Macrofauna associations and formation of shell concentrations in the Early Eocene Roda Formation (southern Pyrenees, Spain)

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The invertebrate macrofauna (mainly molluscs) of the Early Eocene Roda Formation (southern Pyrenees, Spain) is reported and classified in seven biofacies associations, representing ecologically related groups of macro-invertebrates of shallow marine fan-delta environments ranging in depth from intertidal mudflat to shallow carbonate shelf settings (maximum water depth c. 60 m). The most common association is indicative of mixed siliciclastic-carbonate substrates with the characteristics of an abandonment surface in shallow subtidal settings above wave base. The second most frequent biofacies association is found in subtidal normal marine outer-bay carbonate environments with a relatively low sedimentation rate. However, the most prominent associations, although seldomly occurring, are a (par)autochtonous polytypic coral-mollusc hardground association on top of the last major fandelta sandstone body, an autochtonous monotypic oyster association adapted to soft muddy bottoms representing a time span of c. 500 years, and a parautochtonous (probably) brackish water, intertidal mudflat association dominated by Potamididae. The occurrence of the associations is related to the autocyclic shifting of depocentres, waterdepth, and the palaeotopography of the seafloor as evident from lateral transitions between biofacies associations. This facilitated the formation of calcareous horizons of restricted spatial extent. These are explained as a response to local starvation of clastic sediment supply rather than being a manifestation of relative sea-level changes.

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Introduction

The relation of a fossilised invertebrate macrofauna with the palaeoenvironment in which it occurred (which includes substrate, water depth, temperature, and salinity) has been the subject of intensive research (Stanley, 1970; Seilacher, 1984; Goldring, 1991; Kidwell & Bosence, 1991; Alexander et al., 1993 and numerous references therein). Deductions on the sensitivity to environmental factors are for example based on the stratification of shell concentrations (Kidwell, 1991), the morphology of preserved hard parts, the character of the sediment in which the fauna is found, cooccurring species, and life position of the animal if found in undisturbed sediments. Shape and general morphology of bivalve shells directly reflect their mode of life (Stanley, 1970; Alexander et al., 1993). The grouping of fossil bivalves into morphological categories enables the recognition of the type of environment in which they lived.

The occurrence of species and their palaeoenvironmental distribution of benthic foraminifers and molluscs in Early Eocene foreland basins along the southern margin of the axial zone of the Pyrenees (the Tremp-Graus and Ager Basins in northern Spain), and the Corbières of southern France and the Paris Basin have been found to be similar in character (Cossmann & Pissarro, 1906, 1913; Doncieux, 1903, 1908, 1911, 1926; de Renzi, 1971 and pers. comm.; Llompart, 1977; Jimenez, 1987). The mollusc fauna of the Roda Formation has so far poorly been described; the occurrence of several mollusc groups was recorded by Gaemers (1978, reported families indicated by (*) in Appendix 1). It has been shown that in Recent intertidal/shallow shelf environments the faunal composition (classified in biofacies) primarily documents variation in substrate type (Meldahl & Flessa, 1989). The purpose of this study is to identify and document the mollusc species of the Early Eocene Roda Formation of the Tremp-Graus Basin (Fig. 1), and to make an attempt to define biofacies associations and relate their distribution to the distribution of lithofacies. A similar approach was used by Llompart (1977) for a part of the Ilerdian Ager Formation.

Invertebrate macrofaunas have been collected from 75 localities (c. 1500 specimens) spread over the stratigraphic sequence of the Roda Formation. Of these, 69 localities served to classify the invertebrate macrofauna of the Roda Formation in 7 biofacies associations. Six sample localities have been omitted from the biofacies association classification. Four were found in a bed which is interpreted as a storm layer and two localities contained too few specimens.

Due to the poor preservation of the macrofossils no good quantitative data are available to define biofacies using the appropriate cluster-analysis technique. Results from a study by Zenetos (1991) showed that, provided that the appropriate techniques are used, binary data (presence-absence) contain enough information and can give as good a picture as quantitative data. Biofacies associations have been recognised based on the combined information obtained from macrofossils and lithofacies characteristics, an approach advocated i.a. by Goldring (1991, 1993). Lithofacies data include information on sedimentary structures, bioturbation, grain size, clast composition, and cementation.

Geological setting and palaeoclimate

The invertebrate macrofauna is found throughout the deposits of the Roda Formation on the eastern side of the Isábena river between the villages of Serraduy and Roda de Isábena. The Early Eocene Roda Formation is part of the siliciclastic fill of the Tremp-Graus Basin (Nijman & Nio, 1975; Figs. 1-2). The basin (with an E-W axis) was connected with the Atlantic Ocean. The Roda Formation crops out along the northeastern margin of the Tremp-Graus Basin. Deposition of the Roda Formation was related to tectonic activity along fault and fold zones of the northern basin mar-



Fig. 1. Palaeogeographic sketch map of the Roda Formation (modified after Martinius & Molenaar, 1991).

gin (Yang & Nio, 1985; Puigdefábregas & Souquet, 1986). Uplifted areas of the axial zone to the North provided the supply of arkosic sand and probably also caused periodic pulses of subsidence. The Roda Formation was deposited on a shallow shelf on the lower fan-delta plain (Nijman & Nio, 1975; Nio, 1976; Nio & Yang, 1983) and is topped by the Morillo Limestone Formation.

The formation is divided in two members, the lower Roda Sandstone Member and the upper Esdolomada Member. The nannoplankton species and benthic foraminifers of the Roda Formation are indicative of a Late Ypresian (Middle Ilerdian to Middle Cuisian) age (Nijman & Nio, 1975; Gaemers, 1978; Puigdefábregas et al., 1985; Jimenez, 1987). The Roda Sandstone Member is characterised by a number of vertically stacked



Fig. 2. Stratigraphic scheme of the Tremp-Graus Basin in the Isábena valley along a N-S section. Erosional surfaces and hiatuses are indicated (modified after Molenaar, 1990).

sandstone bodies (Roda 1 to 4), interbedded with silty marls and thin limestone beds, which were deposited as depositional lobes in the fan delta. Clastic sedimentation was strongly intermittent due to interruptions in the progradation of delta lobes and tidal bars and to the periodic abandonment of the depositional area. The depositional lobes are separated by major non-depositional surfaces, which are typified by hardgrounds or incipient hardgrounds (Molenaar et al., 1988; Martinius & Molenaar, 1991). The Esdolomada Member is characterised by a thick lobate sandstone body at the base overlain by a sequence of thin sandstone beds interbedded in mudstone, which are as a rule capped by a laterally continuous limestone bed. The sandstone bodies are interpreted as tidally influenced shields with a lobate geometry.

During deposition of the Roda Formation, the Tremp-Graus Basin was situated on the margin of the tropics (Gaemers, 1978). Besides the numerous tropical mollusc species, tropical conditions are also reflected by the presence of coral reefs, large benthonic foraminifers (Gaemers, 1978; Jimenez, 1987), calcareous green algae (Gaemers, 1978). A pollen flora includes Taxodiaceae, Nyssaceae, *Sabal*, and Myricaceae, all of which are tropical fresh water coastal swamp dwellers (Gaemers, 1978). Wood fragments of the tree genus *Carapoxylon* (Meliaceae), characteristic of tropical rain forests, have been recovered from the lower part of the Esdolomada Member (Martinius, 1991).

Fossil preservation

The invertebrate macrofauna of the Roda Formation is poorly preserved. Some gastropod and bivalve specimens are found as external moulds, most however are preserved as internal moulds of which many are weathered. Numerous specimens have remained unidentified and many others were identified only with difficulty. However, some groups at the species level form an exception due to the mineralogy of their shell, their mode of life, or their shell morphology.

Shell remains of Neritidae are relatively well preserved because they have a calcitic outer prismatic layer, which is more stable than aragonite found in the outer and 2 inner layers of almost all other gastropod groups (Cox, 1969). Of these other gastropod groups, shell remains are occasionally preserved on the columella and inside parts of the whorls where dissolution is slowest. Bivalve species with mixed aragonite/calcite shells are frequently preserved with parts of the shell. Examples of the mixed aragonitic/calcitic type are the Mytilidae, Pinnidae, Pectinidae, Spondylidae, Ostreidae, Crassatellidae, and Cardiidae (Taylor et al., 1969). No bivalve shell is entirely calcitic, although oysters are calcitic except for a small aragonitic myophore. In general, oysters are best preserved, mostly with their entire shell intact. Shells of the species *Crassatella depressa* are completely calcified during the fossilisation process.

The mode of life of the Cardiidae and Crassatellidae (shallow burrowing deposit feeders) increases the possibilities for their shell preservation and preservation of articulated valves. They are less affected by physical processes (mechanical erosion, boring, encrusting) than epifaunal species and potentially are more quickly covered by sediment. Dissolution of the shell is primarily due to epidiagenesis (chemical solution in sea water). Closed articulated valves indicate a rapid death within the sediment and a quick burial, whereas partly open valves indicate a relatively slow burial and partial exposure to non-buried conditions. The adductor muscles had time to relax; the shell opened but the valves kept being articulated because the ligament was still intact. Particularly Crassatella depressa exhibits these modes of preservation. Heavy isodont dentition (e.g. Spondylus) is an additional factor increasing the probability of preservation with articulated valves. The dentition even prevents disarticulation of valves of epifaunal species after death by rough environmental conditions (e.g. wave action). Mechanical selection occurs in those cases where one of the valves is considerably lighter and smaller. These are more easily transported and more left valves (usually the heavier one) will be found, e.g. Ostrea (Cubitostrea) multicostata. Many molluscs show scars, due to predation, or borings on different parts of their shell. Clionid borings are commonly found in Crassatella depressa and Velates shells and less frequently in shells of Mytilus, Ostrea (Cubitostrea), and Nautilus. Turritellidae are infrequently bored despite the finding of Kelley & Hansen (1993) that consistently preferred prey taxa of naticid gastropods include Turritellidae in addition to Corbulidae, Lucinidae, Carditidae and Crassatellidae.

Weathering of the fossil remains in the meteoric phase during epidiagenesis is most important in the Roda Formation and is due to tectonic uplift of the strata during the late phases of the alpine orogenic event. Many fossil sites occur on abandonment surfaces on top of fan-delta lobes. The sandstones are immature, rather poorly sorted and poorly cemented. Meteoric water penetrates deep, leading to skeletal and matrix dissolution. This caused complete destruction of the fossils.

Biofacies associations

The invertebrate macrofauna of the Roda Formation is classified in 7 biofacies associations of which the characteristics are described. The descriptive term assemblage is used to denote the general accumulation of non-living faunal material; the term association reflects ecological relationships among the preserved portion of former communities (Kidwell & Bosence, 1991). Assemblages can be autochtonous, composed of specimens derived from the local community and preserved in life positions, parautochtonous, composed of autochtonous specimens that have been reworked to some degree but not transported out of their original life habitat (cf. Cadée, 1984), or allochtonous which denotes assemblages composed of specimens transported out of their life habitats and occurring in a foreign substratum (Kidwell et al., 1986). These workers classified fossil concentrations in three end-members. The first type of skeletal concentration is included in the biogenic end-member, the second can be part of the biogenic or sedimentologic end-member, and the third is part of the sedimentologic end-member.

Appendix 1 lists the invertebrate macrofauna and other fossil remains of the Roda Formation. Tables 1-2 summarise the mode of life of the bivalves and gastropods respectively; Table 3 summarises the biofacies characteristics.

Table 1. Mode of life of the occurring bivalve genera. A = deep burrowing deposit feeders, B = intermediate burrowing deposit feeders, C = shallow burrowing deposit feeders, D = byssaly attached suspension feeders (soft substrate), E = recliner suspension feeders (soft substrate), F = mudsticker suspension feeders (soft substrate), G = boring, H = nestling, I = cementing, and J = swimming. Data from literature reviewed by Llompart (1977), and from Cadée (1968), Cox (1969), Stanley (1970, 1972), Stenzel (1971), Savazzi (1982), Seilacher (1984), and Alexander et al. (1993).

Name	Α	В	С	D	Ε	F	G	Н	Ι	J
Nucula			x							
Nuculana			×							
Mytilus				×						
Botula							×			
Pinna						×				
Chlamys										×
Spondylus									×	
Lima										×
Ostrea									×	
Crassostrea					×					
Lucina	×									
Pseudomiltha	×									
Corbis					×					
Diplodonta		×								
Chama									×	
Cardita			×							
Crassatella			×							
Nemocardium			×							
Trachycardium			×							
Mactra		×								
Libitina								×		
Bicorbula	×									
Teredina	×									
Teredo							×			
Pholadomya	×									
Arcacea				×	×					
Veneridae			×							

Name	Α	В	С	D	
Velates	×		······································	<u></u>	
Nerita	×				
Turritella			×		
Architectonica	×				
Vermetus			×		
Tympanotonos	×				
Pirenella	×				
Pyrazus	×				
Campanile	×				
Sigmesalia	×				
Tibia	×				
Terebellum	×				
Amaurellina		×			
Naticidae		×			
Cassidaria	×				
Clavilithes		×		×	
Athleta		×			
Volutilithes		×			
Lyria		×		×	
Fusidae		×			

Table 2. Mode of live of the occurring gastropod genera. A = browsers on algae and detritus, B = predators, mostly on bivalves, C = ciliary detritus feeder, and D = scavenger. Data from literature reviewed by Llompart (1977), Wenz (1938), Ivany et al. (1990), and Kelley & Hansen (1993).

Table 3. Main	characteristics of	the seven	biofacies a	ssociations	recognised.
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Bio- facies	dominant species	substrate	energy conditions	sediment supply rate	water depth (m)	environmental interpretation
1	Mytilus inflatus Spondylus hispanicus Cardiacea	firm sand	high, above wave base	low	10	shallow subtidal normal marine above wave base with clear water
2	<i>Turritella dixoni</i> Corbulidae	sandy-silt and mud	below fair weather wave base	relatively high	20-60	subtidal normal marine
3A	Goniaraea elegans Crassatella depressa	hard	rather high	very low	< 10	open marine equilibrium hardground community
3B	Patallophyllia sp. Crassatella depressa	rather soft	below wave base	low	20-30	open marine
4	Crassostrea rarilamella	very soft	low	low, mud	< 10	shallow subtidal, normal to slightly brackish marine
5	<i>Clavilithes</i> sp. Naticidae	soft	low, below wave base	low	30-60	normal marine bay
6	Tympanotonos orengae Pyrazus vidali Pirenella figarolense	soft	very low	low	< 5	protected (brackwater?) intertidal mudflat
7	Turritella rodensis	soft	low, occassional storms	moderate	40	sheltered normal marine interdistributary bay

Biofacies association 1 (Mytilus-Spondylus-Cardiidae community)

The invertebrate macrofauna of biofacies association 1 is fou consists of	and at 36 localities and
name:	number of localities:
Serpula sp.	3
Turritella dixoni	10
Turritella dufrenoyi	3
Sigmesalia sp.	2
Clavilithes sp.	3
Naticidae type 1-2, 4	9
Volutidae type 1	5
Mytilus inflatus	11
Chlamys sp. type 3	2
Spondylus hispanicus	11
Ostrea (Cubitostrea) multicostata	3
Ostrea cf. uncifera	14
Cardita boriesi	3
Cardita sp. type 2	6
Crassatella depressa	10
Trachycardium boriesi	10
Nemocardium corbaricum	14
Bicorbula vidali	2
Teredina sp.	2
Teredo sp.	3
Lucinidae type 4	4
Fusidae type 1	3
Veneridae type 1 cf. Meretrix conilhacensis	8
3 unidentified echinoid species	

Biofacies association 1 is characterised by a *Mytilus-Spondylus*-Cardiidae parautochtonous assemblage. This association is the most widespread in the Roda Formation and belongs to the end-cycle coquina group of shell concentrations (cf. Kidwell, 1991). It is found mainly in the Roda Sandstone Member; six localities have been found in the lower part of the Esdolomada Member. The association is even found in the most proximal areas of the Roda Formation and is characterised by epi- as well as infaunal species. It is common in very sandy packstones or calcareous sandstones with grain sizes varying from very coarse sand to medium-sized sand. The more quartzitic the sand, the less invertebrate species are present. The biofacies association is found on top of arkosic sand beds, often forming a stacked sequence of strata, or on top of thick major siliciclastic influxes; it is never found within mudstone intervals. Thickness of the beds in which the fauna is found varies between 20 cm and 1 m. The substrate was firm and stable and sometimes shows characteristics of an abandonment surface with early lithification (Molenaar & Martinius, 1990; Martinius & Molenaar, 1991). The sediment is homogenised due to intense bioturbation.

The microscopic fauna includes Nummulites, Assilina sp., an occasional myliolid

and/or *Discocyclina*, and pelagic foraminifers (e.g. the epiphyte *Rotalia trochidiformis*). In addition to Bryozoa remains, ostracods, red calcareous algae and crab remains, faecal pellets as well as pellets formed by micritization of bioclasts in shallow water (Flügel, 1978) are found.

Turritellidae are quite well adapted to ecological changes and therefore occupy a wide range of environments (Llompart, 1977). Various Recent species of the Turritellidae can endure high sedimentation rates (Cadée, 1968; Gaemers, 1978); they feed on finely sifted sediments. Consistently preferred prey taxa of naticid gastropods are Turritellidae, Lucinidae, Carditidae, and Crassatellidae. One of the criteria for the selection of prey is based on the ratio of cost versus benefit as expressed by the ratio of thickness versus internal volume of the shell (Kelley & Hansen, 1993). Most unidentified gastropod species are of the turbiniform or trochiform types.

Recent relatives of the genus *Crassatella*, and species belonging to the Cardiidae and Carditidae are inhabitants of subtidal environments on siliciclastic sands. Their robust form is a protection against rough environmental conditions, as is the strong dentition of *C. depressa*. The occurrence of Cardiidae in deeper water is dependent on light penetration. They are substrate sensitive (Alexander et al., 1993) and photosensitive, and can only live in clear water (Cadée, 1968; Jones & Jacobs, 1992). Bay environments are most commonly inhabited by species of the Cardiidae (e.g. Recent *Clinocardium*; Alexander et al., 1993). Species of the Lucinidae live in subtidal environments such as estuaries (Cox, 1969). They are slow but deep burrowing bivalves, living in mixed carbonate-siliciclastic sands (Stanley, 1970). The unidentified bivalve species of the biofacies association vary in outline from trigonal-circular with flat, narrow spaced ribs to very elongated smooth shells, occasionally with thick prosogyrate umbo. Bioerosion of mollusc remains is not uncommon.

Indications for the presence of seagrasses come from indirect evidence. Seagrass communities were an integral component of shallow marine ecosystems in the Tethyan Realm during the Eocene. Maximum depth of occurrence of seagrasses is 10 m due to limiting factors as temperature and light penetration. Wave action is another limiting factor; the worst effects of a storm are freshwater influx and increased turbidity which destroys seagrass beds by siltation (Ivany et al., 1990). Characteristic mollusc taxa of seagrass communities include Carditidae, Lucinidae, Chamidae, certain Ostreidae, and *Velates*. They prefer seagrass covered substrates either for attachment to buried stems by a byssus or for food supply (Stanley, 1970; McCoy & Heck, 1976; Ivany et al., 1990). Many disc-shaped benthic foraminifer species (e.g. *Nummulites*) are frequently used as indicators for seagrasses (Ivany et al., 1990).

The bivalves (e.g. *Mytilus* and two species of *Spondylus*) are indicative of a shallow, subtidal, high-energy type of environment (cf. Cox, 1969; Stanley, 1970). The occurrences of biofacies association 1 reflect periods of slow deposition between the influxes of arkosic sand. The depositional environment is interpreted as a bay with relatively clear water above wave base, and with a partly stabilised, firm substratum with occasional soft patches and crevices, covered by seagrasses. Water depth was most probably around 10 m. Based on the occurrence of benthic foraminifers, Jimenez (1987) interpreted the depositional environment as a shallow (brackish) bay.

Biofacies association 2 (Turritella-Corbulidae community)

The invertebrate macrofauna of biofacies association 2 is found a	t 24 localities and
consists of	
name: r	umber of localities:
Patallophyllia sp.	3
Lunulites bugei	2
Turritella dixoni	4
Turritella dufrenoyi	5
Melanatria sp.	1
Tibia sp.	1
Cassidaria sp.	1
Athleta (Volutispina) sp.	1
Strombidae type 3	1
Naticidae type 5 and 6	3
Volutidae type 3	1
Nucula sp. type 2	2
Ostrea (Cubitostrea) multicostata	3
Corbis sp.	1
Crassatella senessei	3
Cardita sp. type 2	3
Libitina sp. type 2	1
Bicorbula vidali	3
Pholadomya konincki	1
Corbulidae type 2	6
Veneridae type 1 cf. Meretrix conilhacensis	2
2 unidentified bivalve species	3
7 echinoid species	4
Zanthopsis dufouri	2

Biofacies association 2 is characterised by a *Turritella*-Corbulidae parautochtonous assemblage and is found in limestone beds intercalated within mudstone intervals mainly in the lower part of the Roda Sandstone Member. It is dominated by Turritellidae and Corbulidae species. Several occurrences are recorded in strata above the major siliciclastic inputs of the Roda Formation. One occurs in the top part of the Roda Sandstone Member just below its upper boundary, others in siliciclastic limestone beds in the upper half of the Esdolomada Member, mainly in more distal areas. The beds in the lower part of the Roda Sandstone Member are bioturbated bioclastic packstones. They contain siliciclastic components and have a relatively low microfauna diversity. Glauconite, indicative of water depths below 30 m, is found in bioclasts and as individual well rounded grains (probably formed by glauconitisation of coprolites; Hughes & Whitehead, 1987). The lateral continuation of the first and second major input of siliciclastics (sandstone bodies Roda 1 and 2) is formed by limestone beds containing biofacies association 2.

Foraminifer genera include Nummulites and Discocyclina; additionally Assilina, Rotalia trochidiformis (associated with seagrasses on siliciclastic-rich carbonatic mud

substrates; Jimenez, 1987), and ostracods occur.

Turritella dixoni, an infaunal inhabitant of sandy carbonate mud, is one of the most frequently occurring mollusc species of this biofacies association. Cardiidae and Carditidae occur in minor amounts. T. dixoni and Crassatella senessei as well as species of Tibia, Cassidaria, and Pholadomya are deposit feeders and browsers, adapted to soft bottoms in or through which they burrow (Stanley, 1970; Llompart, 1977; Savazzi, 1991). Recent Strombidae (e.g. Tibia) occur exclusively in tropical and subtropical seas, mostly in shallow and very shallow water; fossil Strombidae display the same preferences (Savazzi, 1991). Selective thickening in species members of Tibia has a stabilising function preventing accidental overturning; quick growth is the principal defence against predators, e.g. peeling crabs. The recorded maximum water depth of Strombidae is 30 m (Wenz, 1938; Savazzi, 1991). Species of the Nuculidae are deposit feeders living just beneath the surface of the substratum and are classified as substrate specialists (Stanley, 1970; Alexander et al., 1993). They are restricted to substrates relatively rich in organic matter with a narrow range of grain size, mostly at depths between 10 and 100 m. The unidentified bivalves have inequivalved, subcircular to moderately elongate valves, often with elongated posterior side and well developed umbo, which indicates a burrowing mode of life. The coral Patallophyllia is indicative of soft bottoms.

Larvae of the bryozoa *Lunulites bugei* cannot settle on shifting sand or soft mud bottoms. Larvae settle on a small, solid particle (e.g. a quartz grain, shell fragment or foraminifers) which is incorporated in the colony. They live below the wave base in areas with weak to moderate bottom currents (20-100 cm/sec; Cadée, 1975) and can escape shallow burial by crawling upwards (Cook, 1963). High densities of Recent lunulitiforme Bryozoa are reported from mid- shelf areas outside the coastal zone with its silt sedimentation of the Amazon River (20-60 m; Cadée, 1975), and from deltaic environments (Lagaay, 1963). The specimens of biofacies association 2 have been found attached to valves of *Ostrea (Cubitostrea) multicostata*, probably during the life of the oysters. This strategy enabled them to live in areas with a sedimentation rate which they were otherwise unable to cope with.

Biofacies association 2 is interpreted as a subtidal normal marine outer bay environment, occurring on a shallow inner carbonate shelf with a relatively low terrigenous sediment input, just above wave base. It was inhabited by a seagrass community at a water depth which was larger than that of biofacies association 1 (probably 20 to 60 m). Jimenez (1987) concluded that the benthic foraminifers are characteristic of an outer bay or lagoon facies (restricted littoral environment). The beds are interbedded in mudstones which Jimenez (1987) interpreted as restricted bay environments of the fan-delta system.

Biofacies association 3

Biofacies association 3 is found on the hardgrounds developed on top of sandstone bodies in the lowermost part of the Esdolomada Member. Two sub-biofacies associations are distinguished: 3A (1 locality) and 3B (2 localities). Both are autochtonous assemblages and are classified as end-cycle condensed coquinas (cf. Kidwell, 1991).

Biofacies association 3A (Goniaraea-Crassatella community)

The macrofauna of biofacies association 3A consists of: Serpula sp. Entobia sp. (trace fossil of Cliona sp.) Goniaraea elegans Leptomussa variabilis Stylocaenia sanmigueli Turritella dixoni Campanile sp. Strombidae type 3 Crassatella depressa Trachycardium boriesi Nemocardium corbaricum Chlamys pradellensis Spondylus hispanicus Ostrea (Cubitostrea) multicostata Chama boriesi Pectinidae type 4 Veneridae type 2 and 3 coral boring bivalve 2 echinoid species Aetobatis sp. (Miliobatidae) Lamna sp. a sea turtle

This assemblage occurs at one locality only. It is the most distinct example of an end-cycle coquina found in the Roda Formation. The formation of the hardground and its fauna have been described in Martinius & Molenaar (1991). The formation of the sandstone body was the last major stage of deposition of coarse clastic sediment in a shallow marine shelf area. Deposition was the result of progradation of a delta lobe towards the SW. In the terminal phase, the current direction changed from SSW-SW to the W and finally to the NW; sediment supply gradually decreased. In this phase, deposition of the sand was more and more influenced by longshore currents. Eventually sediment supply ceased completely and the uppermost surface of the sand body was exposed to wave action. The sand below this surface became cemented and gradually changed into a hardground.

For the reconstruction of the palaeoenvironment, clionid borings in the shells of *Crassatella depressa* and the functional morphology of the hermatypic coral *Goniaraea elegans* were analysed, supplemented with additional information obtained from other faunal elements. The specific shape of *Chama boriesi*, *Spondylus hispanicus*, and other bivalve species (e.g. *Crassatella depressa*) indicates a highly energetic environment where wave action was important. *C. boriesi* and *S. hispanicus* are dependent on a firm substrate and adapted to rather high energy conditions at shallow depths (Cox, 1969; Stanley, 1970). The genus *Chama* is characteristic for the inner sublittoral benthic zone where water depth is less than 30 m (Cox, 1969). The spines of reef-

dwelling *Spondylus* species act as a protection against fish predation (e.g. parrot fish in Recent times; Stanley, 1970).

Crassatella depressa lived buried in the sediment, with its ventral side protruding from the sand (Stanley, 1970). Therefore, only valves which were lying barren on the sediment could be bored efficiently. It was concluded that shells of *C. depressa* that have borings at both inner and outer side of a valve were empty at the time of boring and exposed to the water on both sides. When the animal was still living, boring could occur only at the outer side of the valve. A second indication of boring of loose shells comes from the fact that most of these shells seldom show repair of the borings at the inside of the valves as a reaction of the living animal upon complete perforation, and the fact that disarticulated valves were much more intensively bored than articulated valves (of 166 disarticulated valves 64% are heavily bored and 14% slightly, against 4% heavily and 91% slightly for double-valved specimens). The time of exposure was of long duration. Biological action (destruction of the ligament) and wave action also must have been responsible for the disarticulation and exposure on the seafloor of part of the shells. The shells, however, were not transported as evidenced by the equal occurrence of left and right valves.

The spherical form of colonies of the abundantly occurring coral species *Gonia*raea elegans, *Leptomussa variabilis* and *Stylocaenia sanmigueli* was interpreted as being the consequence of frequent physical disturbance (cf. Kissling, 1973; Lewis, 1989). The combination of spherical shape and large size (massive form) is a selective advantage for free living colonies in habitats characterised by moderate to heavy wave action, such as that represented in the Roda Formation. For the occurrence of Clionidae it is important that sedimentation and strong water movements do not affect the sponges (Boekschoten, 1966). The part of the water column between the substrate and the mean height of the corals was a zone of lower energy and turbulence. The *G. elegans* coral colonies provided protection for the sponges and other faunal elements in between them. The sponges were attached to disarticulated *C. depressa* valves. Species of the genus *Campanile* are always found associated with hermatypic corals (de Renzi, pers. comm.), which is confirmed for this biofacies association.

Martinius & Molenaar (1991) concluded that development of a fauna on the abandonment surface commenced with the introduction of the first inhabitants: foraminifer species, small coral planulae, echinoids, and species of the Cardiidae and Veneridae. Subsequently, they were followed by very shallow infaunal species as *C. depressa, Turritella dixoni*, and species of the Strombidae. Finally, non-burrowing faunal elements appeared, such as *S. hispanicus, Ostrea (Cubitostrea) multicostata*, and *C. boriesi*. After the hermatypic corals attained a certain height, providing a zone of low turbulence in between them, and the fauna associations reached an equilibrium stage, *Chlamys pradellensis* and *Cliona* could settle. Outside the area of coral growth, wave action must have been too strong.

On the basis of the above data, the palaeoenvironment is interpreted as a shallow open inner shelf (sublittoral benthic zone) with normal marine conditions and clear water, above wave base. Sedimentation rate was episodic and very low, and light penetration optimal. The fauna developed to full maturity, representing an equilibrium community with characteristic species such as *G. elegans* and *C. depressa*. The community can be characterised as a hardground community with bank-reef characteristics. It built a wave resistant structure in relatively protected sub-tropical water, although it lacked the rigidity of a frame. The depth of the water was less than 10 m. The nektonic fauna of rays, sharks and sea turtles indicates open marine conditions.

Biofacies association 3B (Crassatella depressa community)

The invertebrate macrofauna of biofacies association 3B consists of: Entobia sp. Patallophyllia sp. Goniaraea elegans Turritella dixoni Architectonica sp. *Campanile* sp. *Clavilithes* sp. Naticidae type 2 Fusidae type 2 Botula cordata Chlamys pradallensis Cardita boriesi Cardita sp. type 2 Crassatella depressa Trachycardium boriesi Bicorbula vidali Veneridae type 1 cf. Meretrix conilhacensis

This is an autochtonous assemblage dominated by *Crassatella depressa* and occurs at one locality only. Several characteristics of biofacies association 3B differ from biofacies association 3A; they are described in Martinius & Molenaar (1991). In the Esdolomada Member, several thin sheet-like sandstone bodies are intercalated in a silty-sandy marl sequence. Deposition of sand resulted from the lateral migration of tidal channels and formation of tidal lobes. Bioturbation of the sediment was intense and glauconite pellets are common.

Bioerosion of shells was uncommon and mostly caused by gastropod predators, i.e. species of the Naticidae. Members of this family are relatively rapid moving, infaunally operating carnivores, but drilling may take several hours to days (Kelley & Hansen, 1993). Only 20% of the bivalve shells are, albeit slightly, bored by clionids. Cardiidae were probably attached with their byssus to rhizome of the sea grasses (Stanley, 1972), similar to conditions of biofacies association 1. Fig. 3 illustrates the distribution of *C. depressa* valves found in life position on 2 m². The average density of in situ *C. depressa* is 16/m².

Because of the mud, hermatypic corals were almost absent (except an occasional flat specimen of *Goniaraea elegans*). Instead, *Patallophyllia* occurs rather abundantly in life position. *Patallophyllia* is an ahermatypic coral genus of the turbinate-flabellate type (Savazzi, 1982), living below wave base. This solitary coral is specialised to muddy soft bottoms because it has mobility capabilities which allows it to flourish



Fig. 3. Distribution of in situ preserved (*) and isolated valves (\times) of *Crassatella depressa* and in situ preserved *Patallophyllia* (P) of biofacies association 3B on 2 m² of the hardground.

under circumstances that are unfavourable for sedentary forms (Gill & Coates, 1977). Living specimens are capable of righting (the ability of an organism to return actively to life position after accidental overturn) and other activities counteracting burial by sedimentation (Savazzi, 1982). Of the *Patallophyllia* specimens found 40-50% have a curved central axis. This indicates that the animal had been reoriented from its ideal life position. It had to prevent its soft parts from being buried in the mud when e.g. lying in horizontal position on the substrate after a severe disturbance. The animal strived for continued upward growth by curving its central axis (Savazzi, 1982). Apparently, disturbance of the fauna occurred commonly, e.g. due to food-searching fish or rays, or during storms. The bivalve *Botula cordata* found in biofacies association 3B is a commensal of *Patallophyllia* (Savazzi, 1982).

The faunas that developed on top of the lobes are different from the preceding biofacies association (3A) because sedimentation did not cease completely; mud deposition continued slowly after the influx of the coarse clastic sediment. Faunas are preserved in the gradual transition between sand and mud and are adapted to a soft substrate and muddy environment. *C. depressa* had the tendency to bury itself at the most favourable, soft patches of the hardground. The poorly bored shells point to the fact that the faunas represent only a short time interval. The benthonic foraminifers in the mudstones directly overlying the biofacies association are characteristic of an open-platform environment (Jimenez, 1987).

Biofacies association 4 (*Crassostrea* cf. *rarilamella* community)

This association is found at one locality and characterised by a single bivalve species, which occurs in great abundance, viz. the large inequivalved, soft-bottom dwelling oyster (cf. Seilacher, 1984) *Crassostrea* cf. *rarilamella*. It is classified as a monotypic autochtonous assemblage forming an event-concentration (cf. Kidwell, 1991). The bed with the oyster population is intercalated between two fan-delta lobes within a SW-ward prograding system influenced by ebb-tidal currents and occasionally experiencing heavy storms (Nio, 1976; Nio & Yang, 1983; Yang & Nio, 1985). Boring clionids and encrusting bryozoans are also found in this layer. Foraminifers found associated with the oyster population include *Nummulites globulus*, *N. subramondi*, *N. incresens*, *Discocyclina*, and reworked Myliolinidae and *Alveolina* specimens (Jimenez, 1987). The nummulites are indicative of a shallow bay facies with temperatures around 20° and a normal salinity. The population dynamics and growth rates of this oyster population are described in Martinius (1991).

Annual growth increments (calcium-carbonate rich regions between successive growth lines) in the hinge plate of the left valve of 333 oysters were counted from the umbo forward. From the data, a life table was set up and a survivorship curve was constructed. It was concluded that the oyster could reach a maximum age of 38 years; extrapolation of the survivorship curve gave a possible maximum age of 46 years. The mean age was 17 years. The regression coefficient showed that yearly mortality in the population was low and constant after reaching c. 10 years.

The survivorship curve was found to be part of the standard Type I curve of Deevey (1947) with high juvenile mortality, and showed that the oysters could expect a high age. Measured growth curves showed that no gradual decrease occurred at higher age, as is usually the case for bivalves, due to the fact that the oyster shell continued to grow and thicken during the adult stage as an adaptation to mud deposition.

Thus, several characteristics of the animal (high maximum age, constant mortality, heavy thick shell, adaptations to mud sedimentation) indicated that *C. cf. rarilamella* was a K-strategist, well acclimated to muddy soft bottoms in shallow subtidal settings. K-strategists are specialists adapted to stable environments with population abundancies close to the carrying capacity of the environment (Cerrato, 1980). The population represents a time-span of circa 500 years and documents a nearshore, shallow marine environment, confirming short-term time-averaging in the order of up to several thousand years (cf. Fürsich & Aberham, 1990).

Biofacies association 5 (Naticid-Clavilithes community)

This parautochthonous assemblage is found at one locality and consists of: Turritella dufrenoyi Turritella hybrida Turritella sp. type 9 Vermetus (Tubulostium) angulosus Cassidaria sp. Sycum sp. Clavilithes sp. Volutilithes cf. bouziguesensis Volutilithes sp. type 2 Strombidae type 3 Naticidae types 1 (cf. Amaurellina sp.), 2-3, 5-6 Ostrea (Cubitostrea) multicostata Pseudomiltha cf. corbarica Trachycardium boriesi Nemocardium corbaricum Cardiidae type 3 Libitina sp. types 2-3 Teredo sp. Veneridae type 1 cf. Meretrix conilhacensis Nautilus sp. wood fragments of Carapoxylon sp.

It is found in the lower part of the Esdolomada Member, in a distinct, yellow, completely dolomitised, well-cemented bioclastic dolowackestone embedded in mudstones, which contains *Nummulites*, *Discocyclina*, biserial foraminifers, and echinoid remains. Driftwood fragments, often with *Teredo* borings, are identified as belonging to the tree genus *Carapoxylon* (family Meliaceae) which is typical of tropical rainforests (van der Burgh, pers comm.).

The invertebrate macrofauna is slightly dominated by predators (species of the Naticidae, Clavilithes and Volutilithes) feeding on Turritellidae and Lucinidae species (Kelley & Hansen, 1993). Other gastropods are browsers or ciliary detritus feeders. They were all tropical or subtropical soft sediment inhabitants, mostly living infaunally (Llompart, 1977). Recent species of Vermetus often live in colonies cemented to one another; they are commensals of sponges (Wenz, 1938). Species of the genus Pseudomiltha lived in subtidal environments such as estuaries (Cox, 1969). They are slow but deep burrowing bivalves (Stanley, 1970). The specimens of Ostrea (Cubitostrea) multicostata are probably allochtonous. The oysters and the wood fragments might be derived from a nearby deltaic environment were brackish water conditions dominated. One of the O. multicostata specimens shows a large xenomorphic area which strongly resembles an angiosperm structure, e.g. a seagrass axis or root, or a driftwood structure. Xenomorphism is a special form of substratum bioimmuration frequently recorded from oyster specimens (Stenzel, 1971; Rohr & Boucot, 1989; Taylor, 1990) in which the two valves maintain a constant separation during growth across the mollusc shell. The presence of the cephalopod Nautilus indicates open marine conditions, although floating shells can travel enormous distances and reach shallow marine protected environments.

The mudstones formed below the bioclastic dolowackestone were deposited in an upper-shelf environment, those above in a restricted bay or lagoon environment (Jimenez, 1987). Biofacies association 5 is a slightly deeper water association than biofacies association 3B. According to Wilson (1975), light-coloured dolomitic bioclastic wackestones form in lagoons and bays on restricted platforms. Biofacies association 5 is interpreted as a shelf lagoon environment with normal salinity at depths around wave base. Water depth was probably about 30 to 60 m; the platform may have been restricted.

Biofacies association 6 (Tympanotonos-Pyrazus community)

The invertebrate macrofauna of biofacies association 6 consists of:

Turritella aff. bellovacensis Tympanotonos (Eotympanotonos) turris Pyrazus vidali crusafonti Pirenella (Tiaracerithium) figarolense Tibia sp. Amaurellina (Cromnium) intermedia Lyria cf. harpula Ostrea (Cubitostrea) multicostata Mactra aff. semisulcata

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This polytypic (par)autochtonous assemblage is found at one locality only in the lowermost distal part of the Esdolomada Member. The sediment consists of dark blue sandy calcareous siltstone (CaCO₃ content 32.1%). The fossils occur in situ in the laminated mudstone. Laminae thicknesses vary from 2-4 mm; fossil preservation is good, specimens are occasionally found in life position and no bioerosion is observed.

The fauna is dominated by species of the Potamididae which today are found in the intertidal zone on muddy substrates in more or less brackish water in tropical or subtropical regions. *Tympanotonos* species live on estuarine mud bottoms covered with mangroves at the coast of Africa. It is an euryhaline genus which can live in normal seawater as well as in brackish water (Llompart, 1977). Several species of the genus *Tympanotonos* can, under specific environmental conditions, be opportunistic species (de Renzi, pers. comm.). However, the specimens of this association are not found in sufficiently large quantities to qualify as such. Many *Turritella* species are adapted to limited ecological niches. *T. bellovacensis* most probably was a very shallow water species, living at its upper depth limit in this biofacies association. The *Amaurellina* species is the only real predator. It apparently fed on the Turritellidae (Kelley & Hansen, 1993), Potamididae and *Mactra*, and is less common than the *Pyrazus* and *Pirenella* species encountered. *Pyrazus* is the only genus of this biofacies association which can also live in the supratidal zone (Llompart, 1977).

The bivalves are represented with two species. Ostrea (Cubitostrea) multicostata is a shallow marine, mostly cemented, brackish water oyster which lives commonly in estuaries (Stenzel, 1971). The specimens found in this biofacies association are preserved with articulated valves and possess a well developed, uplifted commissure and triangular outline. They were most likely attached to large particles within the sediment, e.g. shells of Potamididae, although impression areas have not been found. Juvenile oysters are found attached to Tympanotonos specimens. Species of the genus Mactra are moderately deep burrowers with posterior inhalant and exhalant current apertures (Stanley, 1970). The valves are thin and approximately oval in outline. The hinge teeth are reduced or absent which permits rocking of the valves about a dorsoventral axis during extension and withdrawal of the siphons and foot. The siphons are long and fused. Shells of this type belong to deep burrowers that occupy more or less permanent burrows (Stanley, 1970; Alexander et al., 1993). Deep burrowing is an adaptation to prevent disturbance by changing tides. In Recent times, the habitats of M. fragilis are intertidal and shallow subtidal settings. The species is restricted to grassy bottoms and sandy substrates (Stanley, 1970).

Based on Recent relatives of the molluscs of this fossil association and the mor-

phological adaptations of the molluscs, biofacies association 6 is interpreted as a protected (brackish water ?) intertidal mudflat association.

Biofacies association 7 (Turritella rodensis community)

The invertebrate macrofauna of biofacies association 7 (found at a single locality) consists of: Patallophyllia sp. Turritella caroli Turritella caroli Turritella figolina Turritella figolina Turritella rodensis Turritella rodensis Turritella sp. type 9 Melanatria sp. Sycostoma sp. Clavilithes sp. Naticidae type 3 Ostrea (Cubitostrea) multicostata Diplodonta sp.

This (par)autochtonous assemblage is found in mudstones at the base of the Esdolomada Member. These mudstones are the lateral continuation of sandstone body Roda 4 with the hardground association of biofacies association 3A on its top. The dark blue sandy mudstone is vaguely laminated with intercalations of yellow-brown micritic layers. These micritic layers are sometimes well cemented, 2-5 cm thick and are mostly barren with respect to macrofossils.

The fauna is characterised by a large amount of mainly well preserved Turritellidae specimens. Other gastropods (e.g. species of Melanatria, Sycostoma, Naticidae) are less frequent. The gastropods sometimes occur in layers and tube-like structures indicating that they are concentrated by bioturbation. T. figolina lived in the same kind of environments as the Recent T. tricarinata communis Risso, 1826 (Gaemers, 1978). The latter lives for example close to the mouth of the river Rhône where fine sediments are rapidly deposited and other molluscs are rare or absent. The species can easily escape burial by crawling upwards to the new sediment surface. It requires large quantities of fine-grained bottom sediments and cannot withstand too much water turbulence. Due to the strong tidal current actions, the upper limit for the occurrence of T. figolina was a depth of 20 m (Gaemers, 1978). The Naticidae, Clavilithes and Volutilithes species preved on the Turritellidae as proven by the numerous boreholes found in turritellid shells. Members of the Turritellidae have been found to be one of the consistently preferred prey taxa of naticid gastropods (Kelley & Hansen, 1993). The *Patallophyllia* specimens found are relatively small; they lived freely on the muddy soft bottom to which they were well adapted. Species of the bivalve genus Diplodonta are very slow burrowers which (in Recent times) prefer muddy substrates and shallow sheltered subtidal conditions (Stanley, 1970).

One of the well cemented micritic layers is a Turritella-boundstone with micrite

matrix. The bed not only contains Turritella rodensis specimens but also large quantities of two small unidentified bivalve species. Specimens of one species are most commonly preserved as internal moulds, specimens of the other as external moulds. Most of the Turritella specimens are broken at the top and/or aperture and are lined in more or less the same direction. In addition, Naticidae specimens, Nummulites, and a few echinoid remains are found. All faunal elements are present in the underlying mudstone interval. Shell beds rarely are the result of pure biological action (Cadée, 1968; Kidwell, 1991); concentration most probably took place by physical action, e.g. a heavy storm or hurricane. The shell bed is classified as an event-concentration (cf. Kidwell, 1991). During the hurricane, mud was brought in suspension and winnowing of (mainly) Turritella shells took place, forming a lag deposit. Turritella-like shells tend to align themselves with their aperture in the direction of the dominant current (Nagle, 1967). As aperture openings are found to point in opposing directions, it is concluded that after waning of the storm Turritella shells were aligned by bi-directional tidal currents. The effect of tides on sediment deposition in the distal part of the Roda fan-delta during the Early Eocene in the Tremp-Graus Basin has been proven by Yang & Nio (1985). A comparable event-concentration formed by wave and/or tidal reworked *Turritella pleibeia* has been reported by Kidwell (1982) from the Miocene of Maryland (U.S.).

Biofacies association 7 is interpreted as a sheltered bay with widespread mud sedimentation and tidal currents, above wave base, and with normal marine salinities. Occasionally, severe storms occurred.

Biofacies association transitions

A depth and substrate related lateral transition between two biofacies associations occurs twice in the deposits of the Roda Formation. The first pair of laterally related biofacies associations is formed by biofacies association 1 and 2, the second pair by biofacies association 3A and 7. In both cases, one biofacies association occurs on top of a sandstone body which pinches out on its seaward side and is replaced by a limestone bed or mudstone deposits containing the second biofacies association. Deposition of sand in the Roda fan delta resulted in local substrate differences and a pronounced seafloor topography.

The top of stacked sandstone beds, and the top of the large sandstone bodies Roda 1, 2 and 3 of the Roda Sandstone Member as well as a sandstone body in the basal part of the Esdolomada Member exhibit the lateral transition between biofacies association 1 and 2, often on a lateral distance of only 100 m. Changing sediment distribution patterns (rapid increase in siliciclastic sedimentation) were responsible for changes in substrate conditions and the change from biofacies association 1 to 2.

The transition between biofacies association 3A and biofacies association 7 is found between the top of Roda 4 (relative clear water above wave base without sand and mud deposition) and its lateral mudstone equivalent (Fig. 4). Sandstone body Roda 4 pinches out southward and laterally changes first into a mudstone sequence with muddy limestone beds and subsequently into a pure mudstone sequence. The limited extent of sand deposition resulted in local differences in water depth, light penetration, and substrate to which different faunas were adapted. An exposure of



Fig. 4. Lateral transition between biofacies association 3A and biofacies association 7.

the intermediate lithofacies contains a fauna characterised by a mixing of some species of biofacies association 3A and some of biofacies association 7 (and even some of biofacies association 2).

Both biofacies association transitions are found in comparable water depths. However, the transition between biofacies association 1 and 2 is located in more central and probably active parts of the fan delta whereas the transition between biofacies association 3A and 7 occurred in less active fan-delta areas. Depth differences between the transitional biofacies associations are 20 to 30 m at the most.

Summary and conclusions

Classification of the invertebrate macrofauna of the Early Eocene Roda Formation and the study of the distribution of the species (by means of the analysis of the 69 fauna localities) resulted in the definition of 7 biofacies associations. The Roda Formation is dominated by biofacies associations 1 and 2 of which the first is the most common: 48% of the occurrences belongs to biofacies association 1, 23% to biofacies association 2 (Fig. 5). Biofacies association 1 is indicative of mixed siliciclasticcarbonate substrates with the characteristics of an abandonment surface in shallow subtidal settings above wave base. It occurs on top of depositional lobes, on their foreslopes and on their more distal toes. Biofacies association 2 is common in subtidal normal marine outer bay carbonate environments with a relatively low sedimentation rate. Micro- as well as macrofauna indicate a more distal and slightly deeper environment, as compared with biofacies association 1. The other biofacies associations occur in the distal areas of the Esdolomada Member and are indicative of local environmental conditions. Biofacies association 3 represents a hardground coral-mol-



Fig. 5. Pie diagram showing percentage of total occurrences represented by each biofacies association.

lusc community with bankreef characteristics, biofacies association 4 a very shallow, subtidal, soft-bottom community in (probably) brackish water, biofacies association 5 a restricted bay or lagoon community in normal marine waters below wave base, biofacies association 6 a protected brackish water intertidal mudflat community, and biofacies association 7 a mud rich sheltered bay community below wave base.

Lateral transitions between biofacies associations 3 and 7, and between biofacies associations 1 and 2 show the relation of the biofacies association with seafloor topography (substrate and water depth) resulting from the formation of lobes in the Roda fan delta. These transitions, which remain identical throughout the deposition of the Roda Formation, witness environmental conditions ranging from shallow, high-energetic conditions to slightly deeper water and more tranquil conditions. Autocyclic lateral shifting of a local siliciclastic depocentre facilitated the formation of calcareous horizons characterised by a restricted spatial extent. These are consequently explained as a response to local starvation of clastic sediment supply rather than being a manifestation of relative sea-level changes and therefore do not reflect maximum flooding surfaces. This conclusion delimits the applicability of sequence stratigraphic methods (i.a. Wilgus et al., 1988) to clastic systems in basins primarily controlled by tectonic forces.

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Appendix 1: Invertebrate macrofauna and other fossil remains from the Roda Formation

A list of identified species from the Early Eocene (Late Ypresian) Roda Formation on the eastern side of the river Isábena is given. A total of 1 annelid species, 2 poriferan species, 5 zoantharian species, 3 bryozoan species, 62 gastropod species, 91 bivalve species, 2 cephalopod species, 12 echinoid species, and 1 arthropod species are reported. In addition, 1 tropical rainforest tree species and 3 vertebrate species are listed. The benthic foraminifers (49 genera) and ostracods of the Roda Formation are listed in Jimenez (1987). Literature used to identify the mollusc specimens includes: Cossmann & Pissarro (1904-1906, 1910-1913), Doncieux (1903, 1908-1926, 1911, 1926), Wenz (1938) and de Renzi (1971).

⁽⁷⁾ indicates mollusc groups reported from the Roda Formation by Gaemers (in Janssen, 1985) from his section X along the eastern bank of the Isábena from La Puebla de Roda to Roda de Isábena (RGM 228 147-280). In addition, *Seraphs* sp. and unidentified molluscs ascribed to the Crenellinae, Tellinidae, Solenidae, Xenophoridae, Anomiidae, and Cypraeidae were recorded by Gaemers (in Janssen, 1985), all of which are not reported in this study. Plates 1-5 illustrate some of the species encountered.

Angiosperms	
Meliaceae	
Carapoxylon sp.	RGM 393 466
Annelida and Porifera	
<i>Serpula</i> sp.	RGM 393 055, 393 098, 393 384
unidentified sponge	RGM 393 487
Entobia sp. (trace fossil of Cliona sp.)	RGM 393 442
Zoantharia	
Goniaraea elegans Leymerie	RGM 393 426-427, 393 452-453, 393 481
Leptomussa variabilis d'Achiardi	RGM 393 450-451
Stylocaenia sanmigueli Sole Sabaris	
Tarbellastraea sp.	
Patallophyllia sp.	RGM 393 058, 393 405, 393 428, 393 449
Bryozoa	
Lunulites bugei Reguant, 1967	RGM 393 408-409
encrusting Bryozoa type 1 and 2	RGM 393 088, 393 432
Gastropoda	
Neritidae ^(*)	
Velates perversus (Gmelin, 1791)	RGM 393 054
Neritopsis vidali (Doncieux, 1908)	RGM 393 416
Turritellidae ^(*)	
Turritella aff. bellovacensis Deshayes, 1833 Turritella caroli Doncieux, 1908	RGM 393 078

Turritella dixoni Deshaves 1833	RGM 393 443, 393 469
Turritella figoling Carez, 1881	RGM 393 396
Turritella cf. dufrenovi Levmerie 1846	RGM 393 435
Turritella hybrida Deshaves, 1833	RGM 393 395
Turritella rodensis Carez, 1881	RGM 393 090, 393 392, 393 393
Turritella cf. carinifera Deshaves, 1833	
Turritella sp. type 9	
Architectonicidae	
Architectonica sp	RGM 393 434, 393 468
Vermetidae	
Vermetus (Tubulostium) angulosus Cheny 1842	RGM 393 444
Thiaridae	
Melanatria sp	RGM 393 083
Potamididae	
Tumnanotonos (Fotumnanotonos) turris (Deshaves 1	830) RGM 393 077
Pirenella (Tiacerithium) figarolense Doncieux 1908	RGM 393 079
Purazus zidali crusafonti da Ronzi 1971	RGM 393 075
Corithiidan	
Campanila sp	RGM 393 446
Trichotropidae(*)	
Sigmesalia sp	
Strombidae	
Tibia sp	RGM 393 074
Strombidae type 2 cf. Strombus sp	RGM 393 052 393 447
Soranhidao	KGIVI 070 002, 070 11,
Terebellum sp	RGM 393 430
Naticidae"	
Amourelling (Crommium) intermedia Deshaves 183	RGM 393 076
Naticidae type 1 cf. Amaurelling sp.	RGM 393 070 393 429
Naticidae sp. unidentified types 2-6	RGM 393 071 393 387 393 401
Wallclude sp. undertined types 2-0	393 425 393 433 393 445
Cassididae	0,
Cassidaria en	RGM 393 061
Caleodidae	KGM 575 001
Sucostoma sp	RCM 393 397
Easciolariidan	KGW 575 577
Clavilithas sp	RCM 393 424
Eascielariidae sp. unidentified types 1-2	K611 050 121
Volutidae	
Athlata (Volutioning) on	RCM 393 067
Volutilithes of houriguesensis Dongioux 1908	RGM 393 465
Volutilithes on turns 2	RGM 393 472
volulillines sp. type 2 Lyria af harmyla do Lomorak 1806	RCM 202 080
Lyrin Ci. imrpuin de Lamarck, 1000 Valutidaa an unidentified turne 1 (af Olividae)	RGM 202 060
Volutidae sp. unidentified type 1 (ci. Olividae)	RGW 393 000 RCM 202 050
Transfer and a	NGIVI 575 037
Incertae seuis	

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	Unidentified gastropod genera: 17 RGI	vi 393 062, 393 394, 393 398-399, 393 402
Biv	valvia	
Nu	lculidae	
	Nucula cf. bouffeti Doncieux, 1911	
	Nucula sp. type 2	RGM 393 403, 393 412
Nu	iculanidae ^(*)	
	Nuculana sp.	
Ar	coidea	
	Arcoidea unidentified species	
My	/tilidae ^(*)	
	Mytilus inflatus Doncieux, 1911	RGM 393 056, 393 404
	Mytilus cf. subrimosus Doncieux, 1911	
	<i>Mytilus</i> sp. type 3	
	Botula cordata (de Lamarck, 1806)	RGM 393 437
Pir	nnidae	
	<i>Pinna</i> sp. types 1-2	
Pe	ctinidae ^(*)	
	Chlamys pradellensis Doncieux, 1905	RGM 393 414, 393 419
	Chlamys aff. infumata (de Lamarck, 1806)	RGM 393 410
	Chlamys sp. type 3	
	Pectinidae sp. unidentified type 4	
Sp	ondylidae ^(*)	
-	Spondylus hispanicus Doncieux, 1911	RGM 393 068, 393 095, 393 385
	Spondylus ? eocenus Leymerie, 1881	
	Spondylus sp. type 3	
Lir	nidae	
	Lima sp.	
Os	treidae	
	Ostrea (Cubitostrea) multicostata (Deshayes	RGM 393 082, 393 084-086
	、 · · · ·	393 417, 393 422, 393 463-464
	Ostrea (Cubitostrea) sp.	
	Ostrea (s.l.) tournali Doncieux, 1911	RGM 393 069, 393 094
	Ostrea (s.l.) cf. uncifera Leymerie, 1881	RGM 393 406
	Ostrea (s.l.) sp. type 4	
	Crassostrea cf. rarilamella (Melleville, 1843)	RGM 393 474-480
Lu	lcinidae	
	Lucina sp.	
	Pseudomiltha argus (Melleville, 1843)	RGM 393 093, 393 438-439
	Pseudomiltha cf. corbarica (Levmerie, 1846)	RGM 393 484
	Lucinidae sp. unidentified type 4	
Fir	mbriidae	
	Corbis sp.	RGM 393 087
Ur	ngulinidae	
	Diplodonta albasiensis Doncieux, 1911	RGM 393 400, 393 440
Cł	namidae(*)	

Chama boriesi Doncieux, 1911	RGM 393 441
Chama sp. type 2	RGM 393 411
Carditidae	
Cardita boriesi Doncieux, 1911	RGM 393 053, 393 064-066, 393 467
Cardita sp. type 2	RGM 393 073, 393 092, 393 389
Crassatellidae ^(*)	
Crassatella depressa Doncieux, 1911	RGM 393 442
Crassatella senessei Doncieux, 1911	RGM 303063
Crassatella sp. type 3	
Cardiidae ^(*)	
Trachycardium boriesi Doncieux, 1911	RGM 393 099, 393 388, 393 461-462
Nemocardium corbaricum Doncieux, 1911	RGM393 471
Cardiidae sp. unidentified type 3	RGM 393 436, 393 459
Mactridae	
Mactra aff. semisulcata de Lamarck, 1806	RGM 393 081
Veneridae ^(*)	
unidentified species type 1 (cf. Meretrix c	onilhacensis Doncieux, 1911)
	RGM 393 420, 393 470
unidentified species type 2	
unidentified species type 3	RGM 393 421
Trapeziidae	
Libitina elongata Levmerie, 1846	RGM 393 431
Libitina sp. types 2-3	RGM 393 460
Corbulidae ^(*)	
Bicorbula vidali (Cossmann, 1897)	RGM 393 091
Corbulidae sp. unidentified type 2	RGM 393 390
Pholadidae	
Teredina cf. personata de Lamarck, 1806	
Teredinidae(*)	
Teredo sp.	RGM 393 448
Pholadomvidae	
Pholadomya konincki Nyst, 1845	RGM 393 386
Incertae sedis	
Unidentified bivalve genera: 39	RGM 393 072, 393 407, 393 413, 393 423
Cephalopoda ^(*)	······································
Nautilus cf. lamarcki Deshaves, 1833	RGM 393 383, 393 473
Eutrephoceras aff. lamarcki (Deshaves, 183	3) RGM 393 057, 393 391
Echinoidea	
Schizasteridae	
Linthia orbignyi Cotteau, 1863	
Linthia aff. levmeriei (Cotteau, 1856)	
Prenaster of monzensis Lambert	
Schizaster sp.	RGM 393 482
Echinolampadidae	
Echinolamnas sp	
Dominowinpus sp.	

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Conoclyp	peidae	
Conoc	clypeus sp.	RGM 393 483
Phymoso	matidae	
Thyle	<i>chinus</i> sp.	
Incertae s	sedis	
6 uni	dentified echinoid species	RGM 393 415, 393 454
Arthropo	oda	
Decapod	a	
Zanth	opsis dufouri Milne-Edwards, 1850	RGM 393 488
Vertebrat	ta	
Pisces		
Miliobati	dae	
Aetob	<i>patis</i> sp.	RGM 393 096, 393 455-456
Lamnida	e	
Lamn	a sp.	RGM 393 097, 393 457
Reptilia	•	
Chelonid	lae	
unide	entified sea turtle	RGM 393 458

Plate 1

- 1. Neritopsis vidali (Doncieux, 1908), RGM 393 416, × 1.6.
- 2. Velates perversus (Gmelin, 1791), $\times 0.8$.
- 3. Turritella dixoni Deshayes, 1833, RGM 393 443, × 1.6.
- 5. Turritella cf. hybrida Deshayes, 1833, RGM 393 395, × 1.6.
- 4. Turritella figolina Carez, 1881, RGM 393 396, × 1.6.
- 6. Turritella rodensis Carez, 1881, RGM 393 392, × 1.6.
- 7. Tympanotonos (Eotympanotonos) turris (Deshayes, 1830), RGM 393 077, × 1.6.
- 8. Vermetus (Tubulostium) angulosus Chenu, 1842, RGM 393 444, × 1.6.
- 9. Amaurellina (Crommium) intermedia Deshayes, 1833, RGM 393 076, × 1.6.



Plate 2

- 1. Melanatria sp., RGM 393 083, × 0.75.
- 2. Strombidae gen. et sp. indet., RGM 393 052, × 1.25.
- 3. Pirenella (Tiacerithium) figarolense Doncieux, 1908, RGM 393 079, × 1.6.
- 4. Neritidae type 2, RGM 393 445, × 1.6.
- 5. Naticidae type 1 cf. Amaurellina sp., × 0.75.
- 6. Clavilithes sp., RGM 393 424, × 1.6.
- 7. Volutilithes sp., \times 1.6.
- 8. Volutidae type 2, RGM 393 059, × 1.6.
- 9. Gastropoda non det., RGM 393 399, × 1.6.
- 10. Mytilus inflatus Doncieux, 1911, RGM 393 404, × 0.9.



Plate 3

- 1. Crassatella depressa Doncieux, 1911, RGM 393 442, × 1.
- 2. Mould of Crassatella depressa Doncieux, 1911, × 1.
- 3. Diplodonta albasiensis Doncieux, 1911, RGM 393 400, × 1.6.
- 4. Chama boriesi Doncieux, 1911, RGM 393 441, × 0.5.
- 5. *Libitina* sp. type $2, \times 0.8$.
- 6. Veneridae type 1 cf. Meretrix conilhacensis Doncieux, 1911, RGM 393 470, × 1.6.



Plate 4

- 1. Eutrephoceras aff. lamarcki (Deshayes, 1833), × 0.75.
- 2. Cardiidae gen. et sp. indet., type 3, RGM 393 459, \times 0.5.
- 3. Veneridae gen. et sp. indet., type 3, RGM 393 421, × 1.6.
- 4. Spondylus hispanicus Doncieux, 1911, RGM 393 385, × 0.75.
- 5. Cardiidae type 2 cf. Trachycardium boriesi Doncieux, 1911, × 0.5.
- 6. Mactra aff. semisulcata de Lamarck, 1806, RGM 393 081, × 0.9.



Plate 5

1. Crassostrea cf. rarilamella (Melleville, 1843), umbo of specimen with single resilifer in left valve, RGM 393 474, \times 0.5.

2. *Crassostrea* cf. *rarilamella* (Melleville, 1843), umbo of specimen with incomplete duplicated resilifer in left valve, RGM 393 475, × 0.5.

3. Crassostrea cf. rarilamella (Melleville, 1843), umbo of specimen with completely duplicated resilifer in left valve, × 0.7.

4. Ostrea (Cubitostrea) multicostata (Deshayes, 1830), RGM 393 463, × 1.6.

5. Carditidae type 1 cf. Cardita boriesi Doncieux, 1911, RGM 393 065, × 0.6.

6. Bicorbula vidali (Cossmann, 1897), RGM 393 091, × 1.6.

7. Ostrea (Cubitostrea) multicostata (Deshayes, 1830) with xenomorphic area, RGM 393 464, × 1.6.

