BIOGEOGRAPHIC RELATIONSHIPS OF THE GALAPAGOS TERRESTRIAL BIOTA: PARSIMONY ANALYSES OF ENDEMICITY BASED ON REPTILES,

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Late Pliocene fossils of Ecuador and their role in the development of the Panamic bioprovince after the rising of Central American Isthmus

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Abstract: Studies carried on in the last several years allow us to date the Canoa Formation as Late Pliocene. The rich paleontological record (foraminifers, mollusks, and otoliths) allowed us to outline a first articulate picture of the biogeographic relationships in the tropical eastern Pacific during the Plio-Pleistocene. The mollusk fauna shows a Panamic connotation, as the majority (88.7%) of the extant species are present between the Gulf of California and the coasts of Ecuador or northern Peru. Benthic foraminifers assemblages indicate a temperate character with a certain affinity with the Mexican Pacific microfauna. More than 7000 otoliths have been found in the Canoa Formation that are attributed to 105 taxa of 46 fish families. Only 65% of the fossil association is living today along the Ecuadorian coasts, while the association as a whole shows closer relationships with the extant Californian fish community (about 80%). In particular, a conspicuous group of fishes (15 taxa) today spread in the boreal East Pacific (from Oregonian to Californian Province or limited only to the Californian area) has been recorded in the Canoa Formation. We named these taxa “Californian guests.” After the rising of the Central American Isthmus, climatic variations may have caused changes in the pattern of surface currents and (or) activated coastal upwelling cells, supporting the diffusion of a part of the boreal biota toward more southern areas. At the present state of knowledge, both proximal causes seem to be compatible with the data presented.

Résumé : Des études effectuées au cours des dernières années nous permettent de déterminer que la Formation de Canoa date du Pliocène tardif. Les nombreuses données paléontologiques (foraminifères, mollusques et otolites) nous permettent d’esquisser la première image claire des relations biogéographiques dans le Pacifique Est tropical au cours du Plio-Pléistocène. La faune des mollusques montre un lien panaméen puisque la plus grande partie (88,7 %) des espèces existantes sont présentes entre le golfe de Californie et les côtes de l’Équateur ou du nord du Pérou. Les assemblages de foraminifères benthiques indiquent un caractère tempéré et une certaine affinité avec la microfaune du Pacifique mexicain. Plus de 7000 otolites ont été trouvés dans la Formation de Canoa et ils ont été attribués à 105 taxons de 46 familles de poissons. Seulement 65 % de l’association fossilifère vit présentement le long des côtes de l’Équateur alors que l’association pris dans son ensemble montre des relations plus étroites avec la communauté existante de poissons californiens (environ 80 %). Plus particulièrement, un groupe de poissons bien en évidence (15 taxons), et de nos jours réparti dans le Pacifique Est boréal (de la province de la Californie à celle de l’Oregon ou limité seulement à la région de la Californie), a été trouvé dans la Formation de Canoa. Nous avons nommé ces taxons des « invités californiens ». Après le soulèvement de l’isthme centraméricain, des variations climatiques peuvent avoir causé des changements dans les patrons de courants de surface et (ou) activé des cellules de remontée côtières, supportant la diffusion d’une partie du biote boréale vers des régions plus au sud. Selon l’état actuel des connaissances, les deux causes proximales semblent être compatibles avec les données présentées.

[Traduit par la Rédaction]

Introduction

During the Neogene, the evolution of the central East Pacific area was marked by several climatic and tectonic events, which influenced circulation mechanisms and determined important biogeographic changes.

The present circulation system consists of three main surface currents and one deep current (Fig. 1). The North Equatorial

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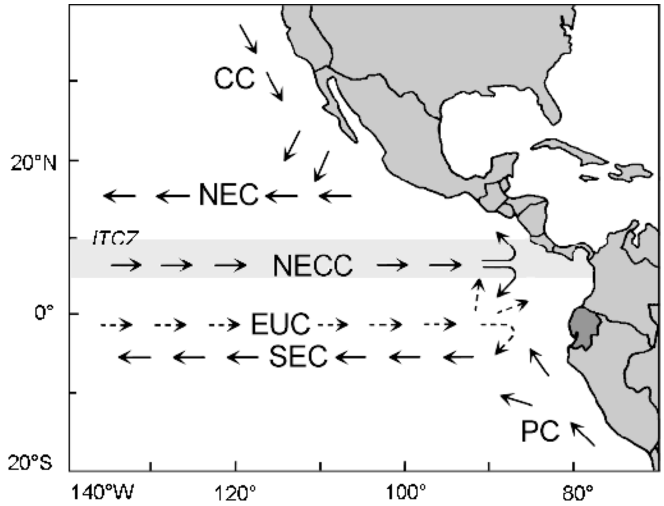
Fig. 1. Generalized circulation system of the equatorial Pacific Ocean showing the latitudinal position of the Intertropical Convergence Zone (ITCZ) and the major surface and subsurface currents: California Current (CC), North Equatorial Current (NEC), North Equatorial Countercurrent (NECC), Equatorial Undercurrent (EUC), South Equatorial Current (SEC), and Peru Current (PC).



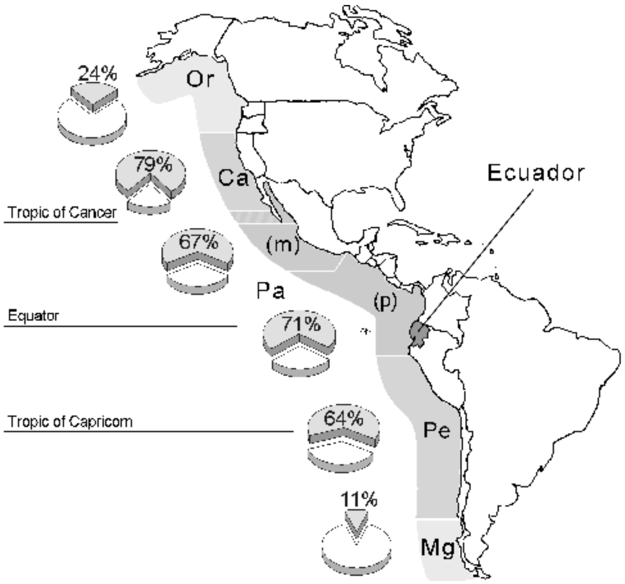
(NEC) and South Equatorial (SEC) currents flow westward and are limited between 8°N–29°N and 10°S–3°N, respectively. The North Equatorial Countercurrent (NECC) is confined between NEC and SEC and flows eastward, while a geostrophic flow, the Equatorial Undercurrent (EUC), goes eastward confined by Coriolis strength between 2°S and 2°N (Chaisson 1995).

This system is strongly influenced by both atmospheric circulation and the position of the Intertropical Convergence Zone (ITCZ), mostly controlled by the balance of the strengths of trade winds; since the southern trade wind is more intense than its northern counterpart, the ITCZ is always located North of the equator (Hovan 1995). Fluctuations in the intensity of trade-wind systems, following the seasonal cycle, move the ITCZ position and change the general arrangement of the equatorial currents. From May to December, in correspondence with the major intensity of the South trade wind, the ITCZ moves to its northernmost limit (about 10°N) and SEC and NEC are strongest. From February to April, related to the strongest North trade wind and a weaker South trade wind, the ITCZ moves to its southernmost position, NECC does not develop, the SEC is weakened by the decrease in intensity of South trade wind, and the Californian Current (CC) increases its strength and penetrates the Panamic basin to 3°N (Pisias et al. 1995).

These patterns of distribution of the eastern Equatorial Pacific surface currents began to develop after the closure of the Indonesian seaway during Middle–Early Miocene (Chaisson 1995) and completed its arrangement with the emergence of the Central American Isthmus (CAI; Pisias et al. 1995; Coates and Obando 1996; Collins 1996; Cannariato and Ravelo 1997; Haug and Tiedemann 1998).

The formation of the CAI was a very complex process which lasted for more than 15 Ma (Coates and Obando 1996), even though it is possible to pinpoint the total end of communications since 3.7–3 Ma on the basis of faunal, isotopic, and sedimentological data (Duque-Caro 1990; Coates and Obando 1996; Ibaraki 1997). Besides ecological and evolutionary effects, the emergence of the isthmus caused substantial variations of regional surface water temperature, changes in oceanic circulation (Keigwin 1978, 1982*b*), modifications of the sedimentation rates, variations of climatic marine conditions in both Atlantic and Pacific oceans, and an increase of salinity in the Caribbean Sea and western Atlantic (Coates and Obando 1996; Ibaraki 1997).

Fig. 2. Biogeographic provinces of the eastern Pacific: Oregonian (Or), Californian (Ca), Panamic (Pa), Peruvian (Pe), Magellanic (Mg). We recognize two different units within the Panamic province: Mexican (m) and Panamic sensu stricto (p). Percentages of the taxa shared by each province and the fossil record from the Canoa Formation are reported.



According to Coates and Obando (1996) and Collins (1996), the emergence of CAI was not a single event and had major consequences on ocean circulation and global climatic patterns. Its biological effects on marine organisms are likely to have spread beginning from the Late Miocene (about 8 Ma) being characterized by different biological responses of the various taxonomic groups in relation to their ecological features. The main orientation (N–S) of the present American coastline conditioned the development of the bioprovinces, whose distribution follows a precise latitudinal gradient (Fig. 2). In particular the tropical waters, constrained to the North by the CC and to the South by the Peruvian Current (PC) are characterized by a limited extension if compared to the other provinces of the tropical area (Caribbean, Indo-West Pacific, and eastern Atlantic) and show a marked asymmetry with respect to the equator.

The biogeographic significance of this area has already been recognized by Forbes (1856), who described a "Panamic province" located between Magdalena Bay and Peru. Later, other authors (see Briggs 1970) contributed to the description of the biological characterization of the Panamic province on the basis of the distribution of several taxonomic groups (mollusks, nemerteans, balanomorphs, fishes). However the northern and southern borders of that province are still objects of debate. In fact, the biogeographic and ecological role played by the Gulf of California is controversial and this area is considered to be either a sub-bioprovince or a distinct province (Briggs 1970) or, according to most of the biogeographers, a northward extension of the Panamic province (Zullo 1991; Walker 1960; Allen and Robertson 1994) with faunal peculiarities.

An important contribution to the evolution of the southern part of the Panamic province has been provided by the Plio-Pleistocene sedimentary successions of Ecuador (especially the Onzole and Canoa formations), known in the literature since the studies by Olsson (1942, 1964) and Sheppard (1930).

Evidence for the presence of taxa with Californian affinity in the Pliocene sediments of Ecuador was provided by Vokes (1988), Landini et al. (1991), and Bianucci et al. (1993) for macrofaunas (mollusks and fishes) and Hasson and Fisher (1986) and Ibaraki (1997) for microfaunas. These faunas allow us to outline a biogeographic framework related to the rising of CAI that is more complex and less influenced by the latitudinal gradient than the present one.

Our studies on the Canoa Formation fossil contents, carried out on foraminifers, mollusks, and otoliths assemblages, together with sedimentologic analyses, allowed us to reconstruct the environmental and geologic evolution of that area during the Late Pliocene (Bianucci et al. 1993, 1997; Cantalamessa et al. 2000*a*, 2000*b*). In the present paper, the fossil record is taken into account to define the biogeographic relationships of the Ecuadorian area within the other Pacific provinces.

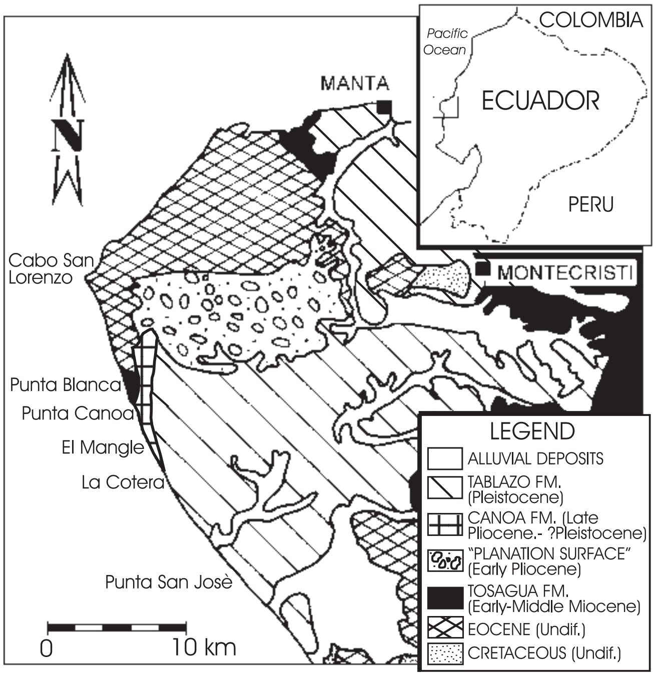
Geological and stratigraphic framework

On the basis of planktonic foraminifers association, the Canoa Formation was referred to Late Pliocene, more precisely to 2.9–2.1 Ma (N 21 Biozone of Blow 1969, according to Bianucci et al. 1997). It has extensive outcrops along the sea cliff south of Cabo San Lorenzo (Manabì), where its beds dip gently south and rest with angular unconformity on the faulted and folded shale of the Tosagua Formation (Fig. 3). The Canoa Formation extends from Punta Canoa to the Quebrada La Cotera disappearing definitively a little further south by dipping beneath the cyclothemic deposits of the Tablazo Formation, which lie unconformably upon it.

Traditional facies analysis and sequence stratigraphy interpretation of the Canoa Formation sediments indicate that it is part of a third-order composite depositional sequence (Cantalamessa et al. 2000*b*; Mitchum and Van Wagoner 1991) formed in shoreface to inner shelf depositional environments by rapid subsidence along the Ecuadorian accretionary wedge, which occurred as the aseismic Carnegie Ridge arrived at the Ecuador Trench.

The Carnegie Ridge is a massive submarine mountain range 3000 m high and 300 km wide, impinging beneath Ecuador between latitudes 1°S–2°S until the Late Pliocene and created at the Galapagos Hot Spot through a complex history (Lonsdale and Klitgord 1978). The nature of the impact, in terms of deformation and evolution of this part of the South American active margin, consists in the progressive decrease of the slab dip, large amount of subsidence on the accretionary wedge related to tectonic erosional processes, and uplift in the fore arc by compressive stresses (Vogt et al. 1976; Von Huene 1984; Lallemand et al. 1992).

Fig. 3. Schematic geological map of the Cabo San Lorenzo area (modified from Whittaker 1988).



The close connection between the creation of favourable conditions for the laying down of the Canoa Formation depositional sequence and the Carnegie Ridge drawing near to the subduction zone, enables this episode to be indirectly attributed to the Late Pliocene.

Interpreting the numerous shellbeds present inside the Canoa Formation as stratal attenuation, we used them as surrogates for seismic discontinuities at outcrop scale. The study of the paleobiological (Bianucci et al. 1997), taphonomic, and ichnologic features of the numerous mollusk shellbeds found inside the succession, and the unconformities associated with them (Kidwell 1991; Kondo et al. 1998), allowed us to reconstruct the internal architecture of the Canoa Formation and to distinguish the systems tracts (Di Celma et al. 2001) present in it.

In accordance with the simple lithostratigraphic description of the Canoa Formation in its typical outcrop, the formation is composed by a ca. 40-m succession of clays and silty clays whose deepest depositional environment can be correlated to the inner shelf. In the upper part the earlier-described lithotypes are rapidly replaced through an erosional surface characterized by the presence of numerous channels arranged orthogonally to the inferred paleoshoreline. They are substituted by ca 30-m-thick intensely bioturbated sandstones, deposited in a shoreface environment.

Paleontological analyses

Detailed paleontological analyses deal with otoliths, mollusks, and foraminifers. In particular, the otolith assemblages furnished, for the first time, a well-diversified list of the fossil ichthyofauna.

The systematic list of the otolith assemblage shows a great number of indeterminate taxa. Taphonomic factors such as the state of preservation, scarce knowledge of the morphology, and intraspecific variability of otoliths (e.g., Ophidiidae,

Table 1. Teleostean fish taxa of the Canoa Formation (Late Pliocene) and their present distribution.

Teleostei of the Canoa Formation		PACIFIC							ATLANTIC	
			EAST PACIFIC							
		IWP	Or	Ca	Pa		Pe	Mg	W	E
					m	p				
CONGRIDAE	*Ariosoma* sp.	●	●	●	●	●			●	●
	Gnathophis sp.	●		●	●	●	●	●	●	●
	Hildebrandia sp.								●	
	Paraconger cf. *guianensis*								●	
	Paraconger californiensis			●	●	●	●			
	Rhechias sp.	●							●	●
	Rhynchoconger cf. *nitens*			●	●	●				
	Rhynchoconger sp.	●			●	●			●	
ENGRAULIDAE	*Anchoa* cf. *compressa*			●						
	Anchoa cf. *nasus*			●	●	●	●			
	Anchoa sp.			●	●	●	●		●	
	Anchovia macrolepidota			●	●	●	●			
	Cetengraulis mysticetus			●	●	●	●			
	Engraulis sp.	●	●	●		●	●		●	●
PRISTIGASTERIDAE	*Ilisha* sp.	●			●	●	●			●
	Neoopisthopterus sp.			●	●	●	●		●	
	Pellona sp.	●							●	
CLUPEIDAE	*Etrumeus teres*	●		●	●	●	●		●	
	Opistonema libertate			●	●	●	●			
ARIIDAE	*Arius* sp.	●		●	●	●	●		●	●
PHOTICHTHYIDAE	*Yarella* sp.	●							●	●
MYCTOPHIDAE	*Hygophum* sp.	●	●	●	●	●	●	●	●	●
	Notoscopelus sp.	●	●	●	●	●	●		●	●
CARAPIDAE	*Echiodon* sp.	●		●	●	●		●	●	●
OPHIDIIDAE	*Brotula* cf. *clarkae*			●	●	●	●			
	Hoplobrotula sp.	●								
	Lepophidium sp.			●	●	●	●		●	
	Lepophidium cf. *cervinum*								●	
	Lepophidium microplepis			●	●	●	●			
	Neobythites sp.	●		●					●	●
	Otophidion sp.			●	●	●			●	
MACROURIDAE	*Coelorinchus* sp.	●		●	●	●	●	●	●	●
BREGMACEROTIDAE	*Bregmaceros* sp.	●		●	●	●	●		●	●
MERLUCIIDAE	*Merluccius gayi*					●	●			
	Merluccius productus		●	●						
BATRACHOIDIDAE	*Porichthys* sp.1		●	●	●	●	●		●	
	Porichthys sp.2		●	●	●	●	●		●	
ANTENNARIIDAE	*Antennarius* sp.	●		●	●	●	●		●	●
MUGILIDAE	*Mugil cf. curema*			●	●	●	●	●	●	●
	Mugil sp.	●		●	●	●	●	●	●	●
ATHERINIDAE	*Atherinops* sp.		●	●						
BELONIDAE	*Strongylura* sp.	●		●	●	●	●		●	●
HEMIRAMPHIDAE	?*Euleptorhamphus* sp.	●		●	●	●			●	●
	Hemiramphus sp.	●		●	●	●	●		●	●
HOLOCENTRIDAE	*Myripristis* sp.	●		●	●	●			●	●
SCORPAENIDAE	Scorpaenidae ind.	●		●	●	●	●		●	●
COTTIDAE	Cottidae cf. Radulinus		●	●						
CENTROPOMIDAE	*Centropomus* sp.			●	●	●	●		●	
SERRANIDAE	*Epinephelus* sp.	●		●	●	●	●		●	●
	Paralabrax sp.		●	●	●	●	●	●		
	Prionodes sp.			●	●	●	●	●	●	
PSEUDOCHROMIDAE	*Pseudochromis* sp.	●								
OPHISTOGNATHIDAE	*Lonchopistus* sp.			●					●	
OPHISTOGNATHIDAE	Opistognathidae ind.	●		●	●	●			●	
APOGONIDAE	*Apogon* sp.	●		●	●	●	●		●	●
LACTARIIDAE	Lactariidae ind.	●								
CARANGIDAE	*Decapterus* sp.	●		●	●	●	●		●	●
	Trachurus sp.	●	●	●	●	●	●	●	●	●
LUTJANIDAE	*Lutjanus* sp.	●		●	●	●	●		●	●
	Pristipomoides sp.	●							●	
LOBOTIDAE	Lobotidae cf. Lobotes	●		●	●	●	●		●	●
GERREIDAE	*Eucinostomus* sp.			●	●	●	●		●	●
HAEMULIDAE	*Anisotremus* sp.			●	●	●	●		●	
	Brachydeuterus sp.									●
	Orthopristis sp.			●	●	●	●		●	
	Pomadasys sp.	●		●	●	●	●		●	●
NEMIPTERIDAE	*Nemipterus* sp.	●								
SCIAENIDAE	*Bairdiella* sp.			●	●	●	●		●	
	Ctenosciaena sp.					●	●		●	
	Cynoscion sp.1		●	●	●	●	●	●	●	
	Cynoscion sp.2		●	●	●	●	●	●	●	
	Equetus sp.								●	
	Genyonemus sp.		●	●						
	Isopistus sp.			●	●	●	●		●	
	Larimus sp.			●	●	●	●		●	
	Mentichirrus sp.			●	●	●	●		●	
	Micropogonias sp.			●	●	●	●		●	
	Nebris sp.				●	●	●		●	
	Paralonchurus sp.				●	●	●		●	
	Pareques sp.			●	●	●	●		●	
	Sciaena sp.						●		●	●
	Sciaenops sp.								●	
	Seriphus sp.		●	●						
	Umbrina sp.	●		●	●	●	●		●	●
CIRRHITIDAE	Cirrhitidae ind.	●		●	●	●	●		●	●
EMBIOTOCIDAE	*Cymatogaster* sp.		●	●						
	Hyperprosopon sp.		●	●						
	Micrometrus sp.		●	●						
POMACENTRIDAE	*Abudefduf* sp.	●		●	●	●	●		●	●
	Chromis sp.	●		●	●	●	●		●	●
LABRIDAE	Labridae ind.	●	?	●	●	●	●		●	●
DACTYLOSCOPIDAE	Dactyloscopidae ind.			●	●	●	●	●	●	
GOBIIDAE	Gobiidae ind.	●	●	●	●	●	●		●	●
STROMATEIDAE	*Peprilus* cf. *medius*			●	●	●	●			
BOTHIDAE	Bothidae ind.1	●		●	●	●	●		●	●
	Bothidae ind.2	●		●	●	●	●		●	●
	Bothidae ind.3	●		●	●	●	●		●	●
PARALICHTHYIDAE	*Citharichthys* cf. *stigmaeus*		●	●						
	Citharichthys cf. *sordidus*		●	●						
	Citharichthys sp.		●	●	●	●	●		●	●
PLEURONECTIDAE	*Eopsetta* sp.	●	●	●						
	Isopsetta sp.		●	●						
	Pleuronectidae ind.	●	●	●			●	●	●	●
SOLEIDAE	Soleidae ind.	●				●				●
CYNOGLOSSIDAE	*Symphurus* sp.	●		●	●	●	●		●	●
Percentage on total number of taxa (105)		47%	24%	79%	67%	71%	64%	11%	71%	42%

Note: IWP, Indo-West Pacific; see Fig. 2 for other abbreviations.

Gobiidae), and the limited diagnostic resolution power (e.g., Gobiidae, Pleuronectidae), are the main reasons of this poor taxonomic resolution (Nolf 1985). Notwithstanding these limitations, it was demostrated that taxonomic ranks such as genera and families can be paleobiogeographically informative (Bisconti et al. 2001), and this enables us to employ them in analysing patterns of general distributions.

Teleostean fishes assemblage

The otolith fauna, represented by about 7000 specimens, consists of 105 taxa, attributed to 46 families and 80 genera (Table 1). Quantitatively, the fish fauna is dominated by six families (Congridae, Engraulidae, Ophidiidae, Sciaenidae, Gobiidae, Paralichthyidae) making up about 90% of the fauna. All these taxa are still living today. To better understand the biogeographic structure of the association, we analysed the present distributions of these taxa in relation to the four principal regions of geographic affinity (Indo-West Pacific, East Pacific, West Atlantic, and East Atlantic).

The greatest faunal affinity is seen with the East Pacific (87%). The West Atlantic component is subordinate (70%), and the similarity with Indo-West Pacific and East Atlantic consistently inferior (47% and 42%, respectively). Taxa exclusively Pacific are 23 (*Paraconger californiensis*, *Rhynchoconger* cf. *nitens*, *Anchoa* cf. *compressa*, *Anchoa* cf. *nasus*, *Anchovia macrolepidota*, *Cetengraulis mysticetus*, *Opistonema libertate*, *Brotula* cf. *clarkae*, *Lepophidium microplepis*, *Merluccius gayi*, *Merluccius productus*, *Atherinops* sp., Cottidae cf. *Radulinus*, *Paralabrax* sp., *Genyonemus* sp., *Seriphus* sp., *Cymatogaster* sp., *Hyperprosopon* sp., *Micrometrus* sp., *Peprilus* cf. *medius*, *Citharichthys* cf. *sordidus*, *Citharichthys* cf. *stigmaeus*, *Isopsetta* sp.); taxa exclusive of West Atlantic are five

Fig. 4. Geographic distribution of some significative eastern Pacific taxa: Pleuronectidae ind. (1), *Engraulis* sp. (2), *Merluccius productus* (3), *Atherinops* sp. (4), Cottidae cf. *Radulinus* (5), *Genyonemus* sp. (6), *Seriphus* sp. (7), *Cymatogaster* sp. (8), *Hyperprosopon* sp. (9), *Micrometrus* sp. (10), *Citharichthys* cf. *stigmaeus* (11), *Citharichthys* cf. *sordidus* (12), *Eopsetta* sp. (13), *Isopsetta* sp. (14), *Anchoa* cf. *compressa* (15), *Neobythites* sp. (16), *Lonchopistus* sp. (17), *Ilisha* sp. (18), *Nebris* sp. (19), *Paralonchurus* sp. (20), *Merluccius gayi* (21), *Ctenosciaena* sp. (22), *Rhynchoconger* sp. (23), Soleidae ind. (24), *Sciaena* sp. (25). For abbreviations see Fig. 2.

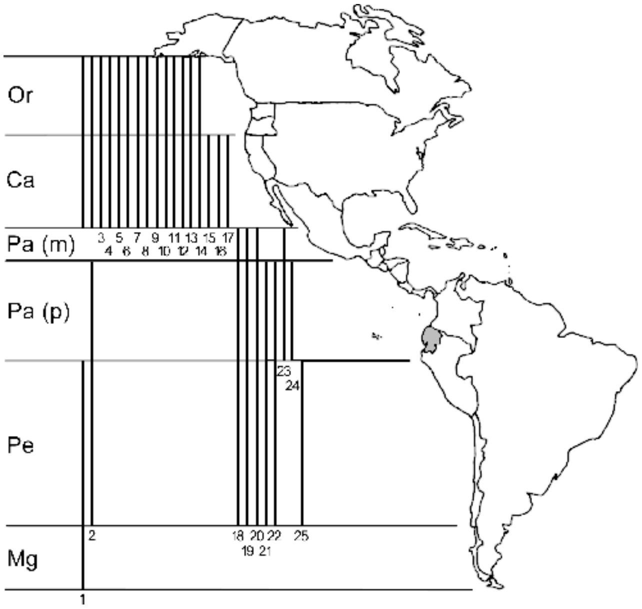
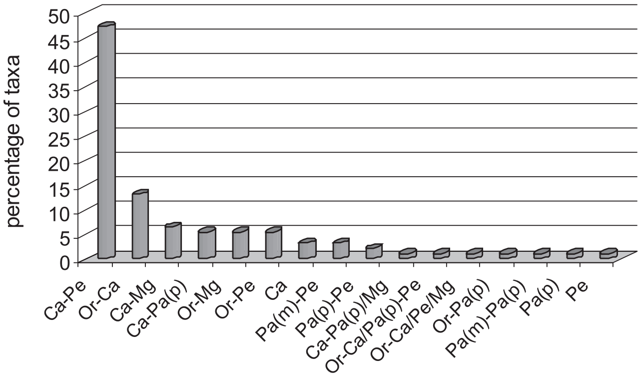


Fig. 5. Percentage of fossil taxa of Canoa Formation shared with the different combinations of biogeographic provinces of the eastern Pacific. For abbreviations see Fig. 2.



(*Hildebrandia* sp., *Paraconger* cf. *guianensis*, *Lepophidium* cf. *cervinum*, *Equetus* sp., *Sciaenops* sp.; Figs. 4, 5).

The taxa shared by the two sides of the CAI, are 23 (*Anchoa* sp., *Neoopisthopterus* sp., *Lepophidium* sp., *Otophidion* sp., *Porichthys* sp.1, *Porichthys* sp.2, *Centropomus* sp., *Prionodes* sp., *Lonchopistus* sp., *Anisotremus* sp., *Orthopristis* sp., *Bairdiella* sp., *Ctenosciaena* sp., *Cynoscion* sp.1, *Cynoscion* sp.2, *Isopistus* sp., *Larimus* sp., *Mentichirrus* sp., *Micropogonias* sp., *Nebris* sp., *Paralonchurus* sp., *Pareques* sp., Dactyloscopidae). The component exclusive to the Indo-West Pacific is limited to four taxa (*Hoplobrotula* sp., *Pseudochromis* sp., Lactariidae, *Nemipterus* sp.) and only the genus *Brachideuterus* is exclusive to the East Atlantic. Furthermore, 35 taxa are uniformly present in the four areas and consequently do not give useful biogeographic information.

Particular noteworthy is the biogeographic status of the genus *Pristipomoides*, living in Indo-West Pacific and in the western Atlantic.

The comparison between the fish fauna of the Canoa Formation and the extant fauna of Ecuador shows substantial differences. In fact, although the fossil association is represented exclusively by living taxa, only 65% of them are still present in Ecuador. Especially significant is the absence of the families Photichthyidae, Pseudochromidae, Lactariidae, Embiotocidae, Pleuronectidae, and Soleidae that indicates a different pattern of biogeographic distribution.

The major affinities of the fossil community have been recognized with the Californian province, where 79% of taxa are present. Twelve of these taxa now live only in the Californian and Oregonian provinces (*Merluccius productus*, *Atherinops* sp., Cottidae cf. *Radulinus*, *Genyonemus* sp. *Seriphus* sp., *Cymatogaster* sp., *Hyperprosopon* sp., *Micrometrus* sp., *Citharichthys* cf. *stigmaeus*, *Citharichthys* cf. *sordidus*, *Isopsetta* sp., *Anchoa* cf. *compressa*) and so we named them “Californian Guests.” In addition, other three taxa (*Eopsetta* sp., *Neobythites* sp, *Lonchopistus* sp.) even if not endemic, have their present East Pacific distribution limited to the Californian province. Lower affinities are shown by Panamic sensu stricto (71%), Mexican (67%), and Peruvian (64%) provinces. Scanty relationships are found with the extreme provinces: Oregonian to the North (24%) and Magellanic to the South (11%) (Fig. 2).

On the contrary the living fauna of Ecuador shows different biogeographic relationships. The greatest affinities have been recognized with the Panamic sensu stricto (86%) and Mexican (84%) areas, lesser affinity with Californian (63%) and Peruvian (68%) provinces, and a poor similarity with Oregonian (4%) and Magellanic (5%).

The evolution of the fish fauna of Ecuador shows two main biogeographic trends from the Late Pliocene to the Recent. The first one was characterized by a more generic Panamic connotation, with high number of Californian guests and still a strong relationship with the Caribbean fauna. In the second phase, the disappearance of Californian guests and a strong decrease of the West Atlantic taxa led to the formation of the modern Panamic province that developed in this area.

Mollusk assemblage

Although the systematic study of the mollusk fauna of Canoa is not complete, taxa listed in Tables 2 and 3 provide a substantial indication of the biogeographic structure of the association as a whole.

The malacofauna, represented by more than 17 000 specimens, consists of 196 taxa, 98 of which refer to Bivalvia, 93 to Gastropoda, and five to Scaphopoda. From a quantitative standpoint, the dominant families are Lucinidae, Crassatellidae, and Veneridae among bivalves and Caecidae, Naticidae, and Nassaridae among gastropods. Fifty-nine of the forms left in open nomenclature are at the generic level (30 bivalves, 28 gastropods, 1 scaphopod), and only two

Table 2. Present geographical distribution of Bivalvia from the Canoa Formation.

Bivalvia of the Canoa Formation	PACIFIC							ATLANTIC	
		EAST PACIFIC							
	WP	Or	Ca	Pa			Pe	W	E
				N	C	S			
Nucula declivis				●	●	●			
Nucula exigua			●	●	●	●			
Nucula spp.									
Saccella bicostata				●	●	●			
Saccella fastigata				●	●	●			
Saccella elenensis			●	●	●	●			
Nuculana spp.									
Anadara concinna				●	●	●			
Anadara esmeralda				●	●	●			
Anadara mazatlantica				●	●	●			
Anadara nux				●	●	●			
Anadara reinharti				●	●	●			
Anadara tubercolosa			●	●	●	●			
Anadara sp.									
Arca sp.									
Arcopsis solida			●	●	●	●			
Barbatia sp.									
Glycymeris lintea					●	●			
Glycymeris maculata				●	●	●			
Glycymeris sp. 1									
Glycymeris sp. 2									
Crenella divaricata				●	●	●			
Atrina sp.									
Ostrea sp.1									
Ostrea sp.2									
Plicatula inezana				●	●				
Plicatula cf. *spondilopsis*				●	●	●			
Undulostrea megodon				●	●	●			
Aequipecten cf. *cracens*		E	X	T	I	N	C	T	
Argopecten circularis			●	●	●	●			
Leptopecten biolleyi				●	●	●			
Pacipecten tumbezensis				●	●	●			
Pecten spp.									
Chlamys sp.									
Pectinidae indet.									
Anomia peruviana			●	●	●	●			
Eucrassatella gibbosa				●	●	●			
Crassinella adamsi				●	●	●			
Crassinella cf. *ecuadoriana*				●	●	●			
Crassinella pacifica			●	●	●	●			
Crassinella varians				●	●	●			
Linga cancellaris				●	●				
Lucina callosana		E	X	T	I	N	C	T	
Lucina centrifuga				●	●	●			
Lucina fenestrata				●	●	●			
Lucina sp.									
Divalinga eburnea				●	●	●			
Pegophysema spherica		E	X	T	I	N	C	T	
Tellidorella sp.									
Mysella compressa				●	●				
Basterotia cf. *subquadrata*				●	●	●			
Basterotia sp. 1									
Basterotia sp. 2									
Trachycardium cf. *procerum*				●	●	●			
Trachycardium cf. *senticosum*				●	●	●			
Trigonocardia granifera				●	●	●			
Trigonocardia obovalis				●	●	●			
Cardium sp.									
Anomalocardia callistoides		E	X	T	I	N	C	T	
Dosinia ponderosa				●	●	●			
Mactra angusta					●	●			
Mactra sp. 1									
Mactra sp. 2									
Anatina sp.									
Chione gorgona		E	X	T	I	N	C	T	
Chione cf. *manabia*		E	X	T	I	N	C	T	
Chione mariae				●	●	●			
Chione squamosa				●	●	●			
Chione cf. *tembla*		E	X	T	I	N	C	T	
Chione sp.									
Petricola denticulata				●	●	●			
Tellina laplata						●			
Tellina cf. *lyra*				●	●	●			
Tellina lyrica				●	●	●			
Tellina sp.1									
Tellina sp.2									
Tellina sp.3									
Tellina (Merisca) brevirostris				●	●				
Tellina (Merisca) sp.1									
Tellina spp.									
Tellinidae indet.									
Solecurtus lineatus					●	●			
Macoma ecuadoriana		E	X	T	I	N	C	T	
Strigilla dichotoma					●	●			
Donax punaensis		E	X	T	I	N	C	T	
Tagelus peruvianus				●	●	●			
Tagelus politus					●	●			
Semele pacifica				●	●				
Semelina subquadrata				●	●	●			
Solen pfeifferi				●	●	●			
Corbula cf. *amethystina*					●	●			
Corbula cf. *inflata*				●	●	●			
Corbula sp. 1									
Corbula sp. 2									
Corbula sp. 3									
Panopea cf. *coquimbensis*		E	X	T	I	N	C	T	
Verticordia ornata				●	●	●		●	
Cyathodonta sp.									

Note: WP, western Pacific; N, northern; C, central; S, southern; see Fig. 2 for other abbreviations.

have a greater indetermination (families Pectinidae and Tellinidae).

Among the 135 recognized species, 37 (27%) are extinct and 98 living. The former are represented almost completely by taxa erected by Pilsbry and Olsson (1941) on the specimens of the Canoa Formation. Data regarding the geographic distribution of the 98 living species have been obtained both from publications of synthesis on the Panamic province, as for example Olsson (1961), Keen (1971), Bernard (1983), Bernard et al. (1991) and Skoglund (1991, 1992), and from studies focussed on particular groups of mollusks, as in Coan (1979), Dushane (1974), and Jung (1989). The collected data show a marked Panamic connotation of the association as a whole (88.7% of the taxa presents a distribution strictly related to the present range of this bioprovince); yet before analysing the faunal biogeographic relationships in more detail, it is important to exactly define the boundaries of the Panamic province referred to in the following discussion. The northern limit corresponds to 31°N at the head of the Gulf of California and to 25°N at Bahia Magdalena on the west coast of the Baja California (Skoglund 1991; Crame 2000). Therefore, some distributional records given only by latitudinal values (Bernard 1983) may be ambiguous if not compared with other sources. Moreover, according to Bernard

Table 3. Present geographical distribution of Gastropoda and Scaphopoda from the Canoa Formation.

	PACIFIC							ATLANTIC	
		EAST PACIFIC							
Gastropoda of the Canoa Formation	WP	Or	Ca	Pa			Pe	W	E
				N	C	S			
Diodora sp.									
Astraea buschii					●	●			
Tricolia sp.									
Alvinia sp.									
Onoba fortis					●	●			
Calliostoma nonurum						●			
Calliostoma sp.									
Circulus occidentalis		E	X	T	I	N	C	T	
Systellomphalus peronatus		E	X	T	I	N	C	T	
Teinostoma ecuadorianum				●	●	●			
Architectonica nobilis				●	●	●		●	●
Turritella broderipiana						●	●		
Caecum compe		E	X	T	I	N	C	T	
Asperiscala cf. *acapulcana*				●	●	●			
Asperiscala emydonesa				●					
Epitonium loripanum		E	X	T	I	N	C	T	
Nitidiscala cumingii				●	●	●			
Nitidiscala durhamiana				●	●				
Nitidiscala cf. *willetti*				●	●	●			
Epitonium sp.1									
Epitonium sp.2									
Epitonium sp.3									
Amaea ferminiana				●	●	●			
Vermicularia frisbeyae				●	●				
Balcis sp.									
Niso imbricata				●					
Niso sp. 1									
Niso sp. 2									
Calyptraea mamillaris				●	●	●			
Calyptraea sp.									
Crepidula aculeata	●			●	●	●	●	●	
Crepidula dorsata	●	●	●	●	●	●	●		
Crepidula sp.									
Crucibulum cf. *springvaleense*		E	X	T	I	N	C	T	
Crucibulum sp. 1									
Crucibulum sp. 2									
Crucibulum sp. 3									
Natica sp.									
Polinices hepaticus								●	
Polinices intemeratus				●	●	●			
Polinices panamensis				●	●	●			
Polinices sp.									
Sinum cymba						●	●		
Cypraea cf. *robertsi*				●	●	●			
Erato cf. *oligostata*					●	●			
Malea cf. *ringens*				●	●	●			
Ficus cf. *ventricosa*				●	●	●			
Bursa corrugata corrugata				●	●	●		●	
Bursa sp.									
Pteropurpura sp.									
Solenosteira boggsi		E	X	T	I	N	C	T	
Cosmioconcha sp.									
Mitrella sp.									
Strombina lanceolata						●			
Strombina recurva				●	●	●			
Strombina sp.									
Nassarius ecuadorianus		E	X	T	I	N	C	T	
Nassarius puntablancanus		E	X	T	I	N	C	T	
Nassarius tinosus		E	X	T	I	N	C	T	
Oliva kaleontina				●	●	●			
Oliva sp.									
Olivella gracilis				●	●	●			
Olivella sp.									
Prunum curtum						●	●		
Subcancilla gigantea				●	●	●			
Cancellaria cassidiformis				●	●	●			
Cancellaria cumingiana				●	●	●			●
Cancellaria dolioides		E	X	T	I	N	C	T	
Cancellaria harpiformis		E	X	T	I	N	C	T	
Cancellaria jijipana		E	X	T	I	N	C	T	
Cancellaria yolandia		E	X	T	I	N	C	T	
Cancellaria cf. *cominella*		E	X	T	I	N	C	T	
Cancellaria cf. *obesa*				●	●	●			
Cancellaria sp.									
Trigonostoma ecuadoriana		E	X	T	I	N	C	T	
Conus cacuminatus		E	X	T	I	N	C	T	
Conus recurvus				●	●	●			
Conus tornatus				●	●	●			
Conus sp.									
Terebra cf. *blanca*		E	X	T	I	N	C	T	
Terebra cf. *subsulcifera*		E	X	T	I	N	C	T	
Terebra spp.									
Strioterebrum cf. *camaronense*		E	X	T	I	N	C	T	
Strioterebrum indocayapum		E	X	T	I	N	C	T	
Glyphostoma spp.									
Nanodiella meridionalis		E	X	T	I	N	C	T	
Kurtziella cf. *esperia*		E	X	T	I	N	C	T	
Kurtziella cf. *heptapleura*		E	X	T	I	N	C	T	
Pyramidella elenensis				●	●	●			
Triptychus incantatus				●	●	●			
Turbonilla loripana		E	X	T	I	N	C	T	
Acteocina puruha		E	X	T	I	N	C	T	
Cylichna cf. *luticola*					●				
Scaphopoda of the Canoa Formation									
Cadulus leptodema		E	X	T	I	N	C	T	
Cadulus quitus		E	X	T	I	N	C	T	
Dentalium cf. *oerstedii*				●	●	●			
Dentalium tesseragonum				●	●	●			
Dentalium. sp.									

Note: See Table 2 and Fig. 2 for abbreviations.

(1983), the southern zone of the Baja California (extending from 25°N, Bahia Magdalena, to 23°N, Cabo San Lucas) may be considered a transitional area with a mixed fauna composed of both Californian and Panamic elements. The southern limit of the Panamic province corresponds to Punta Aguja (6°S, northern Peru) and represents the junction area between the Humbolt Current (cold) and the Equatorial Countercurrent (warm). Finally, it is noteworthy that the following biogeographic data are based on taxa at species level, because distributional ranges at the generic rank are not significant for mollusks.

The majority of the assemblage (63 species, corresponding to 64.2%) consists of species whose present geographic range substantially corresponds with the whole Panamic Province, whereas a small component (7.1%) is represented by bivalves with a Panamic and Californian distribution.

Other faunal components present a more restricted distribution within the Panamic province or show a prevailing geographic range related to the Peruvian province. Quantitatively, the most important group consists of five species of bivalves and four of gastropods (9.2%) restricted to the central–northern part of Panamic province. The presence of *Tellina brevirostris*, *Asperiscala emydonesa*, and *Niso imbricata* is significant in the extant malacofauna of Galapagos Islands, even though these taxa are characteristic of higher mainland latitudes. The taxa present only in the central–southern part of this province reach a slightly lower percentage (eight species, 8.2%), including *Cylichna* cf. *luticola*, until now recorded only in Central America. The last group (5.1%) includes species whose northern distribution does not extend beyond the northern border of the Peruvian province or the southern zone of the Panamic province (Ecuador). These species, including *Tellina laplata* and *Calliostoma nonurum*, show a greater affinity with the northernmost part of the Peruvian province. Also included in this group are those that reached the coasts of Chile, such as *Sinum cymba* and *Prunum curtum*.

The remaining mollusks include a group (3.1%) represented by three transisthmic forms (i.e., forms present in both the Panamic and the Caribbean areas), *Architectonica nobilis, Bursa corrugata corrugata*, and *Verticordia ornata*. *Architectonica nobilis*, in particular, is present both in the Caribbean and in the eastern Atlantic. *Verticordia ornata* is the only representative of the 22 transisthmic bivalves listed by Bernard et al. (1991), but this weak link with the Caribbean area is partly strenghtened by the geminate species (at least 14) present among the bivalves of the association.

Finally, negligible percentages are seen of the Atlantic species *Polinices hepaticus,* currently found from the coasts of Florida to Brazil, the amphipacific *Crepidula dorsata,* occurring in the western Pacific (Japan) and in all the provinces of the eastern Pacific (from Alaska to Chile), and the congeneric *Crepidula aculeata*, considered in literature to have an intertropical-wide range because of its presence in the eastern and western Pacific, as well as in the Caribbean.

Benthic foraminifers assemblage

The foraminifers assemblage of the Late Pliocene Canoa Formation, based on preliminary analyses, is made up of 67 species, among which 25 have not been determined at the species level (Table 4). In general, the specimens are abundant and well preserved. The assemblage is constituted of species living today, with the exception of three species recognized only as fossils: *Bolivina serrata*, *Cibicidoides alazanensis*, and *Uvigerina* cf. *marksi*; it is not possible at the moment to establish if the species labelled “sp.” are still living.

Most of the specimens (more than 80% of the whole foraminifers assemblage) belong, in order, to *Hanzawaia concentrica*, *Cancris sagra*, and *Pseudononion pizarrensis*. These are followed by *Asterigerinata*, *Quinqueloculina*, *Bulimina marginata*, *Brizalina*, and *Bolivina*. The other taxa, listed in Table 4, occur only scattered in the succession and are represented by rare specimens.

According to Murray (1991) *Asterigerinata*, *Cancris*, and *Hanzawaia* are indicative of inner shelf environments; Sgarrella and Moncharmont Zei (1993, cum bibliography) in the Mediterranean area report *Asterigerinata mammilla*, *Cibicides lobatulus*, *Quinqueloculina seminulum*, and *Bolivina aenariensis* (species comparable with *Brizalina subaenariensis*), most frequently from the infralittoral zone. Whittaker (1988), in Ecuador, finds the occurrence of the first three species restricted to shallow-water environments. Other taxa, like *Uvigerina* and *Bulimina* generally found in deeper waters, are cosmopolitan and their occasional occurrence in the Canoa Formation assemblage could be due to vertical migration, linked to cool influence of upwelling current. Therefore, on the basis of these arguments, the foraminifers assemblage of the Canoa Formation is indicative of the upper part of the inner shelf.

As ecological parameters at great depths are very similar and also the foraminifers faunas there are similar, the best way to point out different zoogeographical subdivisions is to study the near-shore assemblages, or at most the shelf and upper slope faunas, which may have several features of the near-shore ones (Boltovskoy 1976). For this reason, the foraminifers assemblage of the Canoa Formation is well suited for studies concerning geographic distribution. This notwithstanding, it is hard, because of the lack of literature, to compare the foraminifers assemblage of Canoa Formation to other associations of the Pacific bioprovinces of South and Central America of the same age and shelf environment and also to perform an exhaustive comparison with the living microfaunas of South America.

However, it is possible to draw a comparison with the living microfaunas, but only those of the bioprovinces for which data are at present available. Therefore, the benthic foraminifers of both the neighbouring Pacific and Atlantic coasts of North America (Table 4) have been considered, concerning respectively the Californian area from about 41°N to 22°N, with the Gulf of California included (Culver and Buzas 1986), and the Gulf of Mexico (Culver and Buzas 1981).

In calculating the following percentages the species sp. occurring in the fossil association are considered exclusive of Canoa Formation.

The Californian and the Gulf of Mexico assemblages consist of 798 and 848 species, respectively. Within the Canoa Formation assemblage, 30 species, corresponding to 44.8%, are shared with the Californian province and 19, corresponding to 28.3%, are species shared with the Gulf of Mexico (see Table 4). In the end, 18 species (*Ammonia tepida*, *Bulimina marginata*, *Cancris sagra*, *Cassidulina laevigata*, *Cibicides lobatulus*, *Fursenkoina pontoni*, *Globocassidulina subglobosa*, *Globulina pyrula*, *Hanzawaia concentrica*, *Lagena laevis*, *Lagena striata*, *Melonis barleeanum*, *Planulina ariminensis*, *Planulina ecuadorana*, *Pseudoparrella exigua*, *Quinqueloculina lamarckiana*, *Quinqueloculina seminulum*, *Uvigerina peregrina*), which make up 26.9% of the Canoa Formation assemblage, are present in the two modern provinces. Moreover, it is noted that 17.9% (12 species) of the species are shared exclusively with California area, while only one species (1.49%) is shared with Gulf of Mexico exclusively (Fig. 6).

If we consider only the most frequently recorded species (Culver and Buzas 1986, 1981) of the Californian and the Gulf of Mexico bioprovinces, they reduce to 130 and to 295, respectively. In this case, the result is that 11 (16.4%) are shared with the modern Californian province, ten (14.9%) with the Gulf of Mexico, and only three species, *Bulimina marginata*, *Quinqueloculina lamarckiana*, and *Uvigerina peregrina*, corresponding to 4.5%, are present in both of the two areas. Therefore, 49 species (73.13% of the whole assemblage) occur only within the Canoa Formation association, while eight (11.94%) are the species shared exclusively with California, and seven (10.45%) exclusively with the Gulf of Mexico. Only three species (*Bulimina marginata*, *Quinqueloculina lamarckiana*, and *Uvigerina peregrina*)

Table 4. Foraminifers of the Canoa Formation compared with the modern assemblages of California and Gulf of Mexico.

Benthic Foraminifers of the Canoa Formation	**RECENT**					
	PACIFIC Cal-Mex			**ATLANTIC**		Gulf of Mexico
t sps (platform assemblage) **67**	**t sps 798**	**f sps 130**	**p sps 83**	**t sps 848**	**f sps 295**	**p sps 114**
Ammonia tepida	●			●		
Ammonia sp.						
Asterigerinata mammilla						
A. planorbis						
Bolivina bicostata	●					
B. serrata (pisciformis)+						
Bolivina sp.						
Brizalina argentea	●	●	●			
Brizalina spissa	●	●	●			
B. subaenariensis				●		●
Brizalina sp.						
Buccella tenerrima	●					
Buliminella curta	●					
Bulimina marginata	●	●	●	●	●	●
B. pagoda	●					
Cancris sagra	●			●	●	●
Cancris sp.						
Cassidulina laevigata	●			●	●	●
Cassidulina aff. *californica*	●					
Cibicides lobatulus	●	●	●	●		
Cibicides sp.						
Cibicidoides alazanensis+						
Cibicidoides mckannai	●	●	●			
Cibicidoides sp.						
Cuneolina angusta						
Cuneolina pavonia						
Elphidium sp.						
Fissurina sp.						
Fursenkoina pontoni	●			●	●	●
Fursenkoina sp.						
Globocassidulina subglobosa	●	●	●	●		●
Globulina pyrula	●			●		
Guttulina communis						
Hanzawaia concentrica	●			●	●	●
Hanzawaia cf. *boueana*						
Hanzawaia sp						
Heterolepa sp.						
Lagena laevis	●			●	●	●
Lagena striata	●	●		●		
Lagena sp.						
Lenticulina clerici						
Lenticulina sp.						
Melonis barleeanum	●	●		●		
Nonion sp.						
Nonionella miocenica	●					
Oolina sp.						
Pararotalia magdalensis						
Planulina ariminensis	●			●	●	●
P. equadorana = *P. ornata*	●		●	●		●
Pseudononion pizarrensis	●					
Pseudononion sp.						
Pseudoparrella exigua	●			●		
Quinqueloculina lamarckiana	●	●	●	●	●	●
Quinqueloculina seminulum	●			●	●	●
Quinqueloculina sp.						
Rosalina globularis	●	●	●			
Stainforthia sp .						
Spiroloculina sp.						
Textularia panamensis	●					
Textularia sp.						
Textulariella sp.						
Trifarina sp.						
Triloculina sp.						
Trochammina sp.						
Uvigerina cf. *marksi+*						
Uvigerina peregrina	●	●	●	●	●	●
Uvigerina sp.						
Shared species	30	11	10	19	10	13
percentages	44.8	16.4	14.9	28.3	14.9	19.4
18 species = 26.9% shared (Canoa Fm. and Pacific and Atlantic provinces)						

Note: t sps, total number of species; f sps, most frequent species; p sps, most frequent platform species; +, extinct.

remain in common with both Californian and Gulf of Mexico areas (Fig. 6).

Finally, comparisons have been made taking in account only the species that at present live in the two provinces at depths to 200 m (platform) and that are ubiquitous. In this case, the Canoa Formation assemblage shares seven species, or 10.4%, with both the California and the Gulf of Mexico provinces: *Brizalina spissa*, *Bulimina marginata*, *Cibicides lobatulus*, *Cibicidoides mckannai*, *Globocassidulina subglobosa*, *Quinqueloculina lamarckiana*, and *Rosalina globularis* with California, and *Cancris sagra*, *Cassidulina laevigata*, *Fursenkoina pontoni*, *Lagena laevis*, *Planulina ariminensis*, *Quinqueloculina seminulum*, and *Uvigerina peregrina* with Gulf of Mexico (Fig. 6).

Boltovskoy (1976), in a study on the distribution of benthic foraminifers of South America, proposed a zoogeographical subdivision of the Pacific side of the continent, describing, among other things, the Panamic and the Chilean–Peruvian provinces, the latter being subdivided in three subprovinces: Peruvian, North Chilean, and South Chilean.

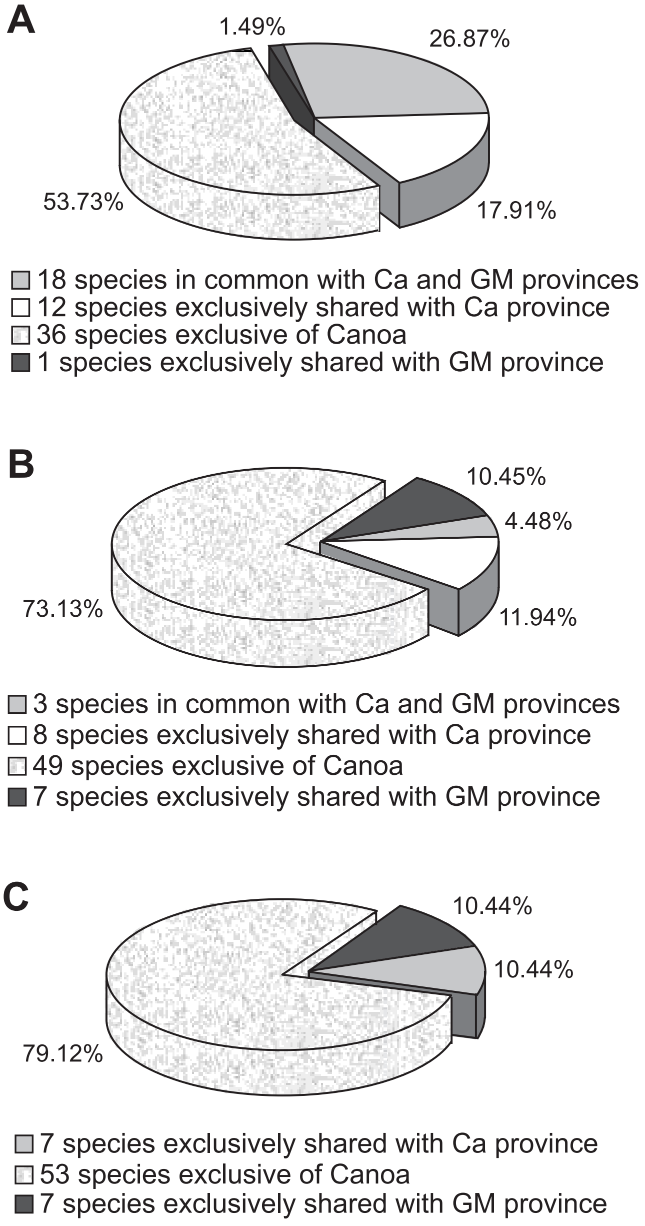
According to Boltovskoy (1976), the boundaries among these areas are linked to the pattern of ocean currents which separate characteristic associations when they reach the coasts. This author finds that the microfauna of the Panamic province, even if it is rather poorly studied, has some affinities with that of the warm-water West Indian and with that of the temperate-water Chilean–Peruvian zoogeographical provinces. But the author admits that the Panamic Province is not close to the Chilean–Peruvian one, neither can it be considered a typical warm-water province. On the contrary, he recognises a closer affinity with the fauna of the Pacific shelf of Central America and Mexico.

Discussion

The biogeographic composition of the Canoa Formation fossil communities shows a precise eastern Pacific affinity and a substantial Panamic connotation, even if the distribution patterns of these three groups exhibit different responses.

The biogeographic setting depicted by the mollusk assemblage is dominated by eastern Pacific forms, which largely outnumber the remaining components making up 93.8% of

Fig. 6. Comparisons between benthic foraminifers assemblages of Canoa Formation with the Californian (Ca) and Gulf of Mexico (GM) areas. (A) Percentage based on the whole assemblage. (B) Percentage based on the most frequent species. (C) Percentage based on the platform species.



the total. A Peruvian affinity is shown by five species (5.1%) exhibiting a northern geographic limit not overcoming the southern part of the Panamic Province (northern Peru – southern Ecuador), whereas negligible percentages are found of the transisthmic (or amphiamerican) species (3.1%), and the Atlantic, amphipacific, and tropical wide-ranging groups are represented only by one species (1%). Within the eastern Pacific area, the prominent stock is represented by typically Panamic taxa (88.7%), a small component of which (7.1%) include the Californian province in their geographic range. Among these, A*nomia peruviana* and *Crassinella pacifica* occur in the Californian province as a whole, but the rest are Panamic species and are only occasionally recorded in the southern-central part of Baja California (Coan and Scott 1997). It seems possible that their presence is due to the northward transport of the mollusk larvae by currents flowing along the coasts of Central America and Mexico during the summer (Finet 1991).

Taking into account a comparison with the extant mollusk assemblage of Ecuador, only 12 species (12.2%) of the Canoa assemblage do not live today along the coast of Ecuador. Apart from *Tellina laplata* and *Calliostoma nonurum*, occurring only at the southern border of the Panamic province (Northern Peru), and *Strombina lanceolata*, living only in the Galapagos Islands (Jung 1989), nine species (9.2%) are known to occur in the central and northern part of this province. Vokes (1988) argued that the lack of some Pliocene species from the modern mollusk assemblages of Ecuador is largely due to extensive changes in current regimes linked to the emergence of the CAI. In particular, the change of water temperature due to the loss of the Caribbean current does not allow these taxa to extend their present latitudinal range as far south.

In summary, the mollusk assemblage does not evidence significant faunal relationships outside of the Panamic province. Nevertheless, on the basis of the biogeographic framework depicted in Table 5, it appears reasonable to infer a Pliocene arrangement of this province, which does not correspond exactly to the modern one. In particular, some species (9.2%) show evidence of northward latitudinal migration from the Late Pliocene to Recent, being represented today by populations living only in the northern and central part of the Panamic province.

Hitherto almost unknown in the stratigraphic record is the presence of a rich otolith association which permits an outline of an interesting biogeographic framework and a depiction of the major evolutionary trends of fish association from Late Pliocene to the Present.

The composition of the modern Panamic ichthyofauna, compared to the other tropical provinces of the Caribbean and Indo-West Pacific, is characterized by a high index of endemicity and a reduced biodiversity index.

The presence of an high number of endemic taxa (14% of genera) is correlated to the progressive isolation of this area, both with the western Pacific and the western Atlantic, during the Neogene. The development of Ekman’s East Pacific barrier and a complex oceanic circulation regime in the tropical eastern Pacific limited the dispersion of organisms from the source areas of the Indo-West Pacific province. Currently, in fact, only 7% of species are shared by both sides of the ocean. Relationships with the Caribbean are also scarce. Nevertheless, the high number of geminate species in the two basins evidences the beginning of intense phenomena of speciation due to the progressive isolation and to the definitive closure of the seaway (between 3.7 and 3 Ma; Duque-Caro 1990; Coates and Obando 1996; Ibaraki 1997).

Besides these historical processes, the impoverishment of Panamic ichthyic association can to be related to the limited size of this area, its scarce environmental diversification and the scarcity of insular and recifal systems (Allen and Robertson 1994).

This decrease in the fish biodiversity involves most of the families that are characteristic of tropical waters (Holocentridae,

Table 5. Biogeographic affinities of the mollusk assemblage.

	Bivalvia		Gastropoda		Scaphopoda		Total	
Biogeographic affinity	n.sp	%sp	n.sp	%sp	n.sp	%sp	n.sp	%sp
Panamic	39	39.8	22	22.4	2	2	63	64.2
South Panamic – Peruvian	1	1	4	4.1	—	—	5	5.1
Central–South Panamic	3	3.1	5	5.1	—	—	8	8.2
North–Central Panamic	5	5.1	4	4.1	—	—	9	9.2
Panamic–Californian	7	7.1	—	—	—	—	7	7.1
Transisthmic	1	1	2	2	—	—	3	3.1
East–West Pacific	—	—	1	1	—	—	1	1
TWR	—	—	1	1	—	—	1	1
Atlantic	—	—	1	1	—	—	1	1

Note: n.sp, number of species; %sp, percent of species; TWR, tropical wide-ranging.

Mullidae, Chaetodontidae, Pomacanthidae, Scaridae, Blenniidae, Acanthuridae, etc.). However, an opposite trend is observed in the wide adaptative radiation of Sciaenidae (Allen and Robertson 1994). The high number of taxa recognized in the Canoa Formation (16 genera), several of which are today extinct in the eastern Pacific but living in the western Atlantic, allows us to infer that a large adaptative radiation of Sciaenidae had already spread in the Late Pliocene and probably derived from a large sciaenid-population spread through the tropical East Pacific and in the Caribbean area during the pre-isthmus rising phase.

To identify the main biogeographic relationships between the fossil community and the extant Antitropical American communities, we analyzed the taxocoenosis at different taxonomic levels (species, genus, and family). At genera and families rank, we note a substantial affinity: about 90% of families and 80% of the genera of the Canoa Formation are presently shared by the western Atlantic. At the species level, we observe a strong eastern Pacific connotation: 16 species (out of 19) are exclusive of the eastern Pacific, nine of which extend from California to Peru, four are exclusive of the Californian waters, one is from California–Panama, and finally one is distributed from Panama to Peru.

Only a very weak relationship with the West Atlantic Ocean has been recognized: one amphiamerican species and two species that are now confined in the West Atlantic. These last taxa represent West Atlantic endemisms, which during the Late Pliocene had an amphiamerican biogeographic status.

To make comparison between the fossil and recent ichthyofauna of the Ecuador, we created, on bibliographic basis, a systematic list of the fish fauna living in this area. Eighty-six percent of the 462 species of teleosts present today are in common with the Panamic sensu stricto area; 84% is shared by the Mexican sector and a smaller component (63%) is also present in the Californian province. No species is shared by Ecuadorian and Californian coasts exclusively.

There is a good degree of affinity (68%) with the adjacent Peruvian province: three taxa exclusively shared and nine ranging from Ecuador to Magellanic area. Therefore, the living ichthyofauna of Ecuador show a clear Panamic connotation and significant relationships with the adjacent Peruvian province.

On the other hand, the presence in the fossil assemblage of a high percentage of species shared with the Californian area and 16 taxa (14%) presently not recorded south of this province allow us to hypothesize the existence, during Late Pliocene, of a wider Panamic bioprovince with a stronger northern influence than the present one.

These geographic relationships evidenced by the fossil fish fauna are partly supported by the analysis of benthic foraminifers and mollusks collected in the same and (or) other geological formations.

The foraminifers fauna shares 30 (44.8%) species with the Californian province and 19 (28.3%) with the Gulf of Mexico. The modern Panamic province, with several temperate taxa, has a larger affinity with the fauna of the Pacific shelf of California and Mexico than with the Caribbean and Peruvian faunas. Also the mollusk fauna shows a generic Panamic connotation, as the majority of taxa are present between California and the coasts of Ecuador and (or) Peru.

Comparing the Late Neogene microfauna and microflora associations of Ecuador to the Neogene ones of Caribbean and California provinces, Hasson and Fisher (1986) emphasized that the uppermost Early Pliocene benthic foraminifers of eastern Pacific had come to diverge sharply from those of the Caribbean, in contrast to the Miocene fauna having much closer affinities with the fauna of California. This fact is undoubtedly linked to the rising of the Central American land bridge, an event which altered the interchanges between the Caribbean and the Pacific, as well as the oceanic current pattern.

Keigwin (1982*a*), on comparing data on stable isotopes at Deep Sea Drilling Program sites 602 (Caribbean) and 603 (Pacific Ocean), evidenced changes starting from the Late Miocene, which may have resulted from the progressive uplift of the Central American land bridge.

A confirmation of the existence of significant faunal relationships between the Californian and the areas of the Panamic province during the Pliocene is given by the studies on the sediments of Camarones (Onzole Formation, northern Ecuador; Vokes 1988; Landini et al. 1991; Bianucci et al. 1993).

Some taxa (e.g., mollusks) closely related to the cooler water species living in the northern Pacific province are recorded by Vokes (1988), while Landini et al. (1991) and Bianucci et al. (1993) describe a well-diversified otolith fauna, which included taxa that currently are strictly associated with the Californian province.

The existence of cold waters (Californian Current) in the central and southern sectors of tropical Pacific was hypothesized by Duque-Caro (1990) to begin in the Late Miocene (about 9.2 Ma) and to continue until the Early Pliocene (3.7 Ma). Similar biotic relationships may be hypothesized between northern and southern extratropical sectors of the East Pacific thanks to paleontological evidences from Plio-Pleistocene sequences of Peru and Chile and the present antitropical distribution of different groups of organisms (Lindberg 1991).

In particular, on the basis of fossils (e.g., mollusks), Lindberg (1991) identifies two major events of dispersion: the first in the Pliocene and the second in the Early Pleistocene. Even if a certain bidirectionality of interchanges has been recognized, the migration of taxa from southern areas toward Panamic and Californian provinces is less consistent, and this evidences a marked asymmetry in the directions of these fluxes. Lindberg (1991) critically examines the different mechanisms of dispersal and vicariance invoked by various authors to explain these antitropical distributions and concludes (p. 316)

> The Pliocene exchanges necessitate a model that does not depend on glaciation to cool the tropics and allows for interchange in both directions. Moreover, these exchanges require a mechanism that would provide both cooling and disrupt the regional current patterns within the region. The closing of the Panamic portal provided both conditions and is consistent with the timing of interchange.

According to several authors, however, the presence of cold water taxa should be linked not to the emergence of CAI but to the activation of coastal upwelling cells. A dispersal mechanism linked to this factor was proposed by Hubbs (1952) for fishes, mollusks, and echinids of the coasts of Baja California. These cells, being ecologically stable in time and space, represented a refuge for temperate species.

More complex is the analysis of the factors determining, in the Late Pliocene, the diffusion of a part of the boreal biota towards more southern areas and the development of a well-diversified fish community in the Ecuadorian waters. After the rising of CAI, climatic variations may have caused changes in the superficial regime of currents and (or) activated coastal upwelling cells, as proposed by various authors in these last years (Duque-Caro 1990; Lindberg 1991; Bianucci et al. 1993; Coates and Obando 1996; Ibaraki 1997).

As already known, the establishment of a superficial circulation similar to the present one is associated with the closure of Panama seaway and to the contemporaneous climatic deterioration related to the onset of the glacial phase.

The modifications of the climatic regime may have changed the seasonal balance of the two trade-wind systems, reinforcing the North-wind system and supporting for a certain period of the year a longer standing of the southern part of ITCZ (which presently reaches 3°N in the period February–April). Therefore, a branch of the CC flew along the coast to the lower latitudes brings more consistent biological effects (concerning at least fish faunas), without changing the general setting of the association.

According to Lindberg (1991, p. 314),

> ... the diversity of taxa, habitats, and life history strategies, as well as the bidirectionality and timing of the exchanges argues against a single causal event or mechanism.

At the present state of knowledge models based on both climatic change and activation of upwelling cells seem able to explain our data. Our studies (in progress) on new fossil associations of the Neogene–Quaternary of Ecuador could allow the definition of the dispersion mechanisms of the biota in greater detail and, over all, the more precise outlining of ways and times of the establishment of the Panamic province and its relationships with the adjacent provinces. < http://www.dst.unipi.it/gruppi/paleontologia/ecuador >.

Conclusions

The paleontological record recognized in the Canoa Formation (foraminifers, mollusks, and, in particular, otoliths) provides some evidence about the evolution of Pliocene Panamic province and its relationships with the other East Pacific and West Atlantic bioprovinces.

Biogeographic pattern

Starting from the rising of CAI, fish, mollusk, and foraminifers assemblages from Late Pliocene of Ecuador are characterized by a very prominent eastern Pacific component. In particular, the overall biogeographic distribution of mollusks and fishes points to a Panamic connotation, but some mollusk taxa are spread in a wider area (Baja California and central California), and closer ichthyofaunistic relationships with temperate northern areas indicate a wider northward extension of this province.

Relationships with the living faunas (fishes, mollusks) of Ecuador

Relationships between the fish and mollusk assemblages of the Canoa Formation and the living assemblages along the Ecuadorian coast are quite weak. Only 66% of the fossil fish taxa are present in the modern community and several fish families, today living in other East Pacific regions, disappeared from this area, probably during the Pleistocene time. This percentage rises to 88.7% when the mollusk species are taken into account.

Relationships with the extant eastern Pacific provinces

Biogeographic relationships of this fossil ichthyofauna with others from eastern Pacific provinces are underscored by large affinities with the Californian province, where 79% of taxa are present, 12 taxa of which presently live only in the Californian and Oregonian provinces. The Panamic sensu stricto (71%), Mexican (67%), and Peruvian (64%) provinces follow, in order of decreasing affinity. Limited relationships are found with the extreme provinces: Oregonian to the North (24%) and Magellanic to the South (11%).

Californian guests

Several authors (Hasson and Fisher 1986; Vokes 1988; Landini et al. 1991; Bianucci et al. 1993) reported taxa (mollusks, fishes, and foraminifers) with Californian affinity in the southern part of the Pliocene Panamic province.

Nevertheless the presence in the Canoa Formation of a consistent and diversified group of fishes (12 taxa), today exclusively living in the Californian and Oregonian provinces, permits us to better define the abundance and the role of the

Californian guests within the southern area of the Panamic province.

At the present state of knowledge, we suggest that different causes could have triggered the southward diffusion of these boreal elements: changes in the superficial regime of currents and (or) the activation of coastal upwelling cells, after rising of CAI.

Tentatively it seems reasonable to hypothesize a possible change in the water circulation in the eastern equatorial Pacific related to global climatic fluctuations and regional tectonics (such as the closure of Panama seaway).

Evolutionary trends of the Ecuadorian ichthyofauna

The local extinction of Californian guests and some other families of fishes and the wider biotic divergence with the West Atlantic, testable also at higher taxonomic levels, are the major evolutionary trends characterizing the transition of the Pliocene Panamic association towards the modern one.

Studies in progress of new fossil associations of the Neogene–Quaternary of Ecuador will permit the definition in a greater detail of the dispersion mechanisms of the biota and, over all, the more precise outlining of ways and times of the establishment of the Panamic province and its relationships with the neighbouring ones.

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