part of the Celendín Formation seems to correspond to the upper part of the Turonian Cajamarca Formation of the type area at Cajamarca studied by Benavides-Cáceres (1956). Therefore, in Fig. 4, we refer informally to this unit as the Cajamarca-Celendín beds (Table 3). The Cajamarca-Celendín beds have been sampled on the right bank of Río Marañón, whereas the whole Celendín Formation has been studied on the left bank of the river.

The Cajamarca-Celendín beds are marked by the successive occurrence of *Plagiostoma grenieri* (Coquand, 1862a), *Plicatula ferryi desjardinsi* Coquand, 1862a, *Mytiloides 'labiatus'* (Schlotheim, 1813), *Hyotissa lombardi* (Freneix, 1957), *Gyrostrea* sp., *Astarte* sp., *Veniella* sp., *Gyrostrea* aff. *roachensis* (Fourtau, 1917), and unidentified inoceramids. Most taxa are epifaunal. The fauna is of Turonian-Coniacian age, as indicated by *Mytiloides 'labiatus'*, which is typical of the Turonian. However, preservation of this latter specimen is poor, which hampers reliable identification.

On the left bank of Río Marañón, the same unit yields, in ascending stratigraphic order: *Plagiostoma grenieri* (Coquand, 1862a) (specimen R141 was bitten by an ammonite or large reptile), *Nicaisolopha nicaisei* (Coquand, 1862a), *Pseudocucullaea lens* Solger, 1903 (loose sample), *Platyceramus* sp. (loose sample), *Plicatula ferryi desjardinsi* Coquand, 1862a, *Plicatula hirsuta* Coquand, 1862a, *Pseudopterna* sp. (not in situ), *Hyotissa lombardi* (Freneix,

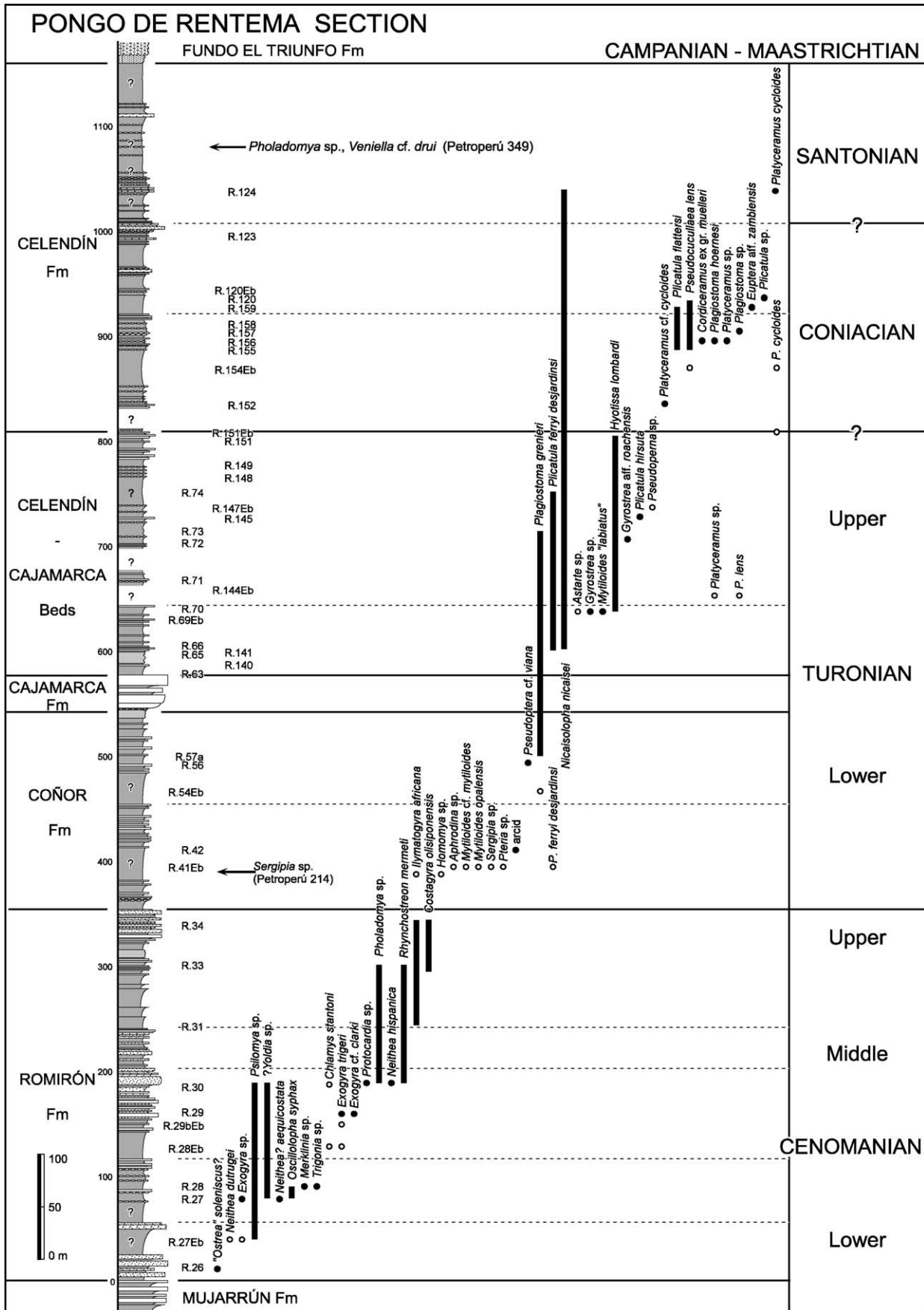


Fig. 4. Lithology of the Rentema section (northern Peru) and distribution of the bivalves. Age indications from Bengtson (in Jaillard et al., 2005). Filled circles and lines, in situ samples; open circles, loose samples.

Table 1
Romirón Formation, Cenomanian, at Pongo de Rentema; material collected in 1995

Taxa	Samples 95R27	95R28	95R29	95R30	95R31	95R33	95R34	epi/inf
<i>Yoldia</i> sp.	X			X				inf
<i>Exogyra</i> cf. <i>clarki</i> (Shattuck, 1903)			X					epi
<i>Exogyra trigeri</i> (Coquand, 1869)			X					epi
<i>Rhynchostreon mermeti</i> (Coquand, 1862a)					X	X		epi
<i>Costagyra olisiponensis</i> (Sharpe, 1850)						X		epi
<i>Ilymatogyra africana</i> (Lamarck, 1801)					X			epi
<i>Oscillolopha syphax</i> (Coquand, 1862a)							?	epi
<i>Chlamys?</i> <i>stantoni</i> (Hill, 1893)				X				epi
<i>Merklinia</i> sp.		X						epi
<i>Neithea?</i> <i>aequicostata</i> (Lamarck, 1819)	X							epi
<i>N. hispanica</i> (Orbigny, 1850)					X			epi
<i>Trigonia</i> sp.		X						inf
<i>Protocardia</i> sp.				X				inf
unidentified heterodonts	X	X	X					? inf
<i>Psilomya</i> sp./ <i>Pholadomya</i> sp.			X	X		X		inf

1957), and a crassatellid. These fauna provide no additional age indications for the Cajamarca-Celendín beds.

The Celendín Formation (Table 4) was sampled on the left bank of Río Marañón, and the following taxa were recognized in ascending stratigraphic order (Fig. 4): *Platyceramus* cf. *cycloides* (Wegner, 1905), *Pseudocucullaea lens* Solger, 1903, a cardiid, *Plicatula flattersi* Coquand, 1862a, *Cordiceramus* ex gr. *muelleri* (Petrascheck, 1906), *Platyceramus* sp., *Plagiostoma hoernesii* (Zittel, 1866), *Nicaiolophina nicaisei* (Coquand, 1862a), *Euptera* aff. *zambiensis* Darteville, 1957, *Plicatula* sp., unidentified inoceramids, and *Platyceramus cycloides* (Wegner, 1905) (sample R 124). Other than the heterodonts, all taxa are epifaunal. The occurrence of *Platyceramus cycloides* (R 124) indicates a Santonian age for the upper part of this unit. *Cordiceramus muelleri* is late Santonian-early Campanian in Europe and North America. The specimen found here (R 156) probably belongs to an earlier form of the same lineage.

In addition, the upper part of the Celendín Formation at Pongo de Rentema yields *Veniella* cf. *druis* (Munier Chalmas, 1881) and *Pholadomya* sp. (sample 349 I of Petroperu).

In the Cajamarca area of northern Peru, two sections were sampled: Baños del Inca and La Encañada. The Baños del Inca section is situated 6 km east of the town of Cajamarca (Fig. 1; see Benavides-Cáceres, 1956). Samples 95.I.1-95.I.9 from the lowermost Albian Inca Formation (Robert et al., 1998; Robert, 2002; Fig. 5) yield *Ceratos-*

treon cf. *flabellatum* (Goldfuss, 1833), an unidentified ostreid, and ?*Scabrotrigonia scabra* (Lamarck, 1819). From the Yumagual Formation of late middle-late Albian age, *Oscillolopha syphax* (Coquand, 1862a) was collected (sample 95-I-16). These taxa suggest a late Albian-Cenomanian age.

The La Encañada section is located approximately 20 km northeast of Cajamarca, along the Cajamarca-Celendín road (Fig. 1). The Cenomanian upper part of the Mujarrún Formation yields *Neithea hispanica* (Orbigny, 1850) and *Costagyra olisiponensis* (Sharpe, 1850) (sample 95-E-12).

The Cenomanian-Turonian strata of the upper part of the Romirón Formation yield *Mytiloides 'labiatus'* (Schlotheim, 1813) of early Turonian age.

2.2. Forearc basins

From the sections at La Tortuga and La Mesa (near Paita, Dept. Piura, Fig. 1), unusually diversified and well-preserved bivalve faunas were collected; their study confirms work by Olsson (1934, 1944) but also indicates a few taxa not described by Olsson. For geological data and the location of the samples, see Jaillard et al. (2006).

2.2.1. The La Mesa formation

Cropping out east of La Tortuga (Cerro La Mesa), this formation is the oldest unit (Fig. 6) of late Campanian-early

Table 2
Romirón Formation, Cenomanian, at Pongo de Rentema; material collected in 1996

Taxa	Samples 96R27	96R28	96R29	96R30	96R34	epi/inf
<i>Exogyra</i> sp.	X					epi
<i>Exogyra trigeri</i> (Coquand, 1869)		X	X	X		epi
<i>Costagyra olisiponensis</i> (Sharpe, 1850)					X	epi
<i>Oscillolopha syphax</i> (Coquand, 1862a)	X	X				epi
<i>Chlamys?</i> <i>stantoni</i> (Hill, 1893)		X		X		epi
<i>Neithea dutrugi</i> (Coquand, 1862a)	X					epi
<i>Psilomya</i> sp.	X					inf
<i>Pholadomya</i> sp.				X		inf

Table 3

Celendín Formation (lower part), ?Turonian, Coniacian, ?Santonian, at Pongo de Rentema, right bank of Río Marañón

Taxa	Samples	66	69	70	71	72	73	74	120	123	epi/inf
<i>Pseudocucullaea lens</i>									X		epi
<i>Mytiloides "labiatus"</i>				X							epi
unidentified inoceramids							X			X	epi
<i>Plagiostoma grenieri</i>	X		X			X	X				epi
<i>Hytissa lombardi</i>				X							epi
<i>Gyrostroma</i> aff. <i>roachensis</i>						X					epi
<i>Gyrostroma</i> sp.				X							epi
<i>Nicaiolopha nicaisei</i>									X		epi
<i>Plicatula ferryi desjardinsi</i>	X				X	X	X	X			epi
<i>Plicatula</i> sp.									X		epi
<i>Astarte</i> sp.				X							inf
<i>Veniella</i> sp.				X							inf

Maastrichtian age. The following taxa were collected (Table 5) in ascending stratigraphic order (Fig. 6): ?*Ambigostrea viliei* (Coquand, 1862a), *Breviarca peruviana* Olsson, 1944, *Plicatula harrisiana* Olsson, 1934, ?*Incardium mellisum* (Olsson, 1944), *Modiolus cervus* (Olsson, 1944), *Trigonarca meridionalis* (Olsson, 1934), *Scabrotrigonia gerthi* (Olsson, 1944), *Vepricardium* (*Perucardia*) *brueggeri* (Olsson, 1944), and *Inoceramus* aff. *sagensis* Owen, 1852. None of these taxa is age diagnostic, but *Inoceramus sagensis* generally is considered Campanian, and *Ambigostrea viliei* in northern Africa is thought to be Campanian-Maastrichtian.

2.2.2. The La Tortuga section

Between La Caleta and El Cenizo beaches (Fig. 6), this section contains many interesting bivalves of Maastrichtian age, presented next in ascending stratigraphic order:

- Middle unit of La Tortuga Formation: *Tellidora* (*Tellipiura*) *peruana* Olsson, 1944.
- Lowermost part of the El Cenizo Formation (Baculites sandstone of Olsson): *Trigonarca meridionalis* Olsson, 1934,

Trochoceramus cf. *nahorianensis* (Kociubynskij, 1968), *Ambigostrea sechura* (Olsson, 1944), *Rastellum* sp., *Scabrotrigonia gerthi* (Olsson, 1944), *Neobuchotrigonia hopkinsi* (Olsson, 1944), *Vepricardium* (*Perucardia*) *brueggeri* (Olsson, 1944), ?*Icanotia pacifica* (Olsson, 1944), *Veniella jamaicensis* (Trechmann, 1927), *Veniella* aff. *cordialis* (Stoliczka, 1871), and *Aphrodina pacifica* Olsson, 1944.

- Lower part of the El Cenizo Formation (upper part of the Baculites sandstone of Olsson): *Ambigostrea* cf. *villiei* (Coquand, 1862a) and *Veniella jamaicensis* (Trechmann, 1927).

In the La Tortuga section, the fauna represent an assemblage typical of a littoral, shallow, and warm environment. The only approximately age-diagnostic bivalve found in the La Tortuga section is *Trochoceramus* cf. *nahorianensis*, which indicates an early or early late Maastrichtian age (Dhondt, 1993).

2.2.3. Additional localities

Additional samples were collected from the Celica and Lancones forearc areas of southwesternmost Ecuador and

Table 4

Celendín Formation (upper part) ? Coniacian-Santonian, at Pongo de Rentema, left bank of Río Marañón

Taxa	Samples	140	141	144	145	147	148	149	151	152	154	155	156	157	159
<i>Pseudocucullaea lens</i>				X							X	X		X	
<i>Platyceramus cycloides</i>	X								X	X	X				
<i>Platyceramus</i> sp.				X									X		
<i>Cordiceramus</i> ex gr. <i>muelleri</i>													X		
<i>Pseudoperma</i> sp.						X									
<i>Euptera</i> aff. <i>zambiensis</i>															X
<i>Plagiostoma grenieri</i>		X	X												
<i>Plagiostoma hoernesii</i>													X		
<i>Plagiostoma</i> sp.														X	
<i>Hytissa lombardi</i>									X						
<i>Nicaiolopha nicaisei</i>	X		X	X			X	X		X	X			X	
<i>Plicatula ferryi desjardinsi</i>				X											
<i>Plicatula flattersi</i>												X			X
<i>Plicatula hirsuta</i>					X										
Crassatellid									X						
Cardiid											X				

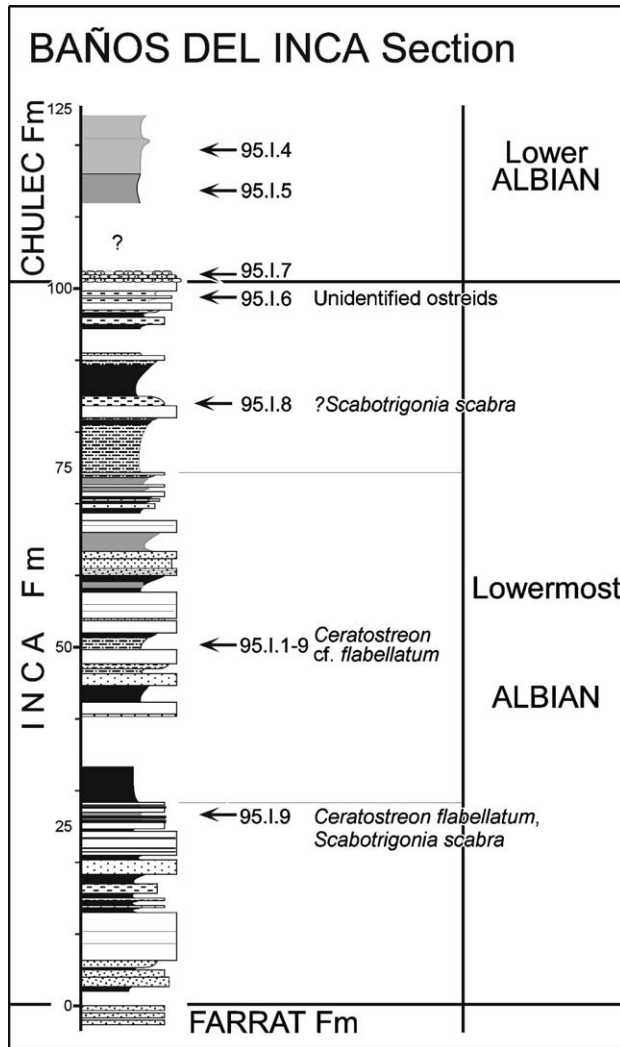


Fig. 5. Lithology of the Inca Formation (Baños del Inca section, west of Cajamarca, northern Peru) and distribution of the bivalve fauna. Age indications from Robert et al. (1998).

northernmost Peru (Fig. 1), which comprise two distinct successions. The Celica-Lancones Basin contains an Albian-Coniacian turbiditic succession unconformably overlain by Campanian-Maastrichtian shales, conglomerates, and subordinate turbidites. The latter represent the infilling of the Paita-Yunguilla forearc Basin (Jaillard et al., 1999) and correlate roughly with the La Mesa outcrops. The sections yield the following taxa, in approximate stratigraphic order:

For the Celica-Lancones Basin:

- Puyango Formation (Ecuador): *Cucullaea* sp., *Cerastostreon* sp. (Albian).
- Copa Sombrero Formation (Ecuador): ‘*Astarte*’ similis Muenster in Goldfuss, 1837.
- El Carmelo Formation (Ecuador): numerous *Mytiloides* sp., including *M. aff. transiens* (Seitz, 1935) and *M. cf. mytiloides* (Mantell, 1822), which indicate the lower Turonian in, for example, Brazil (Hessel, 1988).

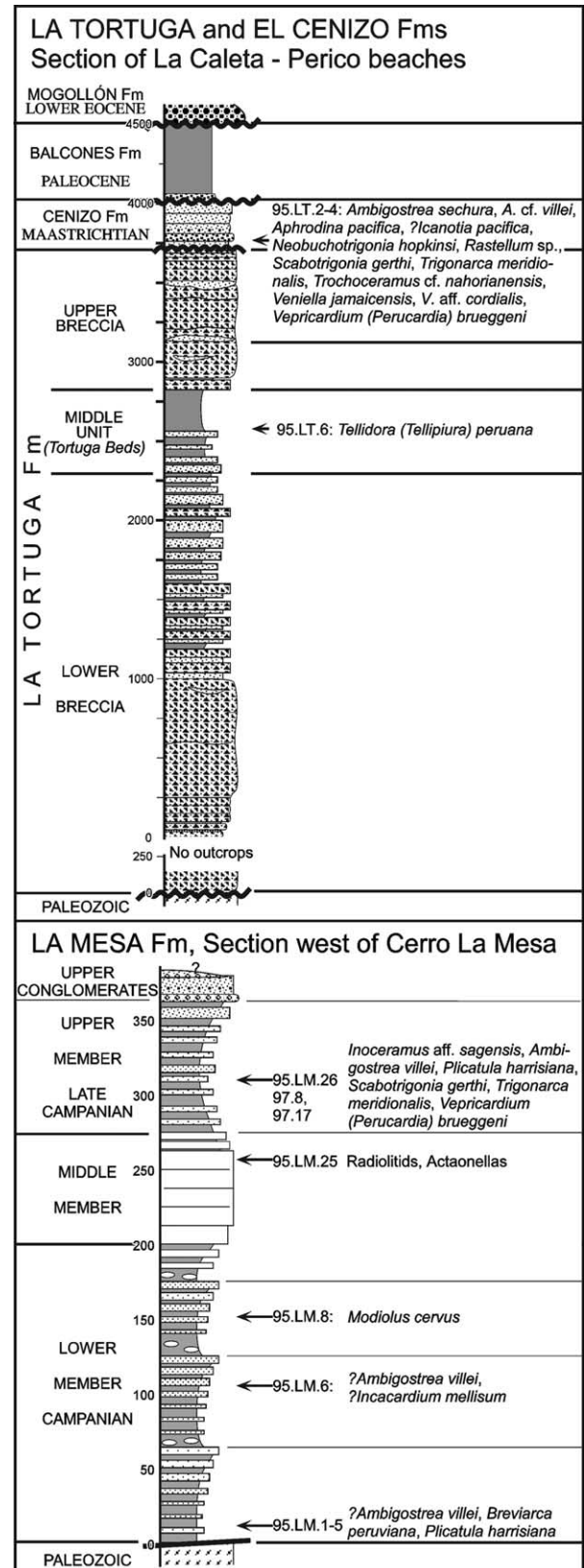


Fig. 6. Lithology of the La Mesa and La Tortuga sections (northern Peru) and distribution of the bivalves. Age indications from Bengtson (in Jaillard et al., 2005). Samples 95.LM.26, 97.8, and 97.17 come from the same beds but distinct localities.

Table 5

La Mesa Formation (Campanian-Lower Maastrichtian) and La Tortuga Formation (Maastrichtian), Paita, Peru (LM1, LM5, LM6, LM26, LT2, LT4, and LT6 collected in 1995; LM97.8 and LM97.17 collected in 1997)

Taxa	Samples LM1	LM5	LM6	LM8	LM26	97.8	97 17	LT2	LT4	LT6	epi/inf
<i>Breviarca peruviana</i>		X									epi
<i>Trigonarca meridionalis</i>					X			X			epi
<i>Modiolus cervus</i>				X							epi
<i>Inoceramus</i> aff. <i>sagensis</i>						X					epi
<i>Trochoceramus</i> cf. <i>nahorianensis</i>								X			epi
<i>Ambigostrea sechura</i>								X			epi
<i>Ambigostrea villei</i>	?	?	?		X		X		X		epi
<i>Rastellum</i> sp.								X			epi
<i>Plicatula harrisiana</i>		X					X				epi
<i>Scabotrigonia gerthi</i>					X		X	X			inf
<i>Neobuchotrigonia hopkinsi</i>								X			inf
<i>Vepricardium brueggeri</i>					X			X			inf
<i>Incardium mellisum</i>			X								inf
<i>Tellidora peruana</i>										X	inf
? <i>Icanotia pacifica</i>								X			inf
<i>Veniella jamaicensis</i>								X	X		inf
<i>Veniella</i> aff. <i>cordialis</i>								X			inf
<i>Aphrodina pacifica</i>					X			X			inf
<i>Corbula tuma</i>					X						inf

For the Paita-Yunguilla Basin:

- El Naranjo Formation (Ecuador): *Platyceramus* cf. *cycloides* (Wegner, 1905).
- From the Zapotillo Formation area (Ecuador), which probably is partly equivalent to the Naranjo Formation: *Platyceramus* aff. *cycloides* (sensu Seitz, 1970) and *Trochoceramus* aff. *monticuli* (Fugger and Kastner, 1885). The Zapotillo Formation extends southward into northwestern Peru, from which *Platyceramus* sp., *Inoceramus* aff. *goldfussianus* Orbigny, 1847 (late Campanian in southwestern France), and *Trochoceramus* sp. were collected. *T.* aff. *monticuli* could indicate a latest Campanian-Maastrichtian age.
- Cazaderos Formation (Cazaderos area, Ecuador): *Platyceramus* sp., *Platyceramus* aff. *cycloides* (sensu Seitz, 1970).

The age bracket for the Naranjo, Zapotillo, and Cazaderos Formations is late Campanian-early Maastrichtian.

3. Paleobiogeography

The paleobiogeographical affinities of the Ecuador/Peru fauna have changed through geological time. Whereas the middle Albian fauna (at Chinimbimi) contain cosmopolitan forms, the upper Albian at Chinimbimi and along Río Misahuallí in Ecuador and the Albian-Cenomanian strata at Pongo de Rentema in Peru (especially the Cenomanian Romirón Formation) contain typical Tethyan faunas and taxa known from North Africa, southwestern Europe, and Texas. A few taxa (*Costagyrta olisiponensis*, *Rhynchostreon*

mermeti, *Ilymatogyra africana*, *Neithea dutrugei*) have a wider Tethyan distribution and reach central Asia (see Dhondt, 1992a; Dhondt et al., 1999).

The lower Turonian faunas at Pongo de Rentema (Coñor Formation) are not very abundant but contain a few remarkable elements, namely, inoceramids such as *Mytiloides mytiloides*, *M. opalensis*, and *Sergipia* sp. The genus *Sergipia* has been described from the Lower Turonian of Brazil; is known from Nigeria, Mexico, and Japan (Hessel, 1988); and recently was mentioned near Cassis, southeastern France (Jolet et al., 1997). It is possible that *Monotis roemeri* (Karsten), described and figured by Gerhardt (1898b, p. 201, pl. 5, Fig. 20) from Colombia, also belongs to *Sergipia* sp.

The Coniacian-Santonian faunas (Celendín Formation) are comparable with those known from northwestern and western Africa (Freneix in Dartevelle and Freneix, 1957), but some oyster taxa have a somewhat younger stratigraphic age in Africa than in South America (Dhondt et al., 1999).

The Campanian-Maastrichtian shallow-marine bivalve faunas in Peru seem partially endemic, which could be an artifact caused by the excellent preservation of the fauna. The result is a fairly complete fauna that contains many identifiable heterodonts. This preservation is unusual among Cretaceous bivalve faunas, which often are restricted to taxa with calcitic shells (generally, oysters, pectinids, limids, and spondylids). Some of these Peruvian taxa might have had a wider distribution, but they have not been recognized in poorly preserved steinkern material known in most Maastrichtian strata. However, the increased endemism of the latest Cretaceous Peruvian shallow-marine fauna also could be a result of the beginning of tectonic deformations on the western margin of South America (the Late Cretaceous

‘Peruvian phase’ of Steinmann, 1929), which probably caused the isolation of marine provinces and basins.

Taxa with a wider distribution include:

- *Veniella jamaicensis* (Trechmann, 1927), also known from the Maastrichtian Providence shales of Jamaica;
- *Ambigostrea villei* (Coquand, 1862a), also known from the Maastrichtian of northern and northwestern Africa (Dhondt et al., 1999);
- possibly *Veniella* aff. *cordialis* (Stoliczka, 1871), closely related to a species from the uppermost Cretaceous of southern India; and
- the inoceramid *Trochoceras nahorianensis*, which is widely distributed in Tethyan and temperate regions (Dhondt, 1993).

4. Taxonomy

Those species represented by well-preserved or numerous specimens are discussed herein more detail; other species will be described separately.

We use the following abbreviations:

- MAFI: Magyar Allami Földtani Intézet, Budapest, Hungary;
 NHMW: Naturhistorisches Museum Wien, Vienna, Austria;
 PRI: Paleontological Research Institution, Ithaca, New York, USA;
 conv: convexity;
 epi: epifaunal;
 inf: infaunal;
 H: height;
 L: left;
 R: right;
 Rb: rib number;
 V: valve; and
 W: width.

Phylum Mollusca

Class Bivalvia

Subclass Pteriomorpha

Order Arcoida

Superfamily Arcoidea

Family Cucullaeidae Stewart, 1930

Genus *Pseudocucullaea* Solger, 1903

Type species *Pseudocucullaea lens* Solger, 1903 (O. D.)

Pseudocucullaea lens Solger, 1903

- * 1903 *Pseudocucullaea lens*-Solger, p. 77, Figs. 1 and 4.
 v. 1927 *Pseudocucullaea perijana* Harris and Hodson-F. and H. Hodson, Harris, p. 1, pl. 1, Fig. 4; pl. 2, Figs. 1, 3, and 4; pl. 3, Fig. 1.

? 1930 *Eusebia stantoni* sp. nov.-Maury, 1930, p. 209, pl. 6, Figs. 5 and 6; pl. 8, Figs. 2 and 3.

v. 1934 *Pseudocucullaea gregoryi*-Olsson, p. 22, pl. 3, Fig. 1.

v. 1944 *Pseudocucullaea gregoryi* Olsson-Olsson, p. 31, pl. 2, Figs. 1 and 2.

v. 1944 *Pseudocucullaea paitana* n.sp.-Olsson, p. 31, pl. 2, Figs. 3–5.

v. 1947 *Cucullaea reesideana* n.sp.-Richards in Knechtel et al., p. 43, pl. 2, Figs. 7–9.

v. 1947 *Cucullaea andersoni* n.sp.-Richards in Knechtel et al., p. 44, pl. 1, Figs. 14 and 15.

p.p.v. 1957 *Pseudocucullaea lens* Solger-Dartevelle and Freneix, p. 39, pl. 4, Fig. 9; pl. 5, Figs. 1–7; pl. 6, Figs. 1 and 2. (with synonymy).

? 1995 *Lopatinia (Pseudocucullaea) gregoryi* (Olsson, 1934)-Alleman, 1995, p. 67, Fig. 1.

Type: Probably in the Naturkunde-Museum Berlin, Germany. The original material came from Balangi on the Mungo River, Cameroon.

Peruvian material: Pongo de Rentema, Celendín Formation, Santonian (samples R120, R144, R154, R155, R157).

Preservation: All specimens are bivalved with slightly decorticated shells to steinkern preservation. Venezuelan specimen of Harris in Hodson et al. (1927) and the Peruvian specimens of Olsson (1934, 1944) are in PRI; Peruvian specimens of Richards in Knechtel et al. (1947) are in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Diagnosis: Suborbicular *Pseudocucullaea* species, with slightly prominent, generally inclined umbones and ornamentation limited to commarginal growth lines, which may be deep (grooves). The dimensions appear in Table 6.

Peruvian Pongo de Rentema specimens: The very special hinge typical of *Pseudocucullaea* is only partially visible in the Pongo de Rentema material.

Ornamentation: The valves seem smooth, except for the commarginal growth lines/grooves; on some rather eroded specimens, faint radial lines are visible near the posterior margin.

Discussion: *Pseudocucullaea lens*, as stated by Riedel (1933) and shown by Dartevelle and Freneix (1957), is a highly variable species. This variability is partly due to allometric growth, which also occurs in other cucullaeid taxa. The Peruvian *Pseudocucullaea* taxa in the literature are mainly different growth stages of the same species and often in different preservational stages. Thus, *P. gregoryi*

Table 6
Pseudocucullaea lens dimensions

Sample no	W (mm)	H (mm)	H/W	conv. (mm)
R120\1	57.2	52.2	0.913	19.5
R 120\2	(68.7)	64.2	0.934	25.8
R 144Eb	64.2	62.0	0.966	27.0
R 154	(69)	(64)	0.928	28.2
R 155	58.0	(55)	0.948	25.5

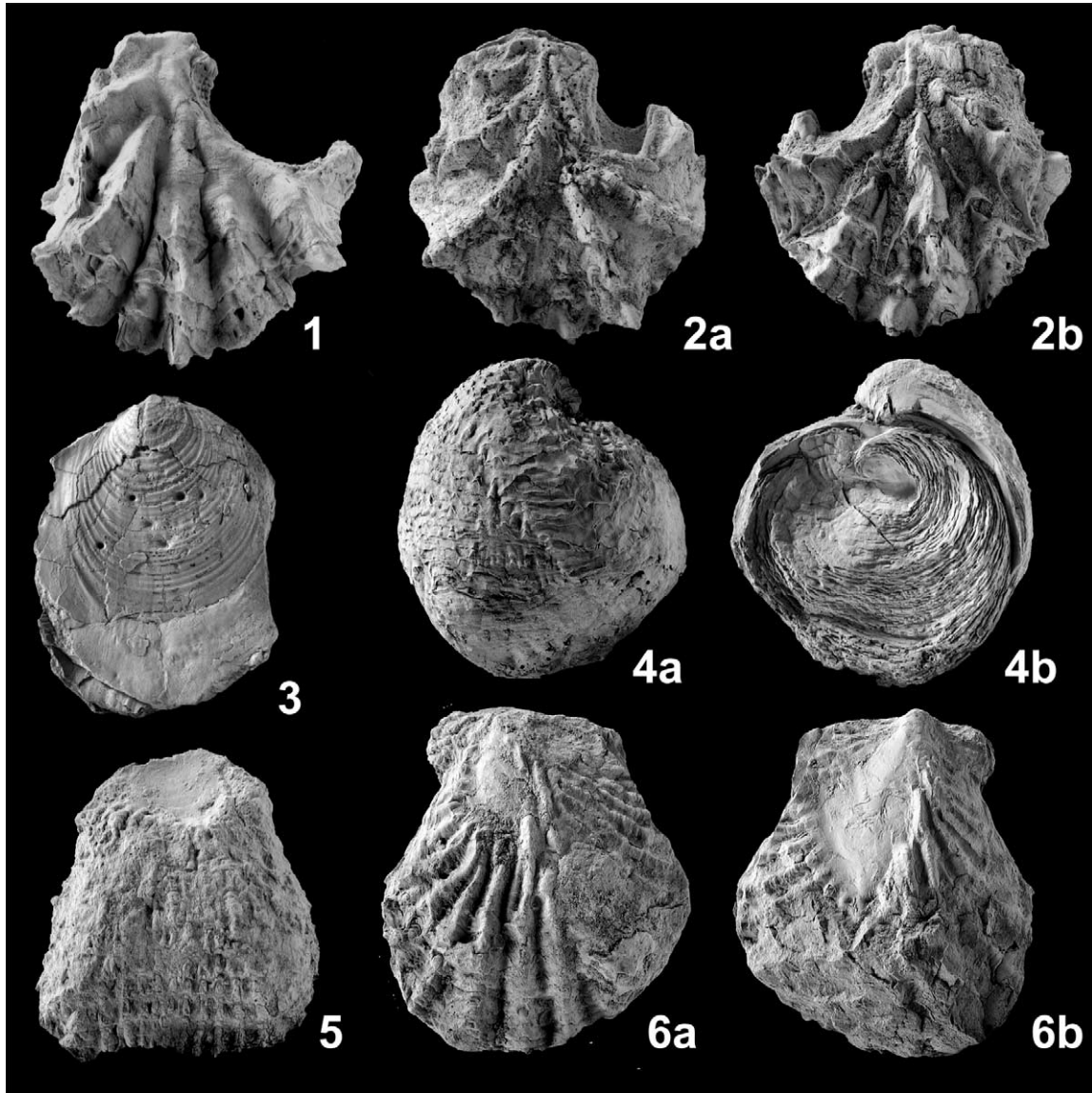


Plate 1. (Fig. 1) *Ambigostrea sechura* (Olsson, 1944): right valve from the El Cenizo Formation, Baculites zone of Olsson (1944), Maastrichtian at La Caleta to El Cenizo beaches, Paita, northern Peru; TC MI 10779 (ex Jaillard 95-LT-2), $\times 0.5$. Fig. 2 *Ambigostrea sechura* (Olsson, 1944): left valve from the El Cenizo Formation, Baculites zone of Olsson (1944), Maastrichtian at La Caleta to El Cenizo beaches, Paita, northern Peru; TC MI 10780 (ex Jaillard 95-LT-2), $\times 0.5$. Fig. 3 *Platyceramus cycloides* (Wegner, 1905): right valve from the upper part of the Celendín Formation, Santonian at Pongo de Rentema, northern Peru; TC MI 10781 (ex-Jaillard R 154), $\times 0.3$. Fig. 4 *Exogyra trigeri* (Coquand, 1869): left valve (4a) and right valve (4b) from the Romirón Formation, Upper Cenomanian at Pongo de Rentema, northern Peru; TC MI 10782 (ex-Jaillard 96 R 30a), $\times 0.25$. Fig. 5 *Ambigostrea villei* (Coquand, 1862a): right valve from the La Mesa Formation, Upper Campanian-Lower Maastrichtian west of Cerro La Mesa, Paita (northern Peru); TC MI 10783 (ex Jaillard 95 LM 26), $\times 0.5$. Fig. 6 *Oscillolopha syphax* (Coquand, 1862a): left valve (6a) and right valve (6b) from the Romirón Formation, Upper Cenomanian at Pongo de Rentema, northern Peru; TC MI 10784 (ex-Jaillard 96 R 28), $\times 0.5$.

Olsson, 1934 (from the Baculites zone at Monte Grande) is a fairly well-preserved, very large specimen of *P. lens*, whereas *P. paitana* Olsson, 1944 (from the *Sphenodiscus* beds at La Mesa) is known from smaller, somewhat more oblique specimens. Olsson did not explain how his taxa differ from the Venezuelan *P. perijana* F. Hodson, H. Hodson, and G. Harris, 1927. The type specimens of the three taxa demonstrate that they fall within the biological variation of one species. Darteville and Freneix (1957) already have mentioned the high similarity between the South American and West African taxa.

Distribution: Coniacian-Campanian of West Africa (from Cameroon to Senegal); Coniacian to Maastrichtian of Brazil, Venezuela, and Peru.

Order Pterioida

Family Inoceramidae Zittel, 1881

Genus *Platyceramus* Heinz, 1932

Type species *Inoceramus mantelli sensu* Barrois, 1879

Platyceramus ex gr. *cycloides* Wegner, 1905

Pl. 1, Fig. 3.

Compare with: 1961, *Inoceramus (Platyceramus) cycloides* Wegner-Seitz, pp. 55–74, pl. 1, Figs. 1–10; pl. 2, Figs. 1 and 7.

Type specimens: Seitz (1961) formally designated as a lectotype the specimen figured by Wegner (1905, p. 163, Fig. 6).

Peruvian material: Pongo de Rentema, Celendín Formation, Santonian (samples 124, 151, 152, 154); most specimens are bivalved, but none is complete or very well preserved.

Discussion: The specimens from Pongo de Rentema are incomplete, and the measurements given by Seitz (1961) cannot be made, nor can a subspecific assignment be given. In the least deformed specimens (R151, R152, R154), the commarginal plications ('Undulationen') seem circular and are accompanied by numerous costellae. The distance between the 'Undulationen' is comparable to that given by Seitz (1961) for *Inoceramus (Platyceramus) cycloides* cf. *vanuxemiformis* Nagao and Matsumoto (Seitz, 1961, p. 70, pl. 2, Figs. 1 and 7), except for that of the figured specimen R154 (Pl. 1, Fig. 3), in which the distance between the 'Undulationen' is only about half of that found on other specimens. R124 is preserved differently, and the 'Undulationen' are not circular but somewhat quadratic.

Distribution: *Platyceramus cycloides* is a typical Santonian species in Europe and apparently also in Peru.

Genus *Trochoceramus* Heinz, 1932

Type species *Trochoceramus helveticus* Heinz, 1932

Trochoceramus aff. *nahorianensis* (Kociubynskij, 1968)
Pl. 2, Fig. 7

Compare with: v. 1944, *Inoceramus*, sp. B-Olsson, p. 197, pl. 1, Fig. 1.

- *. 1968 *Inoceramus nahorianensis* Kociubynskij, sp. nov.-Kociubynskij in Pasternak et al., p. 145, pl. 28, Fig. 4.
- v. 1993 *Trochoceramus nahorianensis* (Kociubynskij)-Dhondt, p. 238, pl. 7, Fig. 4, text-Fig. 15 (with synonymy).

Type specimen: Lectotype NHMW 1965/640 (Naturhistorisches Museum Wien), designated by Dhondt (1993) from Maiersdorf, Hohe Wand, Niederösterreich, Austria and of probable Maastrichtian age.

Peruvian material: Specimen PRI 4810 of the Baculites zone from Paita (original Olsson, 1944, pl. 1, Fig. 1); from the new collection (E.J.), one large, incomplete right valve (steinkern preservation), sample 95 LT 2 Eb, from La Tortuga, Maastrichtian.

Description: Fairly large, flattened *Trochoceramus* species, with more or less subcircular, wide commarginal plications (rugae) and radial costellae.

Dimensions: Maximum H is approximately 120 mm.

Discussion: The figure by Olsson (1944) gives the impression that the specimen is more convex than it really is.

Distribution: The genus *Trochoceramus* is quite common in the Upper Campanian-Maastrichtian of the Tethys and the

southern margin of the White Chalk Sea (Dhondt, 1992b; Walaszczyk et al., 1996), but its species are difficult to define. In the Americas, the genus *Trochoceramus* has been recognized explicitly only by Etayo-Serna (1985) in western Colombia with a specimen that is very close to those from the Maastrichtian of Peru. Stephenson (1941) illustrates as *Inoceramus vanuxemi* (pl. 13, Fig. 3) a specimen from the Nacatoch Sands (Maastrichtian) at Corsicana (Navarro County, Texas, USA), which is also very close to our Peruvian specimen.

Order Limoida

Superfamily Limoidea

Family Limidae Rafinesque, 1815

Genus *Plagiostoma* J. Sowerby, 1814

Type species *Plagiostoma giganteum* J. Sowerby, 1814

Plagiostoma grenieri (Coquand, 1862a)

Pl. 2, Fig. 6

v* 1862a *Lima Grenieri* H. Coq.-Coquand, p. 214, pl. 14, Figs. 7 and 8.

. 1910 *Lima Grenieri* Coqu.-Brüggen, p. 749.

p.p.v. 1957 *Lima (Plagiostoma) grenieri* (Coquand)-Darteville and Freneix, p. 100, pl. 13, Figs. 1 and 2; pl. 14, Figs. 10 and 11; pl. 15, Fig. 1 (with synonymy).

Type specimen: In the Hungarian Geological Survey (MAFI) in Budapest. Originally described by Coquand from the 'Mornasien' (*sensu* Coquand, 1862b = Turonian) of Kenchela, Trik-Karetta, and Tébessa (Algeria).

Ecuadorian/Peruvian material: Pongo de Rentema, Coñor Formation, Turonian (samples 96 R 54 and 96 R 57 a); Cajamarca Formation, Turonian (samples 63 and 65); lower Celendín Formation, right bank of Río Marañón (samples 66, 69, 72, and 73); upper Celendín Formation, left bank of Río Marañón (samples 140, 141).

The specimens have preserved shells and are often bivalved but rarely complete. Auricles are incomplete on all specimens.

Diagnosis: Large, suborbicular *Plagiostoma* species with smooth, equilateral to very oblique, slightly convex to flattened valves, with a very wide umbonal angle.

Dimensions: The specimens from Pongo de Rentema vary in size as follows: W: 59.4–131 mm, average 92.6 mm ($n=15$); H: 60–133 mm, average 90.5 mm ($n=15$); and convexity: 18.6–38 mm, average 36.8 mm ($n=14$).

Description: Larger specimens seem to have relatively less convex shapes, but the sample is too small to prove this statistically. These dimensions agree with those indicated by Darteville and Freneix (1957).

Ornamentation: Restricted to commarginal growth lines, often more clearly visible near the pallial margin.

Discussion: Among the Upper Cretaceous *Plagiostoma* species, large and fairly smooth forms are not uncommon. Pervinrière (1912, p. 150) mentions the Cenomanian *Lima clypeiformis* d'Orbigny from Le Mans, and Darteville and Freneix (1957), among others, discuss the Cenomanian *Lima nuda* Guéranger and *Lima subclypeiformis* Futterer. Dhondt

and Dieni (1993) again describe the latter species, show it to be synonymous with *Plagiostoma hoernesii* (Zittel, 1866), and indicate the differences between *P. hoernesii*, ‘*Lima*’ *clypeiformis* on one side and *P. grenieri* on the other.

Distribution: Turonian of North Africa: Algeria, Tunisia, Libya; Turonian and Coniacian-Santonian of Central Africa: Gabon, Congo; Turonian-Coniacian (?Santonian) of Peru: Pongo de Rentema and Otusco (Brüggen, 1910).

Order Ostreoida
Suborder Ostreina
Superfamily Ostreioidea
Family Gryphaeidae Vialov, 1936
Subfamily Exogyrinae Vialov, 1936
Genus *Exogyra* Say, 1820
Type species *Exogyra costata* Say, 1820

Exogyra trigeri (Coquand, 1869)
Pl. 1, Fig. 4

- * 1869 *Ostrea Trigeri*-H. Coquand, p. 119, pl. 51, Figs. 1 and 2.
- . 1971 *Exogyra (Exogyra) trigeri* (Coquand)-Stenzel, 1971, p. N 1116, Fig. J89, 2a, 2b.
- v. 1977 *Exogyra trigeri* (Coquand)-Cobban, p. 19, pl. 9, Figs. 10–20; pl. 16, Figs. 16–19; pl. 17, Fig. 3, Figs. 5–10; pl. 18, Figs. 3–9; pl. 20, Figs. 98–0 (with synonymy).

The original material from Le Mans comes from the ‘*assises carentoniennes*’ of late Cenomanian age; the original specimens of Coquand are said to be from the Pictet collection and the collection of the Ecole des Mines.

Peruvian material: From Pongo de Rentema, Romirón Formation (Cenomanian): samples 95 R29 (5 specimens) and 96 R28, 29, and 30. Preservation occurs with shells but is not complete.

Diagnosis: Large to very large, elongated to suborbicular *Exogyra* species with mainly concentric ornamentation.

Dimensions: Four specimens from Pongo de Rentema could be measured, as detailed in Table 7.

Table 7
Exogyra trigeri dimensions

Sample no	W (mm)	H (mm) LV	H (mm) RV
96 R 28 Eb	83	85	72.5
96 R 29	73.5	78.5	(65)
96 R 30	128	(160)	(132)
96 R 30a	112	124.5	101.5

Discussion: *Exogyra trigeri* has been described only rarely from Europe but seems fairly common in the US Western Interior, according to Cobban (1977). The Western Interior specimens do not seem to reach the size of those from Le Mans or Peru.

Distribution: Upper but not uppermost Cenomanian of Le Mans (France), Upper Cenomanian-lowermost Turonian of the U.S. Western Interior, and Upper Cenomanian of Peru.

Family Ostreidae Rafinesque, 1815
Genus *Nicaiolopha* Vialov, 1936
Type species *Ostrea nicaisei* Coquand, 1862a

Nicaiolopha nicaisei (Coquand, 1862a)
Pl. 2, Figs. 3–5.

- v* 1862a *Ostrea Nicaisei* H. Coq.-Coquand, p. 232, pl. 22, Figs. 5–7.
- v. 1869 *Ostrea Nicaisei*, H. Coquand-Coquand, p. 34, pl. 6, Figs. 1–17.
- 1877 *Ostrea callacta*, Con.-Gabb, p. 296, pl. 42, Fig. 2, 2a.
- 1903 *Ostrea Nicaisei* H. Coquand-Paulcke, 1903, p. 261
- 1907 *Ostrea Nicaisei* Coqu.-Neumann, p. 101.
- . 1910 *Ostrea Nicaisei* Coqu.-Brüggen, p. 742, pl. 25, Fig. 1.
- v. 1947 *Ostrea nicaisei* H. Coquand-Richards in Knechtel et al., p. 52, pl. 5, Fig. 1, pl. 6, Figs. 1 and 2.
- v. 1966 *Ostrea nicaisei* Coquand-Willard, p. 128, 130, pl. 12, Fig. 3; pl. 13, Fig. 1.
- . 1990 *Nicaiolopha nicaisei* (Coquand)-Malchus, p. 174, pl. 19, Figs. 17 and 19; pl. 20, Figs. 1–8 (with synonymy).

Type-material: The specimens on which Coquand (1862a) based *Ostrea nicaisei* were collected in Campanian-age strata in Algeria. The type series is deposited in the Coquand Collection in MAFI, Budapest.

Malchus (1990) designates as lectotype the original in pl. 6, Fig. 16, of Coquand (1869), though Malchus incorrectly attributes it to pl. 11, which actually is the original of pl. 22, Fig. 5 in Coquand (1862a).

Peruvian material: Pongo de Rentema, Celendín Formation, ?Coniacian-Santonian (samples R 120, R 124, R 141, R 144, R 148, R 149, R 152, R 154, R 157, R 158).

Ostrea callacta: Hacienda of Macanga, Patá province (added by Gabb [1877]: “Conrad’s type from: ‘the Pampa del Sacramento, Eastern Peru’”). We have not been able to discover the whereabouts of this specimen.

Diagnosis of the Peruvian material: Equilateral, elongated to suborbicular, plicated, large *Nicaiolopha* taxon; valves are almost equivalve.

Dimensions: Among the Pongo de Rentema material, 10 specimens were sufficiently well preserved to be measured, as detailed in Table 8.

The material of Benavides-Cáceres (1956) in the American Museum of Natural History in New York (USA) shows a different pattern. Samples VB50, VB71, VB88, and VB89 contain much smaller specimens. In VB50, W varies between 46.0 and 80.5 mm, with an average of 57.5 mm ($n=10$); and H varies between 48.5 and 86.0 mm, with an average of 66.1 mm ($n=10$). The number of plicae varies between 6 and 11.

In VB88, W ranges 32.0–68.5 mm, with an average of 50.6 mm ($n=11$); H ranges 34.4–78.0 mm, with an average of 56.8 mm ($n=11$); and the number of plicae varies between 6 and 11.

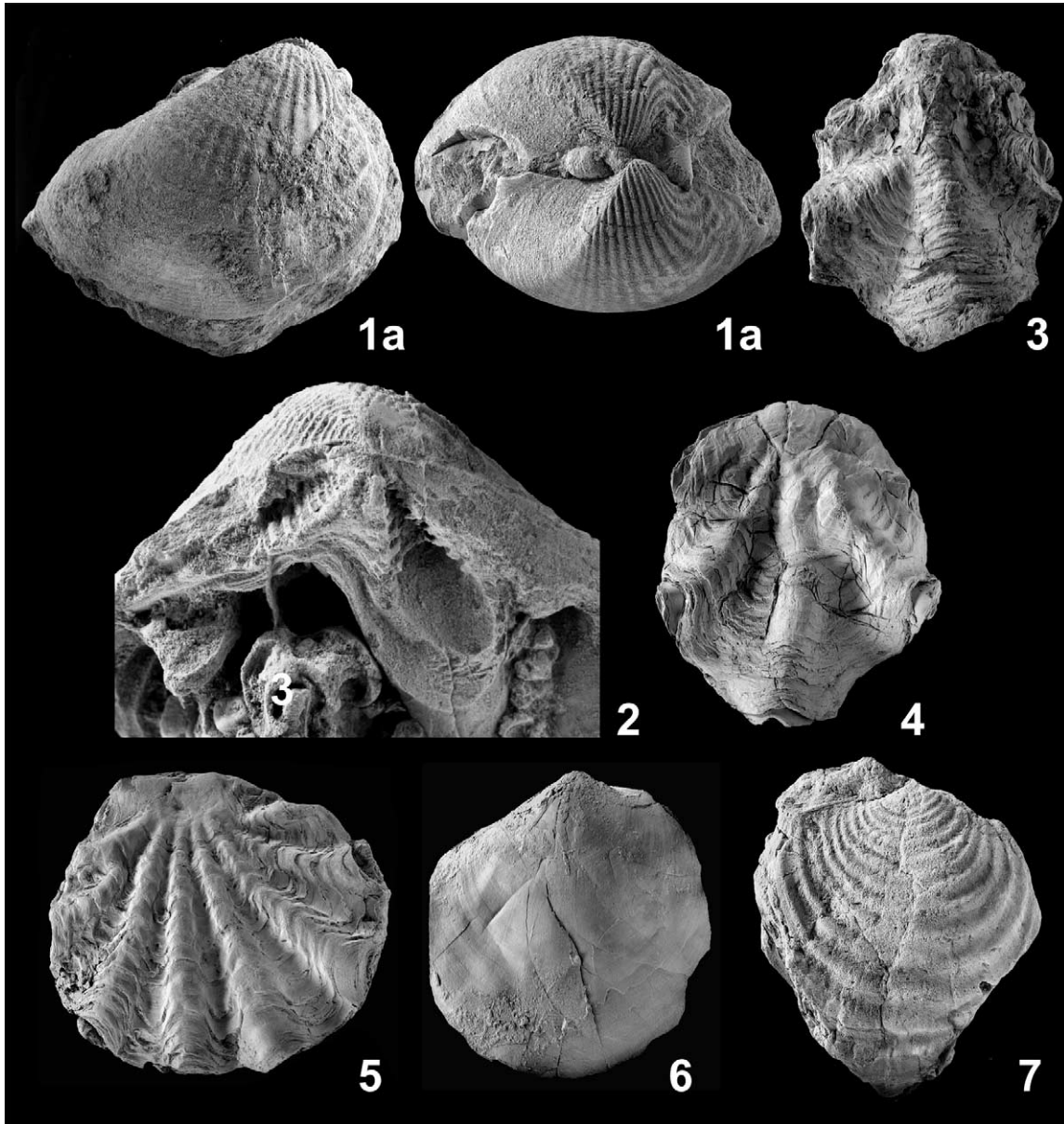


Plate 2. (Fig. 1) *Neobuchotrigonia hopkinsi* (Olsson, 1944): left valve (1a) and bivalved specimen seen from the umbo (1b) from the El Cenizo Formation, Baculites zone of Olsson (1944), Maastrichtian at La Caleta to El Cenizo beaches, Paíta, northern Peru; TC MI 10785 (ex Jaillard 95-LT-2), $\times 0.4$. Fig. 2. *Neobuchotrigonia hopkinsi* (Olsson, 1944): hinge of left valve from the El Cenizo Formation, Baculites zone of Olsson (1944), Maastrichtian at La Caleta to El Cenizo beaches, Paíta, northern Peru; TC MI 10786 (ex Jaillard 95-LT-2 Eb), $\times 1$. Fig. 3 *Nicaisolopha nicaisei* (Coquand, 1862a): Celendín Formation, ?Coniacian at Pongo de Rentema, left bank of Río Marañón, N. Peru; TC MI 10787 (ex Jaillard R 149), $\times 0.5$. Fig. 4 *Nicaisolopha nicaisei* (Coquand, 1862a): Celendín Formation, ?Coniacian-Santonian at Pongo de Rentema, left bank of Río Marañón, N. Peru; TC MI 10788 (ex Jaillard R 152), $\times 0.25$. Fig. 5 *Nicaisolopha nicaisei* (Coquand, 1862a): Celendín Formation, ?Coniacian-Santonian at Pongo de Rentema, left bank of Río Marañón, N. Peru; TC MI 10789 (ex Jaillard R 144 Eb), $\times 0.5$. Fig. 6 *Plagiostoma grenieri* (Coquand, 1862a): Coñor Formation, Turonian at Pongo de Rentema, N. Peru; TC MI 10790 (ex Jaillard 96 R 57 A), $\times 0.25$. Fig. 7 *Trochoceramus nahorianensis* (Kociubynskij, 1968): right valve from El Cenizo Formation, Baculites zone of Olsson (1944), Maastrichtian at La Caleta to El Cenizo beaches, Paíta, northern Peru; TC MI 10791 (ex Jaillard 95-LT-2), $\times 0.5$.

Samples VB71 and 89 are small but contain specimens of similar size.

Samples VB90, VB212, VB213, and VB214 each contain a few, large specimens, comparable to those from Pongo de Rentema. The number of plicae of these specimens varies from 4 to 7.

Discussion: The shape of *N. nicaisei* varies widely and probably depends on the size of the attachment area. When

the attachment scar is small and round, it results in an elongated valve shape, whereas when it is elongated and oval (longest dimension parallel to the width), it seems to result in a suborbicular valve shape.

The Peruvian *N. nicaisei* specimens from Pongo de Rentema are on average larger and possibly more plicate than those from North Africa (Malchus [1990] indicated 79 mm as H max for *N. nicaisei* specimens). The specimens

Table 8
Nicaisolopha nicaisei dimensions

Sample no	W (mm)	H (mm)	H/W	plicae
R124	63	76	1.16	4
R144	95	85	0.89	8
R148	73	82	1.12	9
R149/1	97.5	103	1.06	4
R149/2	107	(107)	(1.00)	8
R152\1	108.5	128	1.18	5
R152\2	88	95	1.08	6
R154	104	106	1.02	6
R157	84	87	1.04	6
R158	87.5	88.5	1.01	5

W varies 63–108.5 mm, average 90.75 mm ($n=10$); H varies 76–128 mm, average 95.75 mm ($n=10$); and the number of plicae varies between 3 and 9.

collected from different Peruvian localities by Benavides-Cáceres (1956) vary in size. Growth characteristics are thus almost certainly locally induced by the environment (ecotypes).

Distribution: In northern Peru, *N. nicaisei* is restricted to the Celendín Formation of the Coniacian-Santonian (Benavides-Cáceres, 1956; Jaillard et al., 2006). In northern Africa and the Near East, it is found in Campanian-Maastrichtian strata (Malchus, 1990; Dhondt et al., 1999).

Previously, Neumann (1907) mentioned *O. nicaisei* from La Quinua at the ‘Santonian-Campanian’ transition; Brügger (1910) reported it from Otusco and La Quinua near Celendín in Peru in rocks of Santonian age.

Genus *Ambigostrea* Malchus, 1990

Type species *Ambigostrea pseudovillei* Malchus, 1990

?*Ambigostrea sechura* (Olsson, 1944)

Pl. 1, Figs. 1 and 2

v.* 1944 *Ostrea (Lopha) sechura*, n. sp.-Olsson, p. 199, pl. 1, Figs. 7 and 8.

1995 ‘*Ostrea*’ *sechura* Olsson, 1944-Alleman, 1995, p. 68, Figs. 5 and 6.

Holotype: Specimen PRI 4804 from the Baculites zone, at Paita, northern Peru.

New Peruvian material: 95-LT 2 of two bivalved specimens, one right valve, two left valves, Maastrichtian at La Tortuga.

Diagnosis: Medium-sized, sickle-shaped oyster with plicae.

Dimensions: H of largest specimen: 122 mm.

Discussion: The Peruvian specimens of ?*Ambigostrea sechura* are similar but not identical to the Maastrichtian North African *A. tripolitana* (Krumbeck) as described and illustrated by Malchus (1990, p. 182, pl. 23, Figs. 4–9; pl. 24, Figs. 1–4). We have not studied the microstructure of ?*A. sechura* and therefore are not absolutely certain that the taxon belongs to *Ambigostrea*.

Distribution: ?*Ambigostrea sechura* so far has been recorded only from the Maastrichtian of northern Peru.

Ambigostrea villei (Coquand, 1862a)

Pl. 1, Fig. 5

v* 1862a *Ostrea Villei* H. Coq.-Coquand, p. 231, pl. 21, Figs. 10–12.

v. 1869 *Ostrea Villei*, H. Coquand-Coquand, p. 27, pl. 4, Figs. 1–8; pl. 5, Figs. 1–4.

. 1990 *Ambigostrea villei* (Coq.)-Malchus, p. 180, pl. 21, Fig. 26, 27; pl. 22, Figs. 1–7; pl. 23, Figs. 1–3 (with synonymy).

Lectotype: Specimen figured by Coquand (1869, pl. 5, Figs. 1 and 2) from Djelail (Algeria) (Malchus, 1990). It is the original of Coquand (1862a, pl. 22, Figs. 1 and 2).

Age: ‘Dordonien’ (=Maastrichtian).

Peruvian material: LT4 from El Cenizo Formation, La Caleta to El Cenizo beaches, Baculites sandstone, one bivalved specimen. West of Cerro La Mesa: 95 LM1, 95 LM5, 95 LM6, and 95 LM26 with 5 valves, and LM97.17 and LT4. The specimens are fairly well preserved but somewhat incomplete.

Diagnosis: Medium-sized, thick-shelled, trapezoidal to triangular or even elongate oyster species with numerous riblets on both valves.

Dimensions: As shown in Table 9.

Table 9
Ambigostrea villei dimensions

Sample no	L (mm)	W (mm)	Rib	V
95 LM26/1	87.0	82.5	26	L
95 LM26/2	65.0	69.0	22	L
95 LM26/3	63.5	66.0	35	L
95 LM26/4	43.5	43.5	20	R
97 LM17/1	88.5	92.0	31	R
97 LM17/2	73.6	66.0	32	R

Description: The shape is more trapezoidal than triangular. The attachment area seems larger than in the North African specimens figured by Malchus (1990). The shape of the attachment area might induce the shell shape.

Discussion: Malchus (1990) gives a detailed description and discussion of *Ambigostrea villei*. His material was better preserved than the specimens from Peru. Just as with *N. nicaisei* (Coquand), specimens of *A. villei* from Peru seem to reach somewhat larger sizes than in northern Africa.

Distribution: Campanian-Maastrichtian of Peru; Maastrichtian of Algeria; Campanian of Egypt and the Near East (Malchus, 1990; Dhondt et al., 1999).

Subclass Palaeoheterodonta

Order Trigonioida

Superfamily Trigonioidea

Family Trigonidae Lamarck, 1819

Genus *Pterotrigonia* Van Hoepen, 1929

Type species *Pterotrigonia cristata* Van Hoepen, 1929
 Subgenus *Scabrotrigonia* Dietrich, 1933
 Type species *Trigonia scabra* Lamarck, 1819

Pterotrigonia (Scabrotrigonia) gerthi (Olsson, 1944)

- v. 1928 *Trigonia crenulata* Lam. var. Peruana-Gerth, p. 234. (non *Trigonia peruana* Paulcke, 1903).
 v.* 1944 *Trigonia (Scabrotrigonia) gerthi* n. sp.-Olsson, p. 200, pl. 3, Figs. 4, 5, 10.
 . 1995 *Pterotrigonia (Scabrotrigonia) gerthi* (Olsson, 1944)-Alleman, 1995, p. 69, Fig. 7.

Holotype: Specimen PRI 4812, paratype PRI 4813 from the Baculites zone at Paita, northern Peru (Maastrichtian).

Number of specimens: Right valve of 95 LT2EB; left and right valves of 95 LT2; preservation is good, but none of the specimens is complete. In the collections of ‘Naturalis’ (Leiden), six incomplete, relatively poorly preserved specimens from the northern end of Playa Tortugas, Pta. Perico (472. P.18., No. 147) from the material of Gerth (1928).

Nomenclature: According to the International Commission of Zoological Nomenclature (1999, Article 72.4), the type series of this taxon contains the Gerth (1928) and Olsson (1944) specimens. In the choice of holotype, we prefer to follow the opinion of Olsson (1944), in agreement with recommendation 73B (preference for specimens studied by author). This choice is also preferable because the specimens chosen by Olsson (1944) are better preserved.

Diagnosis: A typical *Scabrotrigonia* species with numerous, narrow, closely spaced, spinose ribs on the flank.

Dimensions: As shown in Table 10.

Table 10

Pterotrigonia (Scabrotrigonia) gerthi dimensions

Sample no	H (mm)	W (mm)	R	S
95 LT2/1	57.0	(64.0)	(28)	RV
95 LT2/2	45.0	(54.0)	(30)	RV
95 LT2/3	54.6	(59)	(28)	LV
95 LT2/4	33.0	45.0	25	LV
95 LT2/5	46.8	51.3	25	LV

Description: Rib number is relatively high (R up to 28), and the spines on the ribs are small, especially toward the umbo.

Discussion: Olsson (1944) gives a detailed description of the material from La Tortuga, which seems to agree with our specimens except for the number of ribs. We counted more ribs but include the small ribs near the umbo, which Olsson may have omitted. How much the material of Gerth (1928) agrees with the species described by Olsson, we cannot judge. If both prove identical, contrary to Olsson’s statement, the type *Trigonia gerthi* should be the specimen described by Gerth (1928) as *Trigonia crenulata peruana*.

Distribution: Maastrichtian of northern Peru.

Genus *Neobuchotrigonia* Pérez and Reyes, 1996

Type species *Buchotrigonia (Buchotrigonia) topocalmensis* Pérez and Reyes, 1980

Neobuchotrigonia hopkinsi (Olsson, 1944)
 Pl. 2, Figs. 1a,b, and 2

- ? 1928 *Trigonia* spec. nov.-Gerth, p. 239.
 v.* 1944 *Trigonia hopkinsi*, n. sp.-Olsson, p. 201, pl. 3, Fig. 1.
 . 1996 *Neobuchotrigonia hopkinsi* (Olsson)-Pérez and Reyes, p. 205, pl. 2, Figs. 4–7

Holotype: Specimen PRI 4819 from the Baculites zone near Paita, Peru.

New Peruvian material: One bivalved specimen and one incomplete left valve from the El Cenizo Formation.

Dimensions: PRI 4819: H: 74 mm; W: 84 mm; and 95 LT2 specimen: H: 82.5 mm; W: 103 mm.

Description: The marginal carina is sharply delimited in the youngest stages and then broadens. The area is wide and smooth except in the very young stages, in which transverse costellae are present and curve toward the hinge margin.

The flank has centrally located, shallow costae restricted to the young stages of the shell, and some of these ribs curve toward the anterior margin. In older stages, commarginal elevations occur, which are more strongly developed near the anterior margin.

Discussion: At first glance, this taxon does not look like a trigoniid (Olsson, 1944, pl. 3, Fig. 1). However, the presence of trigoniid teeth (Pl. 2, Fig. 2) leaves no doubt as to its family relationship. Similar buchotrigoniid taxa have been described from Cretaceous Tethyan strata in South America, Spain, the Near East, and New Zealand. Whether the taxa described by Pérez and Reyes (1980, 1996) really represent different species, we cannot judge without studying the material on which these taxa are based.

Distribution: Maastrichtian of Peru.

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