



UNIVERSITÀ  
DEGLI STUDI  
FIRENZE

## FLORE

# Repository istituzionale dell'Università degli Studi di Firenze

### **Statistical analysis on benthic foraminifers of the Pliocene Canoa Formation (Manabí Basin, Ecuador)**

Questa è la Versione finale referata (Post print/Accepted manuscript) della seguente pubblicazione:

*Original Citation:*

Statistical analysis on benthic foraminifers of the Pliocene Canoa Formation (Manabí Basin, Ecuador / E. INTRIERI; G. VALLERI. - STAMPA. - Coccioni R. & Marsili A., (eds) 2007. Proceedings of the Giornate di Paleontologia 2005. Grzybowski Foundation Special Publication n 12, 109+viii pp.:(2007), pp. 20-35. (Intervento presentato al convegno Giornate di Paleontologia 2005 tenutosi a Urbino nel May, 20-22, 2005).

*Availability:*

This version is available at: 2158/353816 since:

*Terms of use:*

Open Access

La pubblicazione è resa disponibile sotto le norme e i termini della licenza di deposito, secondo quanto stabilito dalla Policy per l'accesso aperto dell'Università degli Studi di Firenze (<https://www.sba.unifi.it/upload/policy-oa-2016-1.pdf>)

*Publisher copyright claim:*

(Article begins on next page)

# Statistical analysis on benthic foraminifers from the Pliocene Canoa Formation (Manabì Basin, Ecuador): a tool for palaeoenvironmental reconstruction

EMILIO INTRIERI and GIGLIOLA VALLERI

Dipartimento di Scienze della Terra – Università di Firenze Via G. La Pira, 4 – 50121 Firenze

## ABSTRACT

This paper concerns detailed qualitative, quantitative and multivariate analyses carried out on the Pliocene Canoa Formation benthic foraminifer assemblages (Sheppard, 1930) to investigate palaeoenvironmental conditions. Throughout the more than sixty metres of section, more than a hundred samples have been collected, generally with half a metre spacing. Qualitative and quantitative analyses have been performed on the larger than 0.125 mm fraction. The 146 recognised species have been grouped in 11 morphotypes by means of morphotype analysis (Corliss & Fois, 1990; Jones & Charnock, 1985), among which one is here first defined. For each sample percentage abundances of each species and morphotype have been calculated and elaborated by means of Q-mode cluster analysis. Also the abundance of the planktonic specimens (P/P+B), the diversity index (Fisher's  $\alpha$ ) and the weight percentages of the residues have been considered for each sample.

The cluster analysis pointed out six typologies of samples, on the bases of morphotype assemblages. The comparison of these data with other statistical data and with the autoecology of the species, enabled us to recognise the environment parameters, the oscillations of which caused microfaunal changes. Five palaeoenvironmental phases have been recognised.

**Keywords.** benthic foraminifera, statistical and multivariate analyses, palaeoenvironment, Pliocene, Ecuador.

## INTRODUCTION

Recently interest in the study of benthic foraminiferal assemblages as a reliable tool for ecological and palaeoecological interpretation has greatly increased. Since the 1960's, many authors have been studying foraminiferal ecology, with implications on palaeoecological reconstructions. Among them, Phleger (1960); Boltovskoy & Wright (1976); Corliss (1985); Boltovskoy *et al.* (1991); Murray (1973, 1991); and Mancin & Pirini (2002).

This work is focused on the detailed qualitative and quantitative analysis of the benthic foraminifers of the Canoa Formation, with the aim of understanding the palaeoenvironmental evolution of the basin.

The Canoa Formation (Sheppard, 1930) consists of clays, sandy clays and sands, transgressively deposited on the Miocene Tosagua Formation, outcropping along the coast of Ecuador, south-west of Manta (Fig. 1), a highly tectonically active area, near the Nazca-South America subduction zone (Lonsdale, 1978). The Canoa Formation has been

referred, according to Bianucci *et al.* (1997), to the Late Pliocene (N21 Biozone of Blow, 1969).



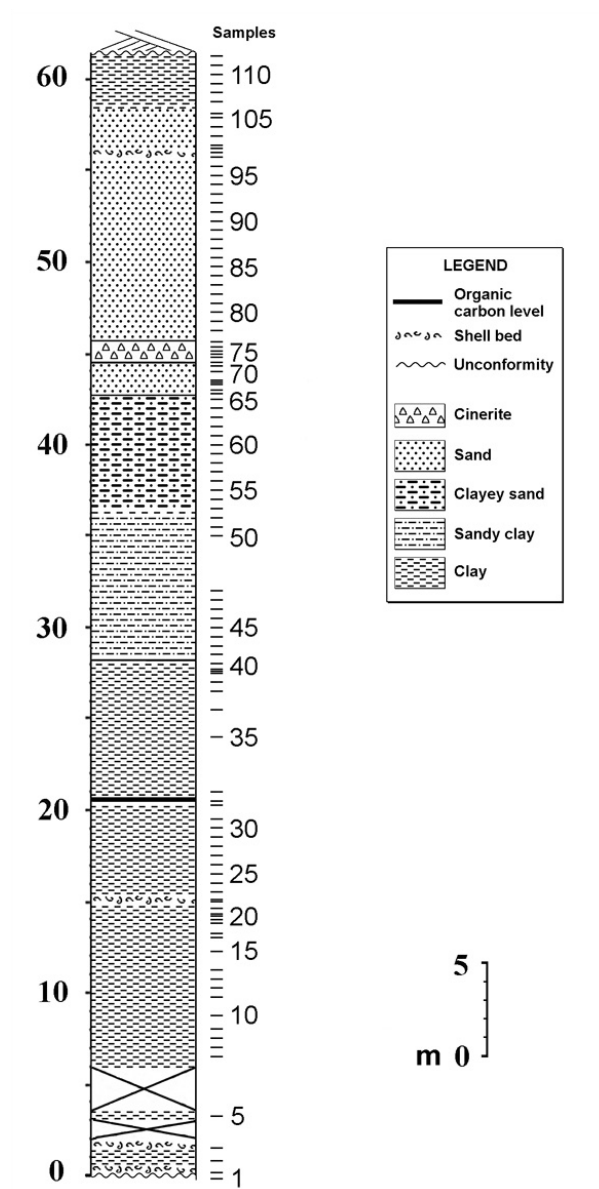
**Figure 1.** Geological map of the study area (modified from Landini *et al.*, 2002).

Several studies have been carried out during the last years on the Canoa Formation molluscs, ooliths and foraminiferal assemblages, as well as on sedimentological characters (Whittaker, 1988; Bianucci *et al.*, 1997; Cantalamessa *et al.*, 1999, 2000a, 2000b; Di Celma *et al.*, 2002; Landini *et al.*, 2002). These authors have interpreted an inner neritic depositional environment in a basin partially isolated from the open ocean by means of a sill. The intense tectonic activity in the area has caused vertical shifts of the sill, so that the basin would have experienced periods of alternating better and worse communication with the ocean. Such tectonic activity influenced the ecological parameters of the basin as well as the foraminiferal assemblages during the deposition of the Canoa Formation.

### MATERIALS AND METHODS

Throughout the more than 60 metres of composite section (Fig. 2) 116 samples have been collected, generally with 50 cm spacing from each other. The Canoa Formation beds very gently dip southward, therefore it is possible to follow the vertical extension along some kilometres of the coast. About 56 m of the formation was measured and sampled from Punta Canoa to Quebrada El Mangle while the top-most about 5 m at Quebrada La Cotera, a locality about three kilometres southwards. For each sample 100 to 150 g of dried sediment was disaggregated with hydrogen peroxide (30 vol.) and washed through 0.063 and 0.125 mm sieves. Detailed foraminifers analyses were carried out on 106 samples, the others resulted barren. The larger than 0.125 mm residue fractions were considered for counting and for each sample the residues have been split by means of a microsplitter, spread on gridded picking trays and observed; this operation was repeated a sufficient number of times to determine about 300 benthic and 300 planktonic specimens. Percentages of the recognised 146 benthic taxa have been calculated. At the same time on a total of 300 specimens, the ratio between the planktonic and the total foraminifers,  $P/(P+B)$ , was calculated for each sample. This value, concerning the Canoa Formation, may be considered as a proxy for evaluating the communication degree of the basin with the open ocean (see Discussion). Other characteristics have also been considered for each sample: the weight percentage of the washed residue, to evaluate the percent sand (finer sediment than 0.063 mm being eliminated during sieving), the percentage of epifaunal specimens on the total number of benthic specimens (% E); and the diversity index (Fisher's  $\alpha$  index), i.e. the number and the relative abundance of the species in benthic assemblages (Murray, 1991).

Moreover, morphotype analysis (Corliss 1985; Jones & Charnock, 1985; Corliss & Fois, 1990) has



**Figure 2.** Schematic section of the Canoa Formation, samples position is indicated.

been performed on the benthic assemblage and the 146 taxa, included those not defined at specific level, have been grouped into 11 morphotypes (Tab. 1).

For every morphotype, as well as for every species, the percentage abundances were calculated and elaborated by means of descriptive statistics (frequency histograms) and by means of multivariate analysis, Q-mode cluster analysis (PAST software, Hammer *et al.*, 2001). This last analysis performed on percentage abundances of the 11 morphotypes and of the 146 species shows similar results, corroborating the use of this method as a reliable tool for palaeoecological interpretations. Therefore, because of the simplicity of elaboration, the morphotype abundances have been used for the interpretation, together with considerations on the autoecology of the species.

**Table 1.** Life adaptations of the morphotypes and their relationships with some environmental factors. (Data after Corliss, 1985, 1991; Jones & Charnock, 1985; Bernhard, 1986; Murray, 1991; Kitazato, 1994; Duleba *et al.*, 1999). \* Shallow infaunal: 0-2 cm; intermediate infaunal: ~1-4 cm; deep infaunal: 4-15 cm (Corliss, 1991). ° Aerobic: >1.0 ml/l O<sub>2</sub>; dysaerobic: 0.1-1.0 ml/l O<sub>2</sub>; anaerobic: <0.1 ml/l O<sub>2</sub> (Murray, 1991).

		Planconvex	Biconvex	Milioline	Rounded trochospiral			
Style of life	Microhabitat	Epifaunal/Epiphytic	Epifaunal	Epifaunal/Epiphytic	Epifaunal			
	Feeding strategy	Herbivorous/detritivorous	Herbivorous/detritivorous	Herbivorous	Herbivorous/detritivorous			
	Mode of life	Sessile/crawling	Free/crawling	Free/crawling	Free			
	Depth in sediment*	-	-	-	-			
Environment factors	Substrate grain size	Coarse	Fine to coarse	Coarse	Medium-fine			
	Energy	Relatively higher	Relatively higher	Relatively higher	Relatively lower			
	Oxygen status°	Aerobic	Aerobic	Aerobic	Aerobic			
	Salinity	Normal	Normal	Normal	Hyposaline-hypersaline			
		Rounded planispiral	Pseudoplan.	Conical/cylindrical	Spherical	Flattened conical/cyl.	Ovoid	Agglutinating
Style of life	Microhabitat	Infaunal	Infaunal	Infaunal	Infaunal	Infaunal	Infaunal	Infaunal
	Feeding strategy	Herbivorous/detritivorous	Detritivorous	Detritivorous	Detritivorous	Detritivorous	Detritivorous	Detritivorous
	Mode of life	Free	Free	Free	Free	Free	Free	Free
	Depth in sediment*	Shallow	Deep	Shallow-intermediate	Shallow	Deep	Shallow	Intermediate-deep
Environment factors	Substrate grain size	Medium-fine	Fine	Fine	Fine	Fine	Fine	Fine to coarse
	Energy	Relatively lower	Relatively lower	Relatively lower	Relatively lower	Relatively lower	Relatively lower	Relatively lower
	Oxygen status°	Aerobic	Aerobic	Dysaerobic	Aerobic	Anaerobic	Anaerobic	Aerobic
	Salinity	Hyposaline-hypersaline	Hyposaline-normal	Normal	Normal	Normal	Normal	Normal

## BENTHIC SPECIES OF THE CANOA FORMATION

In the Canoa Formation 146 benthic species were recognised, belonging to 59 genera. Agglutinating taxa have been in general determined only at a genus level because of their difficult specific determination and their sometimes bad preservation.

The most abundant species is *Hanzaavaia concentrica*, present in 96 of the 106 studied samples, reaching on average about 16%. Other common species are *Pseudonion pizarrensis* (about 14%, present in 104 samples) and *Bulimina marginata* (about 11%, present in 105 samples). Only these

three species of the whole association exceed average abundances of 10%. These last three species, along with *Pararotalia magdalenensis* (7.5% abundance), *Ammonia tepida* (about 6%), *Criboelphidium poeyanum* (about 5%), *Uvigerina peregrina* and *Nonionella miocenica* (both about 4%) make up about 66% of the association. Only 16 species exceed 1% abundance on average and altogether reach 83% of the whole association. All the above mentioned values on the abundance have been calculated averaging of the relative abundances of the species in all of the 106 samples.

The dominant species in the assemblages of the

considered samples are indicative of very shallow water. So, in agreement with Whittaker (1988) and Cantalamessa *et al.* (1999), the Canoa Formation sediments are referable to an inner shelf environment. Therefore water depth does not need to be enumerated as a limiting environment factor, because the limited depth oscillations may have affected the foraminifer associations only to a small degree.

The presence of the temperate to cool water species *Uvigerina peregrina* (Murray, 1991) and the rare occurrence of the warm water species of milioline group may be consistent with the influence of northern cool currents into the basin and/or the presence of coastal upwelling, as suggested by Landini *et al.* (2002). According to these authors, such palaeoceanographic features can be linked to the closure of Panama Isthmus in the Late Pliocene.

#### BENTHIC FORAMINIFERAL AUTOECOLOGY

Benthic foraminiferal assemblages are used as a reliable tool for palaeoenvironmental reconstructions (Boltovskoy *et al.*, 1991; Murray, 1991). Many species show preferences for certain environmental conditions and parameters including substrate composition (sediment type and grain size), organic carbon and oxygen content, salinity, turbidity, turbulence and depth of the waters.

In this work information on the autoecology of the most common species has been considered to interpret palaeoenvironmental evolution of the basin (the following species are listed in order of decreasing abundance in the assemblages of the Canoa Formation):

- *Hanzawaia concentrica* - According to Murray (1991), this species is a dominant component in inner shelf assemblages, down to a few tens of metres depth, mainly associated with sandy substrates.

- *Pseudononion pizarrensis* - This species was first described from Recent muddy sediments of a hypo-saline river mouth environment (Berry, 1928).

Van Morkhoven *et al.* (1986) referred *P. pizarrensis* to neritic environments and Miller *et al.* (1997) reported this species from mainly fine-grained substrates. According to Boltovskoy (1976), this is a temperate water species (cited as *Nonion pizarrense*).

- *Bulimina marginata* - A living species reported from 20 to 1400 m (Murray, 1991), but according to Duleba *et al.* (1999) it is a typical shelf species. It mainly lives within muddy sediments (Murray, 1991).

This is an opportunistic species, able to take advantage of an increase in organic carbon and to well tolerate oxygen depletion at the sea floor (Sen Gupta & Machain-Castillo, 1993). *Bulimina marginata* can therefore become dominant in shallow dysaerobic waters.

- *Ammonia tepida* - It is an inner shelf to lagoonal species (Murray, 1991) and is widely regarded as an euryhaline species, ranging from hypo-saline to hyper-saline environments (Bandy, 1961; Boltovskoy, 1976; Murray, 1991).

- *Criboelphidium poeyanum* - Murray (1991) reports this species (as *Elphidium poeyanum*) living at very shallow water depth (less than 12 m), in muddy-sandy substrate. It can live within a very wide range of salinities, from hypo- to hyper-saline lagoons, in some cases up to 90‰ (Boltovskoy, 1976; Murray, 1991).

- *Uvigerina peregrina* - This species lives at various depths, ranging from 45 to 4500 m. Similarly to *Bulimina marginata*, this species may tolerate bottom oxygen depletion and high organic carbon concentration (Boersma, 1984; Murray, 1991), in which case its relative abundance can increase in shallow waters, although it is normally more abundant in deeper waters (Boersma, 1984). It is often related to cold water temperatures (Murray, 1991), due either to high water depth or to upwelling, in shallower waters. This species is usually associated with muddy substrates (Murray, 1991).

#### MORPHOGROUPS

Several authors (Severin, 1983; Corliss 1985, 1991; Jones & Charnock, 1985; Bernhard, 1986; Corliss & Chen, 1988; Corliss & Fois, 1990, among others) have emphasized the influence of environmental parameters on the morphology of the foraminiferal test. These authors defined the morphotypes according to the shape of the test and the nature of the wall. Morphogroup analysis allows to draw palaeoenvironment features considering also taxa undetermined at a species level, since the morphotypes are independent of taxonomy.

Substrate is the main factor controlling distribution of the benthic foraminifer morphogroups (Tab. 1). According to Corliss (1991), living foraminifers can be referred to the epifaunal morphogroup when dwelling on the sediment-water interface or, taking into account sediment reworking, in the top centimetre of sediment, and to the infaunal morphogroup when living at various depths within the sediment (shallow infaunal: down to 2 cm; intermediate: ~1-4 cm; deep: 4-15 cm).

Most of the specimens belonging to the epifaunal morphogroup normally live on relatively harder and/or coarser sediments than the infaunal ones, some live free also on soft/muddy substrates (Kitazato, 1994). Most of the epifaunal species either crawl on the sediment by extending their pseudopodia, grazing on algae (herbivores) and organic detritus (detritivores) (Murray, 1991; Kitazato, 1994), or adopt a sessile life-style. Some species of the latter, belonging to the planoconvex morphotype, can permanently or temporarily

attach their test to the substrate by means of an organic glue (Langer, 1993), which allows them to tolerate current movements and relatively high water turbulence at the bottom (Corliss & Fois, 1990). Some epifaunal species are epiphytic and live on vegetated substrates (Langer, 1993). Their recovery in fossil assemblages is indicative of shallow water depth, within the photic zone, and of well oxygenated environments.

Foraminifers belonging to the infaunal morphogroup live free within the sediment, feeding mainly on organic detritus. Most infaunal species need a finer and/or softer sediment than the epifaunal ones. Compared to epifaunal species, the tests of the infaunal ones exhibit a higher surface/volume ratio, as well as a greater pore density throughout the whole test surface. Such features are advantageous for living in oxygen-limited conditions (Corliss & Fois, 1990). The use of morphogroup methodology has allowed to deal in statistic analysis with much less numerous variables than species, making it simpler to interpret the relationships between variation of the benthic assemblages and the palaeoenvironment changes.

### MORPHOGROUPS OF THE CANOA FORMATION

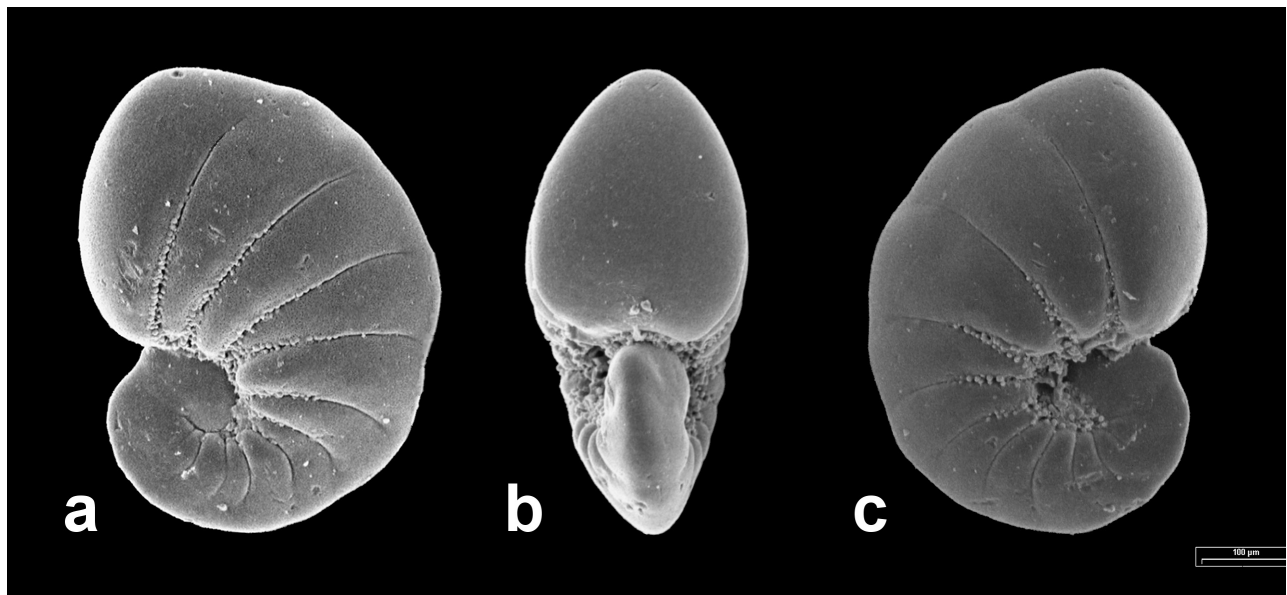
In this study the 146 benthic foraminifer species of the Canoa Formation have been grouped into 11 morphotypes (Tab. 2), nine of which (Planoconvex,

Biconvex, Milioline, Rounded trochospiral, Rounded planispiral, Conical/cylindrical, Spherical, Flattened conical/cylindrical and Ovoid) have been described by Corliss & Fois (1990); one (Agglutinating) is defined on the basis of the work of Jones & Charnock (1985), another one (Pseudoplanispiral) is first introduced in this work.

We have here introduced the Pseudoplanispiral morphogroup (Fig. 3) to differentiate, from the similar Rounded trochospiral and the Rounded planispiral ones, those numerous specimens which are characterised by a trochospiral coiling (even if very low), but that present a nearly planispiral external shape. This type includes mostly *Pseudononion pizarrensis* and secondarily *Nonionella miocenica* (Tab. 2) and is present with significant percentages, on average 18.9%, up to sample 65 (Tab. 3). Moreover, this morphotype has been differentiated from the Rounded trochospiral one to point out different adaptations of the two morphotypes: pseudoplanispiral *Pseudononion* and *Nonionella* are infaunal, fine-sediment dwelling genera, while Rounded trochospiral specimens, constituted essentially by *Ammonia*, present an epifaunal style of life. Furthermore, Pseudoplanispiral, differentiated from the Rounded planispiral morphogroup, although they are both infaunal, puts in evidence other different adaptations. The first group includes species indicative of normal to low salinity, such as within estuaries, and inner shelves environments

Table 2. List of species of each morphotype. (Dominant species within each morphogroup are in bold).

EPIFAUNAL MORPHOGROUPS	Planoconvex	Biconvex	Milioline	Rounded trochospiral			
	<i>Anomalinooides</i> sp.1 <i>Anomalinooides</i> sp.2 <i>Asterig. planorbis</i> <i>Asterigerinata</i> sp.1 <i>Cibicides lobatulus</i> <i>Cibicides</i> sp.1 <i>Cibicides</i> sp.2 <i>Cavertinopsis</i> sp.1 <b><i>Hanzawaia concentrica</i></b> <i>Heterolepa</i> sp.1 <i>Heterolepa</i> sp.2 <i>Planulina ariminensis</i> <i>Rosalina globularis</i> <i>Rosalina</i> sp.1 <i>Rosalina</i> sp.2 <i>Rosalina</i> sp.3	<i>Alliatina</i> sp.1 <i>Ammonia</i> sp.1 <i>Ammonia perlucida</i> <i>Buccella haroui</i> <i>Buccella tenerima</i> <i>Buccella</i> sp.1 <i>Cancris</i> sp.1 <i>Cancris panamensis</i> <i>Cancris sagru</i> <i>Cibicoides crebbii</i> <i>C. mckamui</i> <i>C. pseudoungerianus</i>	<i>Cibicidulites</i> sp.1 <i>Cibicidulites</i> sp.2 <i>Cibicidulites</i> sp.3 <i>Cibicurbis hitchcockiana</i> <i>Cibicurbis</i> sp.1 <i>Cibicurbis</i> sp.2 <i>Elphidium crispum</i> <i>Epistominella pacifica</i> <i>E. pulchella</i> <i>Lenticulina americana</i> <i>Lenticulina rotulata</i> <i>Lenticulina</i> sp.1 <b><i>Pararot. magdalensis</i></b>	<i>Pyrgo</i> sp.1 <b><i>Q. lanarckiana</i></b> <i>Quinqueloc. semibulatum</i> <i>Spiratoculina</i> sp.1 <i>Tritulacina</i> sp.1	<b><i>Ammonia tepida</i></b> <i>Ammonia</i> sp.1 <i>Cyroidina aliformis</i> <i>Cyroidina soldani</i> <i>Cyroidina</i> sp.1 <i>Valvulineria bradyana</i> <i>V. venezuelana</i> <i>Valvulineria</i> sp.1		
INFAUNAL MORPHOGROUPS	Rounded planispiral	Pseudoplanispiral	Conical/cylindrical	Spherical	Flattened conical/cyl.	Ovoid	Agglutinating
	<i>Astrononion</i> sp.1 <b><i>Cribroelph. poeyanum</i></b> <i>Cribroelphidium</i> sp.1 <i>Elphidium incertum</i> <i>Elphidium spinatum</i> <i>Melonis</i> sp.1 <i>Melonis</i> sp.2 <i>Melonis</i> sp.3 <i>Melonis</i> sp.4 <i>Nonion depressulum</i> <i>Protelphidium</i> sp.1 <i>Protelphidium</i> sp.2	<b><i>P. pizarrensis</i></b> <i>Pseudononion</i> sp.1 <i>Pseudononion</i> sp.2 <i>Nonionella miocenica</i> <i>Nonionella</i> cf. <i>twyida</i> <i>Nonionella</i> sp.1	<b><i>Bulinina marginata</i></b> <i>Bulinina pagoda</i> <i>Bulinina rostrata</i> <i>Bulinina</i> sp.1 <i>Bulinella curta</i> <i>B. elegantissima</i> <i>Fursenkonia pontoni</i> <i>Fursenkonia</i> sp.1 <i>Globobulimina pyrula</i> <i>Globobulimina</i> sp.1 <i>Nodosaria catesbyi</i> <i>Nodosaria</i> sp.1 <i>Nodosaria</i> sp.2 <i>Nodosaria</i> sp.3 <i>Reussella spinulosa</i> <i>Stainforthia</i> sp.1 <i>Stainforthia</i> sp.2 <i>Stifosomella</i> sp.1 <i>Trifarina</i> sp.1 <i>Uvigerina peregrina</i> <i>Uvigerina</i> cf. <i>galloway</i> <i>Uvigerina</i> sp.1 <i>Uvigerina</i> sp.2	<i>Globocass. subglobosa</i> <i>Lagena laevis</i> <i>Lagena setigera</i> <b><i>Lagena striata</i></b> <i>Oolina hexagona</i> <i>Pullenia bulloides</i>	<i>Bifarina</i> sp.1 <i>Bolivina advena</i> <i>Bolivina</i> cf. <i>advena</i> <i>Bolivina bicostata</i> <i>Bolivina floridana</i> <i>Bolivina multicostrata</i> <b><i>Bolivina pisciformis</i></b> <i>Bolivina plicata</i> <i>Bolivina serrata</i> <i>Bolivina sinuata</i> <i>Bolivina spathulata</i> <i>Bolivina</i> sp.1 <i>Bolivina</i> sp.2 <i>Bolivina</i> sp.3 <i>Brizalina oenariensis</i> <i>Brizalina alata</i> <i>Brizalina argentea</i> <i>Brizalina inflata</i> <i>Brizalina spissa</i> <i>Brizalina</i> sp.1 <i>Fronducularia</i> sp.1	<i>Cassidulina californica</i> <i>Cassidulina laevigata</i> <i>Cassidulina</i> cf. <i>laevigata</i> <i>Cassidulina neocarinata</i> <i>Fissurina</i> sp.1 <i>Fissurina</i> sp.2 <i>Fissurina</i> sp.3 <i>Pseudoparrella exigua</i> <i>Siphonina tenuicarinata</i>	<i>Figuerella</i> sp.1 <i>Karverella</i> sp.1 <i>Milhamina</i> sp.1 <b><i>Textularia panamensis</i></b> <i>Textularia soldani</i> <i>Textularia truncata</i> <i>Textularia</i> sp.1 <i>Textularia</i> sp.2 <i>Textularia</i> sp.3 <i>Textularia</i> sp.4 <i>Textularia</i> sp.5 <i>Vernethina</i> sp.1



**Figure 3.** *Pseudononion pizarrensis* (a: spiral view, b: edge view, c: umbilical view) belonging to the Pseudoplanispiral morphotype.

with runoff input; the second, Rounded planispiral group, on the contrary, consists of species tolerant of hypo- to hyper-saline waters.

The Rounded trochospiral and Rounded planispiral morphotypes include, in a very large percentage, respectively *Ammonia tepida* and *Criboelphidium poeyanum*. These are both euryhaline species that are tolerant of hypo- to hyper-saline conditions (Boltovskoy, 1976; Murray, 1991). The two morphotypes themselves are here considered as salinity indices, although salinity is normally a limiting factor at species level.

The Planoconvex morphogroup (present with an average of 26,8%) is mostly constituted by *Hanzawaia concentrica* and, in a lower amount, by *Rosalina* spp., *Asterigerinata* spp. and *Cibicides* spp. The species belonging to these three last genera (sessile species) may permanently or temporarily attach their test to the substrate (both sediment and seaweeds/plants) by means of an organic glue (Langer, 1993). This allows them to tolerate relatively high energy of the waters (Corliss & Fois, 1990). Planoconvex specimens are associated with medium/coarse grain size sediments.

The Biconvex morphotype is found with significant percentages (about 19% on average) in most of the samples throughout the Canoa Formation (Tab. 3). This may be due to the wide adaptation of the species that can crawl on hard/coarse sediments or live free on mobile/fine sediments, being either organic detritus feeders or herbivores (Murray, 1991; Tab. 1 and 2).

The Conical/cylindrical morphotype is present with average value of 17.1%. This group reaches more notable values of abundance with an average of 26.7% only in the lower half of the succession (up

to sample 43), and is generally associated with fine grained sediments. The most abundant species grouped here, are *Bulimina marginata* and *Uvigerina peregrina*, opportunistic taxa which well tolerate lower oxygen levels. This group itself can be used as a proxy for dysaerobic conditions at bottom.

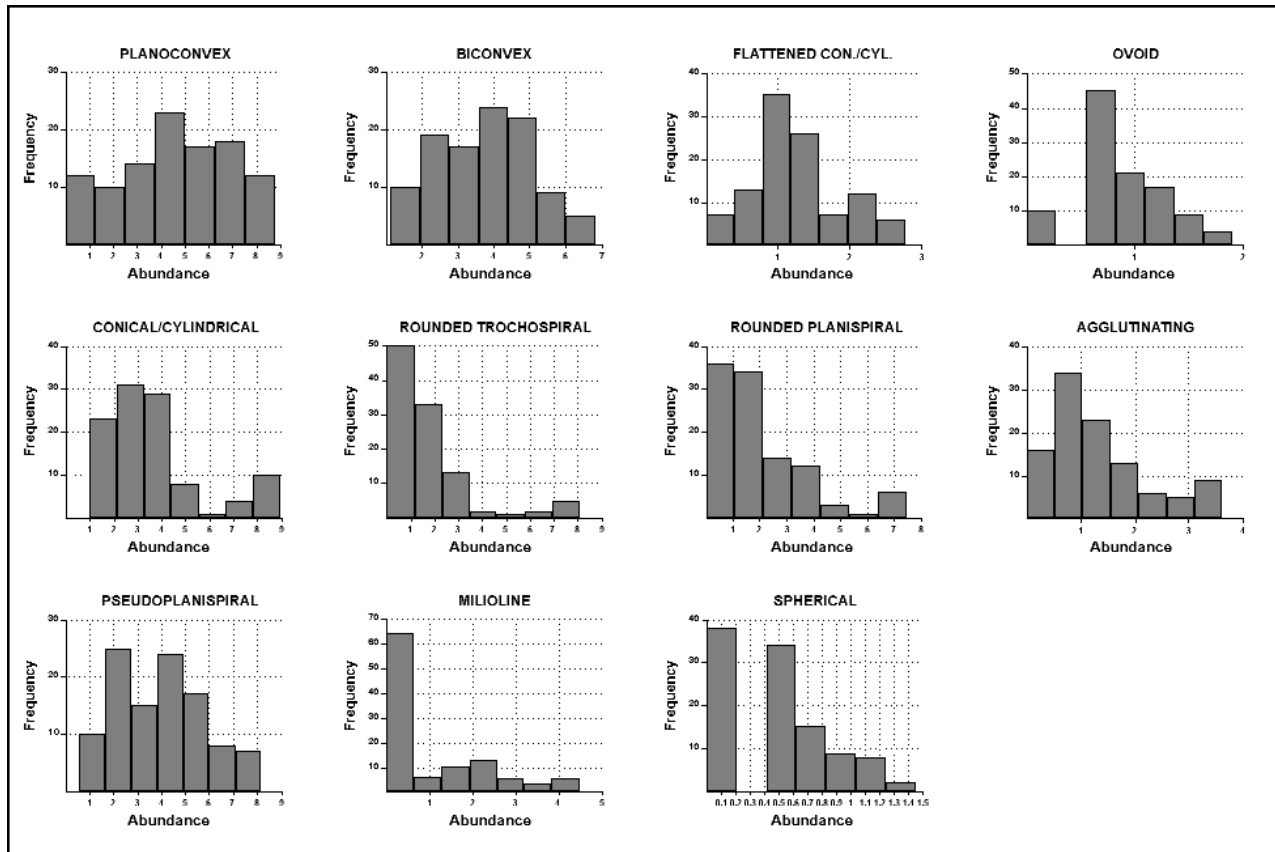
The milioline morphotype in the Canoa Formation is hardly present with average value of 2.5% and is linked to relatively coarse sediments. The species of this group are indicative of free living life on the substrate or crawling on seaweeds and plants, showing an epiphytic adaptation (Duleba *et al.*, 1999).

All the agglutinating specimens, mainly represented by species belonging to the Textulariidae, are present with very low percentage (average value of 2.6%) in the studied samples, and can be referred to the Morphogroup C of Jones & Charnock (1985). This group is characterised by an elongated test and infaunal style of life. Since foraminifers with an agglutinated wall are able to sort out grains to build their test in a variety of grain-size sediments, unlike most infaunal species, they can live also within relatively coarse sediments (Murray, 1991).

Agglutinated tests are more fragile than the porcellanaceous and hyaline ones, and because of their fragility they may not be present in the fossil assemblages, or may be present in lower amounts with respect to the original assemblage. Therefore this morphogroup has not been here considered for palaeoecological purpose. Murray (1991) asserts that the agglutinating foraminifers have a controversial ecological significance, and the occurrence of agglutinating fossil specimens is most likely linked to diagenetic processes rather than to particular environmental characters.







**Figure 4.** Frequency histograms for the percentage abundances of each morphogroup. Data have been transformed according to the expression:  $x_1 = \sqrt{x}$ .

The histogram of the Pseudoplanispiral morphogroup presents a clear bimodal distribution. The first peak indicates that samples with low abundance (abundance class from 2.8 to 7.5%) are the most frequent. The second frequency peak corresponds to samples with medium abundance values (abundance class 14.6-24.1%) (Fig. 4). The species belonging to this morphogroup (mainly *Pseudonion pizarrensis* and *Nonionella miocenica*) which have a good fitness to low and normal salinity conditions (see Morphogroup of the Canoa Formation), undergo an appreciable reduction in the uppermost samples, while in the same samples the Rounded trochospiral and Rounded planispiral morphogroups (hypo- to hyper-saline species *Ammonia tepida* and *Criboelphidium poeyanum* respectively) become dominant (Fig. 5). The reduction in the abundance of the Pseudoplanispiral species may be explained by a change in the environment towards hyper-saline conditions which allow *A. tepida* and *C. poeyanum* to become dominant (see Discussion) at the top of the formation (samples 103-111; Fig. 5 and 6).

The other non-normally distributed morphogroups display a positive asymmetry, with the highest frequencies corresponding to low abundance values. The Rounded trochospiral, Rounded planispiral and Conical/cylindrical morphogroups

have a bimodal distribution, with a secondary peak of markedly lower frequencies corresponding to anomalously very high abundance values (abundance classes 47.5-64.7%, 40.7-55.3% and 60.6-79.6% respectively). These distributions can be explained by the influence of limiting factors with anomalous values that favour the abundance of opportunistic, more adaptable, forms (see Benthic foraminifers autoecology and Morphogroups of the Canoa Formation). The Milioline morphogroup is present with very low abundances or is absent, with the exclusion of few samples in which the abundances have values of 10-20%. The most frequent abundance class in fact includes values near 0. The overall low abundance of the milioline group (mainly constituted by warm-water, epiphytic species) may be related both to the lack of vegetation on the substrate or to cool water temperatures, due to the activation of coastal upwelling cells and/or the arrival of cool water currents from northern areas (Landini *et al.*, 2002). The frequency histogram for the Spherical morphogroup shows maximum frequency for the lowest class, representing abundance values practically equal to 0. In fact in the Canoa Formation this morphogroup reaches the maximum value of 2% only in two samples (Tab. 3). Species belonging to the Spherical morphogroup are commonly indicative of deep-water environments:

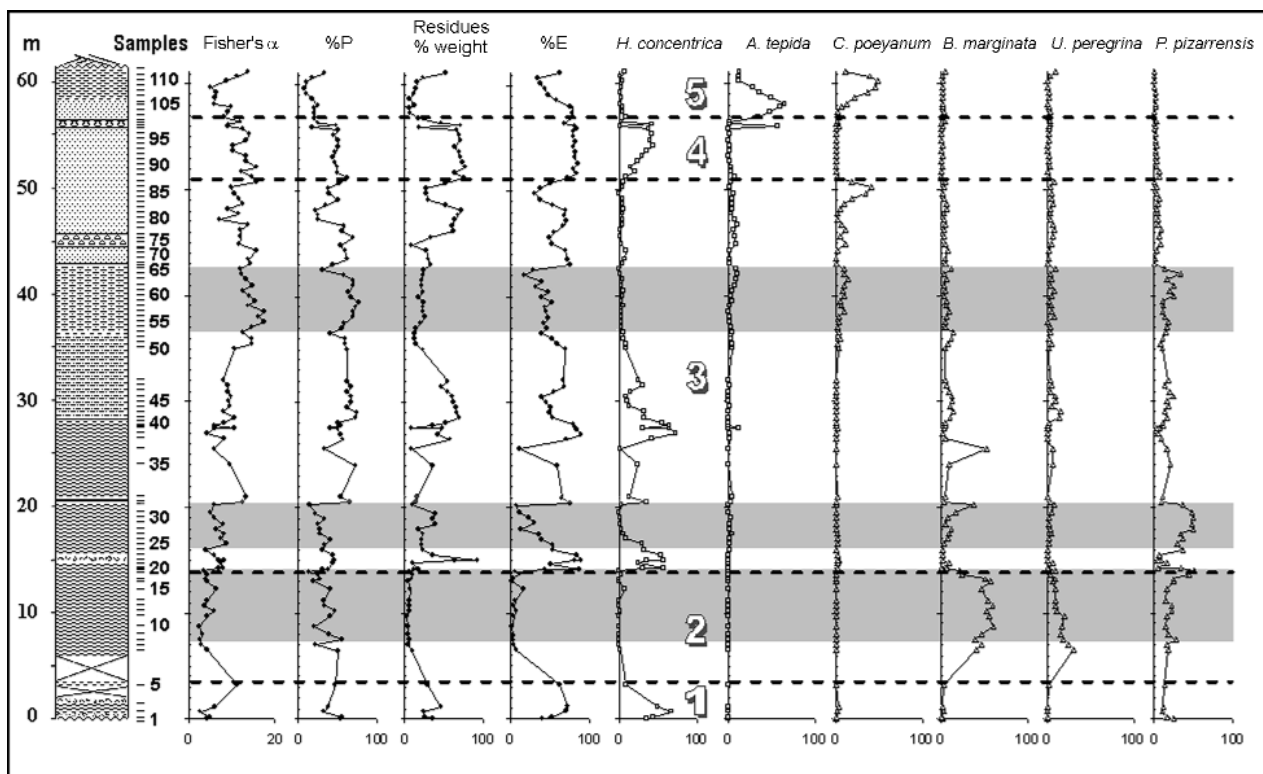


Figure 5. Variations of Fisher's  $\alpha$ , plankton percentage abundance, percentage weight of washed sample residues, epifaunal percentage abundance and of selected species percentage abundance. The five recognized evolutionary phases are separated by dashed lines and numbered, grey intervals indicate the rainy periods. Symbols: open squares: epifaunal species; open triangles: infaunal species.

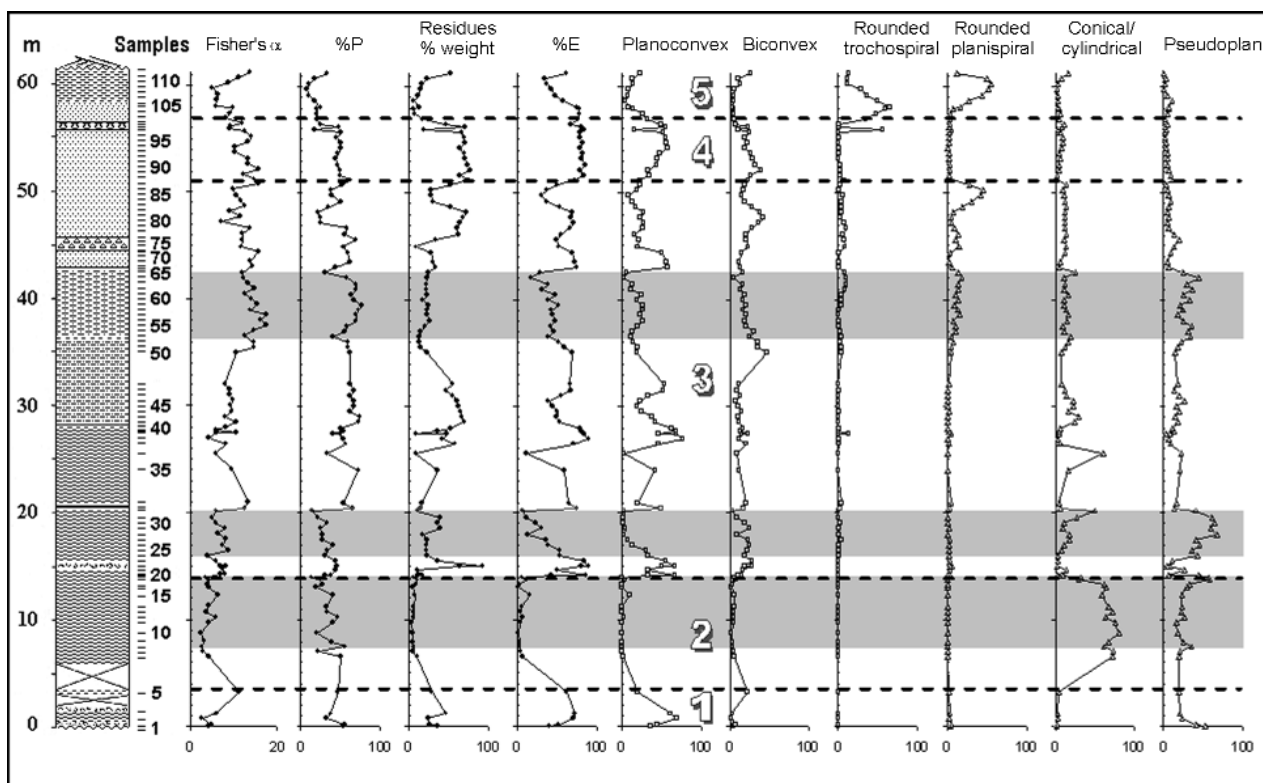


Figure 6. Variations of Fisher's  $\alpha$ , plankton percentage abundance, percentage weight of washed sample residues, epifaunal percentage abundance and of selected morphotypes percentage abundance. The five recognised evolutionary phases are separated by dashed lines and numbered, grey intervals indicate the rainy periods. Symbols: open squares: epifaunal morphogroups; open triangles: infaunal morphogroups.

among the others Corliss & Chen (1988) report for the spherical species depths between 200 and 1600 m and Corliss & Fois (1990) depths down to more than 3000 m, which can explain their very low abundance in the inner shelf sediments of the Canoa Formation.

The Agglutinating morphogroup shows the peak of highest frequencies corresponding to low abundance values (0.27-1.1%). As already pointed out, the abundance of agglutinating specimens can be altered because of their test fragility, therefore this morphogroup has not been considered for the palaeoecological interpretation.

### CLUSTER ANALYSIS

Multivariate analysis, Q-mode cluster analysis grouping samples on the basis of the similarity of their content, has been performed both on the species and on the morphotype percentage data, using the unweighted pair-group average method and Euclidean distance algorithm. The resulting dendrograms show only negligible differences between the two analyses. For palaeoenvironment interpretations, we have chosen to consider the results of cluster analysis on the morphogroups that subdivides the samples into six clusters (Fig. 7), each grouping samples with similar morphogroups assemblage (Tab. 4).

Cluster 1: This is the most numerous sample-cluster, gathering 46 of the analysed 106 samples. In these samples, benthic foraminifers belong to different morphogroups, none of which shows a clear

dominance. The Planoconvex, Biconvex and Pseudoplanispiral morphotypes are equitable and well represented, each attaining medium values higher than 20% (Tab. 4). Also the Conical/cylindrical morphogroup is remarkable, with an average of 12%. Altogether, these samples show a well diversified benthic assemblage with equivalent percentages of epi- and infaunal specimens, which shows normal values of the limiting factors in the marine environment.

Cluster 2: This cluster is the second most dominant: it groups 27 samples (Fig. 7) in which Planoconvex is the dominant morphotype, with average value of 56%. The Biconvex morphotype is also common, averaging 17%. Overall, specimens belonging to the epifaunal morphogroup are clearly predominant in these samples and *Hanzawaia concentrica* is the most common species with an average of about 40%. These samples are characterised concurrently also by coarse grain-size of sediments (in which the washed residues have an average value of the weight percentage sand of about 50%, Figs. 5 and 6).

Cluster 3: The six samples are located in the top-most part of the Canoa Formation. Rounded planispiral, with average value of 48%, is the prevailing morphogroup which includes *Criboelphidium poeyanum* as the most abundant species (40%). The Rounded trochospiral and Planoconvex morphotypes average 16% and 12% respectively (Tab. 4).

Cluster 4: Six samples are grouped here, located

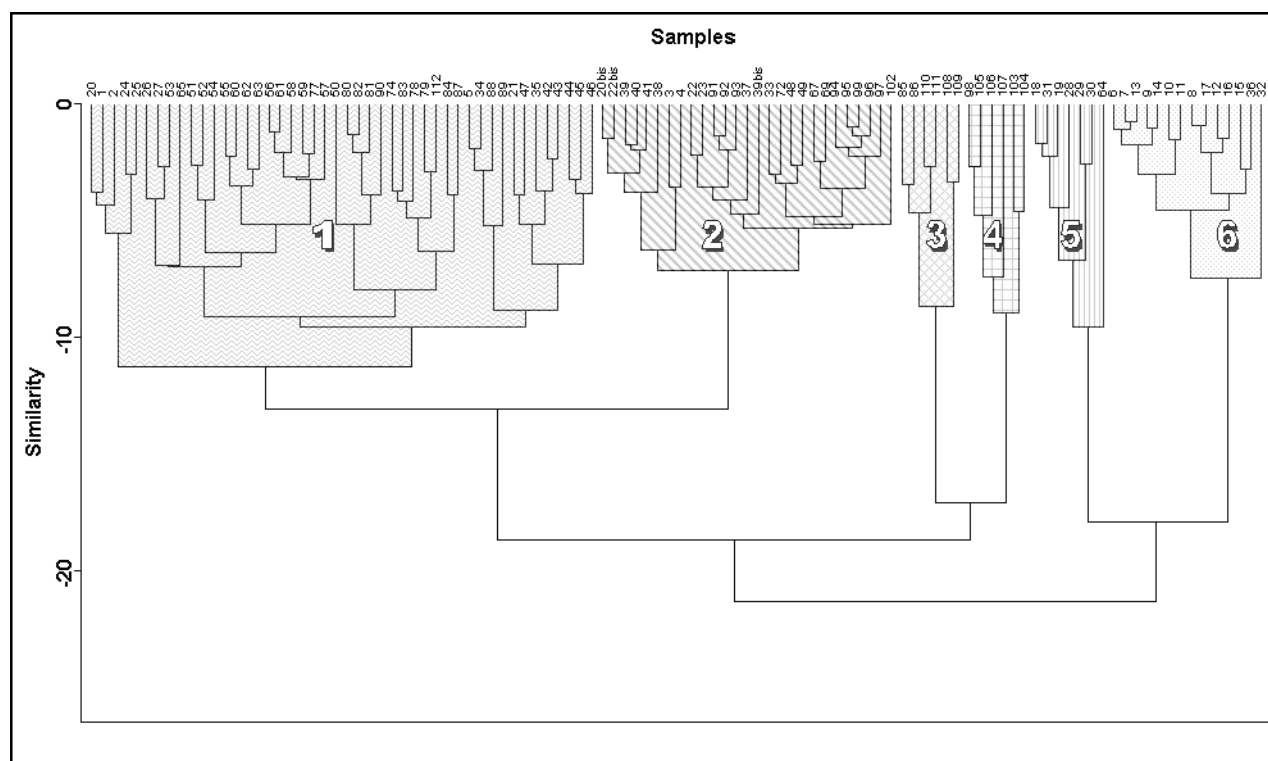


Figure 7. Dendrogram resulting from the Q-mode cluster analysis on the percentage abundances of morphotypes.).

**Table 4.** Minimum, maximum and mean values of the percentage abundances of each morphogroup within each cluster. Morphogroups are listed by decreasing mean abundance within each cluster. (E = Epifaunal; I = Infaunal).

Cluster 1				
	Morphogroup	Minimum	Maximum	Mean
E	Planoconvex	6	45.3	24
E	Biconvex	4.3	46	21
I	Pseudoplanispiral	0.7	52	21
I	Conical/cylindrical	1	29	12
I	Rounded planispiral	0.3	30	7.2
E	Rounded trochospiral	0	13	3.6
E	Milioline	0	20	3.5
I	Agglutinating	0	13	2.6
I	Flattened con./cyl.	0	7.7	2.6
I	Ovoid	0	3.3	1.1
I	Spherical	0	2	0.5
Cluster 2				
	Morphogroup	Minimum	Maximum	Mean
E	Planoconvex	44	76.7	56
E	Biconvex	1.3	32	17
I	Pseudoplanispiral	1	23	7.7
I	Conical/cylindrical	1.3	12	5.5
I	Agglutinating	0	12	3.9
E	Milioline	0	10	3.5
I	Rounded planispiral	0	5.3	2.1
E	Rounded trochospiral	0	13	1.3
I	Flattened con./cyl.	0	3.9	1.1
I	Ovoid	0	2.6	0.9
I	Spherical	0	2.1	0.2
Cluster 3				
	Morphogroup	Minimum	Maximum	Mean
I	Rounded planispiral	43	55	48
E	Rounded trochospiral	2	36	16
E	Planoconvex	6.7	18	12
E	Biconvex	4.7	17	11
I	Conical/cylindrical	2	10	5.4
I	Pseudoplanispiral	0.3	6	3.1
I	Flattened con./cyl.	0	7	2.6
I	Agglutinating	0	2.7	1.3
I	Ovoid	0.3	2	0.9
I	Spherical	0	0.3	0.2
E	Milioline	0	0.3	0.1
Cluster 4				
	Morphogroup	Minimum	Maximum	Mean
E	Rounded trochospiral	35	65	52
E	Planoconvex	4.7	32	17
I	Rounded planispiral	2.3	27	9.8
E	Biconvex	2.3	11	5.3
I	Pseudoplanispiral	1.7	11	5.2
I	Agglutinating	0.3	10	4.3
I	Conical/cylindrical	2.3	6	4
I	Flattened con./cyl.	0.3	2	1.2
E	Milioline	0	4.7	1
I	Ovoid	0	0.7	0.4
I	Spherical	0	0.3	0.1
Cluster 5				
	Morphogroup	Minimum	Maximum	Mean
I	Pseudoplanispiral	44	67	58
I	Conical/cylindrical	8	32	19
E	Biconvex	3.7	24	11
I	Rounded planispiral	0	17	2.9
E	Planoconvex	0.4	4	2.5
E	Rounded trochospiral	0	11	2.4
I	Flattened con./cyl.	0.3	6.7	2
I	Agglutinating	0	2.3	0.9
I	Spherical	0.3	1	0.6
I	Ovoid	0	1	0.6
E	Milioline	0	0	0
Cluster 6				
	Morphogroup	Minimum	Maximum	Mean
I	Conical/cylindrical	49	80	65
I	Pseudoplanispiral	17	41	25
E	Biconvex	1.7	11	4.4
I	Flattened con./cyl.	0	3	1.6
E	Planoconvex	0	9.7	1.4
I	Spherical	0.3	1.4	0.8
I	Agglutinating	0	2.7	0.6
I	Ovoid	0	1.3	0.5
I	Rounded planispiral	0	0.3	0.1
E	Rounded trochospiral	0	0.3	0.1
E	Milioline	0	0.3	0.1

near the top of the section. These are dominated by the Rounded trochospiral morphotype (52%), completely consisting of *Ammonia tepida*, which is the most abundant species. The Planoconvex and Rounded planispiral morphogroups are also common (17% and 10%, respectively).

Cluster 5: This cluster groups 7 samples in which the Pseudoplanispiral morphotype is dominant (average 58%), followed by the Conical/cylindrical (19%) (Tab. 4). *Pseudononion pizarrensis* is here the most abundant species, averaging 48%. Specimens with infaunal adaptation are clearly dominant (average abundance 84%) in these samples, characterised also by fine-medium grain sediment (Figs 5

and 6) .

Cluster 6: Samples included in this cluster are limited to the lower part of the Canoa Formation. Specimens belonging to the Conical/cylindrical morphotype are dominant (average 65%) (Tab. 4). There are also notable amounts of Pseudoplanispiral forms (25%). The most abundant species is *Bulimina marginata* (50%) and the other common forms are *Pseudononion pizarrensis* and *Uvigerina peregrina* (average values of 20% and 13%, respectively). In these samples the overwhelming dominance of infaunal specimens (over than 94%) is concurrent with very fine grain sediments (Figs 5 and 6).

## DISCUSSION

The comparative analyses of the foraminifer assemblages, percentage weight of the sample residues, the relationships among the morphogroups, (Figs. 5), the results of the cluster analysis (Fig. 7) together with data on the autoecology of the species have allowed us to reconstruct microhabitat conditions and to identify changes in the palaeoenvironment of the Canoa Formation through five successive phases (Fig. 5).

1) The lowermost part of the Canoa Formation (samples 1-5, belonging to Clusters 1 and 2), is characterised by relatively coarse sediments (percent sand changes from 24% to 47%) and by a high value of E % (average value about 60%); the percentage of planktonic specimens oscillates between 32% and 55% with an average of 45%, and the Fisher index  $\alpha$  has variable values (from 3 to 11) with an average of 6. The benthic foraminiferal assemblage is clearly dominated by the Planoconvex morphogroup (Tab. 3), indicative of water turbulence. All these features allow us to propose a first phase of the evolutionary history of the basin characterised by normal values of salinity and by rather high energy regime, linked to the initial transgression of marine waters.

2) From sample 6 to 19, belonging to Clusters 5 and 6, the percent sand sharply decreases (with values from 3% to 10% and an average of 6%), as well as the percentage of epifauna (oscillating from 3% to 16%, with an average value of about 6%); the planktonic percentage is also lower, oscillating from 10% to 50%, with an average of about 33%, and the diversity values are constantly low, from 3 to 6 (average  $\alpha = 4$ ). According to Murray (1991) values of a lower than 5 are typical of stressed environments. The benthic foraminiferal microfauna is here strongly dominated by infaunal morphogroups (Tab. 3), in particular by the Conical/cylindrical morphotype and secondly by the Pseudoplanispiral type. Two of the most abundant species in this interval, *Bulimina marginata* and *Uvigerina peregrina*, are considered as opportunistic species tolerating low-oxygen conditions. *Pseudonion pizarrensis* is the third most abundant species. In this study we consider this taxon indicative of hypo-salinity since it shows a pattern of the percentage abundance opposite to that of the Rounded trochospiral/Rounded planispiral morphogroups, which signify hyperhaline conditions (Fig. 6).

According to Bernhard (1986) and Jorissen *et al.* (1995), in oxygen depleted environments infaunal species and morphotypes are normally dominant over the epifaunal ones. This interval therefore indicates a period of poor communication with the open ocean during which low amount of turbulence may have favoured water stratification, oxygen depletion at the sea floor and fine grained sedimentation. A further cause of the low oxygen level is the oxi-

dation of abundant organic matter carried in by rivers owing to more intensive transport activity, linked to periods of major tectonic movements, or because of more intensive runoff activity, linked to rainy climate. A high level of organic matter is supported by the abundance of *Uvigerina peregrina*, a species favouring high organic carbon content, according to Boersma (1984) and Murray (1991). Moreover, the high abundance of *Pseudonion pizarrensis* (averaging 30.2% in the samples 8-19), highlighting rather low values of salinity, possibly suggests a rainy climate period during this second phase.

3) A third phase (samples 20-87, the most of which [39] are grouped in Cluster 1, Fig. 7) is characterised by a gradual increase of the diversity index and of the presence of planktonic specimens, (which both reach the maximum values of the whole succession:  $\alpha = 17.7$  in samples 55 and 57, plankton abundance = 77% in sample 59) with values from 4 to 17.7 and average of 10 for the diversity index, and from 15% to 77%, average 50% for planktonic percentage. Percent sand shows wide oscillations, spanning from 8% to 93% with an average of 35%. Epifaunal abundances also show oscillating values: most samples have a rather good balance between epifaunal and infaunal forms, with only some short intervals dominated by either group. It is possible to distinguish within this phase two shorter intervals of major abundance of the Pseudoplanispiral morphotype (Fig. 6). Particularly the first interval, from sample 24 to 32, is characterised by a remarkable abundance of Pseudoplanispiral specimens, on average 50%, as well as by rather low values of diversity, plankton abundance, sand and % epifaunal (on average respectively 6.6, 28%, 26% and 30%). While the second interval, from sample 53 to 65, besides a minor dominance of Pseudoplanispiral specimens, with average of about 29%, is characterised by an average value of  $\alpha = 14$  and about 60% of planktonic specimens, by a lower percentage of sand (about 21% on average) and by a minor prevalence of infaunal specimens (average % E = 40%). Tentatively, it is possible to link these intervals to rainy episodes and/or to small oscillations of the sill. Altogether, this large interval is characterised by oscillations, even if weak, of the parameters that well fit in with conditions of basin opening and better marine connections.

4) In the fourth phase the samples (88-102, belonging to Cluster 2, two excluded) are characterised by high amount of sand (average 64%), by the dominance of epifaunal taxa, which present values from 68% to 85% with an average of 80%, and by an average of about 45% of planktonic specimens (values from 18% to 62%). The diversity index has high values (varying from 9 to 16 and on average

about 12), Planoconvex species are the most common, namely *Hanzawaia concentrica* and *Rosalina* sp.p.. The dominance of the Planoconvex morphotype and the high percent sand indicate an increase of energy in the basin. On the whole this can be considered an interval of good communication with the ocean, characterised by favourable environmental conditions that promote high taxonomic diversity.

5) Samples 103-111 of the upper part of the Canoa Formation, are grouped in the Clusters 3 and 4 (excluding the anomalous topmost sample 112) and consist of fine-grained sediments (the average % sand is about 13%). These samples contain very few planktonic foraminifers (oscillating from 7% to 25% and with average of 16%) and are characterised by decreased diversity values (average  $\alpha = 8$ ) and by a decreasing trend (from 77% to 35%) of the epifaunal species percentage. The benthic foraminifer associations in this interval (Fig. 5) are decidedly dominated first by *Ammonia tepida* (samples 103-107, Cluster 4) with values from 35% to 65% and successively (samples 108-111, Cluster 3) by *Criboelphidium poeyanum* with values from 36% to 48%. These taxa, significant of shallow waters, are euryhaline species and their dominance, concomitant with the absence of the low salinity pseudoplanispiral *Pseudononion pizarrensis*, indicates anomalous salinity conditions, most likely in a hyper-saline lagoon, which together with the very low P/(P+B) points out the complete closure of the communication of the basin with the ocean.

Considering the whole succession *Hanzawaia concentrica*, always associated with coarse grained sediments and with other species with an attached life style, has been here considered an index of rather turbulent waters. The presence, even if with oscillating percentages, in the lower and middle part of the succession (beginning from the sample 6 to the sample 65, up to about 43 m) of Pseudoplanispiral species, which are tolerant of low salinity values, may be consistent with fluvial input linked to more rainy periods. Subsequently, from 43 m to the top (sample 67 to 112), the presence of the Pseudoplanispiral morphogroup decreases from an average percentage of 26% to 5%, which possibly indicates a reduction of more rainy weather and of river influx.

## CONCLUSIONS

A detailed study has been performed on the benthic foraminifer assemblage from the Pliocene Canoa Formation with the aim to investigate the palaeoecological evolution of the basin: species and morphogroup associations have been considered for 106 samples from the succession, collected every fifty centimetres, when possible. The obtained data have been elaborated by means of descriptive and multivariate analyses and compared with the autoecolo-

gy of the species.

This study has emphasized the peculiar palaeoenvironmental significance of some species and morphogroups. In particular *Hanzawaia concentrica* may be considered an index of high energy. *Ammonia tepida*, *Criboelphidium poeyanum* and *Pseudononion pizarrensis* have been assigned a meaning of hyper-salinity to the first two taxa and of hypo-salinity to the latter. Since the above mentioned species are the almost exclusive components of the respective morphogroups, we consider these morphotypes themselves indices of salinity levels: i.e., Rounded trochospiral and Rounded planispiral signify hyper-salinity and Pseudoplanispiral means hypo-salinity. Also the Conical/Cylindrical morphogroup, made up almost exclusively of *Bulimina marginata* and *Uvigerina peregrina*, is itself an index of low oxygen levels at the sea floor.

The results of this integrated analysis have allowed us to reconstruct the characteristics of the microhabitat and to depict the palaeoenvironmental evolution of the Canoa Formation. Multivariate analysis performed on morphotypes and on species has provided similar results, which confirms the use of morphotypes as a reliable tool for palaeoecological interpretations.

The foraminiferal associations confirm the deposition of the Canoa Formation in a shallow coastal basin and show the existence of a tectonic oscillating sill which, at intervals, partially isolated the basin from the ocean. The variation of the planktonic/benthic ratio has been here considered not as the expression of the minimum variations of the water depth, but as a good indicator of the connections between the basin and the open ocean. The vertical tectonic movements of the sill are believed to be the major cause of changes in palaeoenvironment parameters and consequently of the variations of the abundances and of the interrelationships of the species in the assemblage.

On the basis of the presence and of the fluctuations in the abundance of significant species, it has been possible to recognise variations in salinity that we have interpreted as due to alternating periods of humid and dry climate. In the lower and middle part of the succession (Fig. 6) in fact the three recognizable intervals characterised by high percentages of the pseudoplanispiral species *Pseudononion pizarrensis*, are related to rainy periods and to relevant freshwater influxes. In the upper part of the succession, the successive interval characterised by scarce presence of *P. pizarrensis* and contemporaneously by dominance of *A. tepida* and *C. poeyanum*, attests to increasing of aridity and of the consequent evaporation rate.

On the whole the characteristics of the microfungal associations have made it possible to individuate five major phases in the palaeoenvironmental

evolution (Fig. 5).

An initial transgressive phase led to the beginning of deposition in a shallow coastal basin. A second phase saw the uplift of a tectonic sill causing relative isolation of the basin. During this period the reduced ingress of oceanic waters hindered the ingress of planktonic foraminifers and the concurrent reduced energy established water stratification in the basin, with limited oxygen conditions at the sea floor. A third phase was characterised by a sinking trend of the sill with consequent restored good communication with the ocean, abundant ingress of planktonic forms, renewed energy and re-oxygenation of the waters, favouring, possibly in rather good environmental conditions, a high microfaunal diversity. During this phase, climatic oscillations can be recognised with the occurrence of rainy periods, causing stronger runoff of fresh-water from continent into the basin. During a fourth phase a lowering of the tectonic sill has favoured the complete communication with the open ocean, as pointed out by the abundance of planktonic foraminifers, by the high diversity index and by the remarkable abundance of the Planoconvex morphogroup indicative of a rather high level of energy in the basin. The successive final phase saw the complete isolation of the basin with a substantial lowering of water depth. The upper samples of the succession are characterised by an oligotypic lagoonal assemblage with species indicative of hyper-saline waters indicating strong evaporation, linked to the lack of connection with ocean waters and to dry climate conditions.

At present it is difficult to discern, on the basis of the available foraminifer data, whether during this period the tectonics influenced the evolution of the basin more than the global eustatic oscillations. In any case, the continuing regressive trend later led to final emersion. Further multidisciplinary studies would be required in the future to better understand the detailed moments of the whole evolution history of the basin.

#### ACKNOWLEDGMENTS

The authors are very grateful to Prof. Elena Ferrero of the Department of Earth Sciences Torino University, and to Prof. Michael A. Kaminski of the Department of Earth Sciences, London University, for critically reviewing the paper and the useful suggestions for improving English. The research has been supported by MIUR grants assigned to G. Valleri.

#### REFERENCES

- Bandy, O.L., 1961. Distribution of foraminifera, radiolaria and diatoms in sediments of the Gulf of California. *Micropaleontology*, **7**, 1-26.
- Bernhard, J.M., 1986. Characteristic assemblages and morphologies of benthic foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene. *Journal of Foraminiferal Research*, **16**, 207-215.
- Berry, E.W., 1928. A new *Nonion* from Peru. *Journal of Paleontology*, **1**, 269-270.
- Bianucci, G., Cantalamessa, G., Landini, W., Ragaini, L. & Valleri, G., 1997. Paleontological and sedimentological observation on the Canoa Formation (Manabí Basin, Ecuador). *Bollettino della Società Paleontologica Italiana*, **36** (1-2), 85-96.
- Blow, W.H., 1969. Late Middle Eocene to Recent Planktonic Biostratigraphy. In: P. Brönnimann & H.H. Renz (eds.), *Proceedings of the First International Conference on Planktonic Microfossils*, Geneva, 199-422.
- Boersma, A., 1984. *Handbook of common Tertiary Uvigerina*. Microclimates Press, Stony Point, New York, 207 pp.
- Boltovskoy, E., 1976. Distribution of Recent foraminifera of the South American region. In: R.H. Headley & C. G. Adams (eds.), *"Foraminifera"*, vol. **2**, 171-236, Academic Press, London.
- Boltovskoy, E., Scott, D.B. & Medioli, F.S., 1991. Morphological variations of benthic foraminiferal tests in response to changes in ecological parameters: a review. *Journal of Paleontology*, **65** (2), 175-185.
- Boltovskoy, E. & Wright, R., 1976. *Recent foraminifera*. Junk, The Hague, 515 pp.
- Cantalamessa, G., Di Celma, C., Bianucci, G., Carnevale, G., Ragaini, L., Landini, W. & Valleri, G., 2000a. Pleistocene sediments along the Central Ecuador convergent margin. *II Congreso Latinoamericano de Sedimentología, y VIII Reunion Argentina de Sedimentología, Mar del Plata* (Ar.). Resúmenes, 57-58.
- Cantalamessa, G., Di Celma, C., Bianucci, G., Carnevale, G., Ragaini, L., Landini, W. & Valleri, G., 2000b. A Plio-Pleistocene composite third order depositional sequence generated by ridge subduction along the Ecuadorian convergent margin. *Proceedings of 15th Australian Geological Convention*, Sydney.
- Cantalamessa, G., Di Celma, C., Cimarelli, M., Bianucci, G., Landini, W., Ragaini, L. & Valleri, G., 1999. The Canoa Formation (Manabí Basin, Western Ecuador): an example of Late Pliocene shelf asymmetrical sequence. *Proceedings of the 14th Argentine Geological Congress, Salta* (Ar.), **1**, 496-499.
- Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. *Nature*, **314**, 435-438.
- Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. *Marine Micropaleontology*, **17**, 195-236.
- Corliss, B.H. & Chen, C., 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. *Geology*, **16**, 716-719.
- Corliss, B.H. & Fois, E., 1990. Morphotype analysis of Deep-Sea Benthic Foraminifera from the Northwest Gulf of Mexico. *Palaeos*, **5**, 589-605.
- Di Celma, C., Ragaini, L., Cantalamessa, G. & Curzio, P., 2002. Shell concentrations as tools in characterizing sedimentary dynamics at sequence-bounding unconformities: examples from the lower unit of the Canoa Formation (Late Pliocene, Ecuador). *Geobios*, Mem. Spec., **24**, 72-85.
- Duleba, W., Debenay, J.P., Eichler, B.B. & de Mahiques, M.M., 1999. Holocene Environmental and water Circulation Changes: Foraminifers Morphogroups

- Evidence in Flamengo Bay (SP, Brasil). *Journal of Coastal Research*, **15**, 554-571.
- Hammer, O., Harper, D.A.T., & Ryan, P.D., 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, **4** (1), 9 pp.  
[http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm).
- Jones, R.W. & Charnock, M.A., 1985. "Morphogroups" of agglutinating foraminifera, their life positions and feeding habits and potential applicability in paleoecological studies. *Revue de Paléobiologie*, **4**, 311-320.
- Jorissen, F.J., de Stigter, H.C. & Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Marine Micropaleontology*, **22**, 3-15.
- Kitazato, H., 1994. Foraminiferal microhabitats in four marine environments around Japan. *Marine Micropaleontology*, **24**, 29-41.
- Landini, W., Bianucci, G., Carnevale, G., Ragaini, L., Sorbini, C., Valleri, G., Bisconti, M., Cantalamessa, G. & Di Celma, C., 2002. Late Pliocene fossils of Ecuador and their role in the development of the Panamic bioprovince after the rising of the Central American Isthmus. *Canadian Journal of Earth Sciences*, **39**, 27-41.
- Langer, M., 1993. Epiphytic foraminifera. *Marine Micropaleontology*, **20**, 235-265.
- Lonsdale, P., 1978. Ecuadorian subduction system. *Bulletin of the American Association of Petroleum Geologists*, **62**, 2454-2477.
- Mancin, N. & Pirini, C., 2002. Benthic and planktonic Foraminifera of the Paleogene Epiligurian successions (Northern Apennines, Italy): a tool for palaeobathymetric reconstruction. *Bollettino della Società Paleontologica Italiana*, **4** (2-3), 187-213.
- Miller, K.G., Rufolo, S., Sugarman, P.J., Pekar, S.F., Browning, J.V. & Gwynn, D.W., 1997. Early to middle Miocene sequences, systems tracts, and benthic foraminiferal biofacies, New Jersey coastal plain. In: K.G. Miller & S.W. Snyder (eds.), *Proceedings ODP, Scientific Results*, 150X: College Station, TX (Ocean Drilling Program), 361-373.
- Murray, J.W., 1973. Distribution and Ecology of Living Benthic Foraminiferids. Heinemann, London, 288 pp.
- Murray, J.W., 1976. A method of determining proximity of marginal seas to an ocean. *Marine Geology*, **22**, 103-119.
- Murray, J.W., 1991. Ecology and Palaeoecology of Benthic Foraminifera. Longman, Harlow, 397 pp.
- Phleger, F.B., 1960. Ecology and Distribution of Recent Foraminifera. Johns Hopkins Press, Baltimore, 297 pp.
- Severin, K.P., 1983. Test morphology of benthic foraminifera as a discriminator of biofacies. *Marine Micropaleontology*, **8**, 65-76.
- Sen Gupta, B.K. & Machain-Castillo, M.L., 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology*, **20**, 183-201.
- Sheppard, G., 1930. Geology of Southwest Ecuador. *Bulletin of the American Association of Petroleum Geologists*, **14** (3), 263-309.
- Van Morkhoven, F.P.C.M., Berggren, W.A. & Edwards, A.S., 1986. Cenozoic cosmopolitan deep-water benthic foraminifera. *Bulletin des Centres de Recherches Exploration-production Elf-Aquitaine*, Memoir **11**, 421 pp.
- Whittaker, J.E., 1988. Benthic Cenozoic Foraminifera from Ecuador. British Museum (Natural History), London, 194 pp.

