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Fossil associations from the middle and upper Eocene strata of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees)

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Abstract

Fossil associations from the middle and upper Eocene (Bartonian and Priabonian) sedimentary succession of the Pamplona Basin are described. This succession was accumulated in the western part of the South Pyrenean peripheral foreland basin and extends from deep-marine turbiditic (Ezkaba Sandstone Formation) to deltaic (Pamplona Marl, Ardanatz Sandstone and Ilundain Marl formations) and marginal marine deposits (Gendulain Formation). The micropalaeontological content is high. It is dominated by foraminifera, and common ostracods and other microfossils are also present. The fossil ichnoasssemblages include at least 23 ichnogenera and 28 ichnospecies indicative of *Nereites*, *Cruziana*, and ?*Scoyenia-Mermia* ichnofacies. Body macrofossils of about 80 taxa corresponding to macroforaminifera, sponges, corals, bryozoans, brachiopods, annelids, molluscs, arthropods, echinoderms and vertebrates have been identified. Both the number of ichnotaxa and of species (e. g. bryozoans, molluscs and condrichthyans) may be considerably higher. Body fossil assemblages are comparable to those from the Eocene of the Nord Pyrenean area (Basque Coast), and also to those from the Eocene of the west-central and eastern part of South Pyrenean area (Aragon and Catalonia). At the European scale, the molluscs assemblages seem endemic from the Pyrenean area, although several Tethyan (Italy and Alps) and Northern elements (Paris Basin and Normandy) have been recorded. Palaeontological data of studied sedimentary units fit well with the shallowing process that throughout the middle and late Eocene occurs in the area, according to the sedimentological and stratigraphical data.

Keywords: Fossil associations, Paleogene, turbidites, delta, shallow-marine, South Pyrenean basin

Resumen

Se describen las asociaciones fósiles del Eoceno medio y superior (Bartoniense y Priaboniense) de la sucesión sedimentaria de la Cuenca de Pamplona. Esta sucesión se acumuló en la parte oeste de la Cuenca de antepaís periférica surpirenaica y comprende desde turbiditas marinas profundas (Formación Areniscas de Ezkaba) hasta depósitos deltaicos (Formaciones Margas de Pamplona, Areniscas de Ardanatz y Margas de Ilundain) y marinos marginales (Formación Gendulain). El contenido micropaleontológico es alto y está dominado por los foraminíferos. Los fósiles de ostrácodos y otros organismos son también abundantes. Las asociaciones de icnofósiles incluyen al menos 23 icnogéneros y 28 ichnoespecies, indicativas de las icnofacies de *Nereites*, *Cruziana*, y ?*Scoyenia-Mermia*. Se han identificado fósiles corporales de unos 80 taxones, correspondientes a macroforaminíferos, esponjas, corales, briozoos, braquiópodos, anélidos, moluscos, artrópodos, equinodermos y vertebrados. El número de icnotaxones y de especies (p. e. briozoos, moluscos gasterópodos, bivalvos y peces condríctios) puede ser considerablemente mayor. Las asociaciones de fósiles corporales son comparables a las del Eoceno del Área norpirenaica (Costa vasca) y de las partes central y este del Área surpirenaica (Aragón y Cataluña). A escala europea, la asociación de moluscos parece endémica del Área pirenaica, aunque contiene elementos del Tetis (Italia y Alpes) y de las cuencas del norte (Cuenca de París y Normandía). El contenido paleontológico de las unidades sedimentarias analizadas es coherente con el proceso de somerización que tiene lugar a lo largo del Eoceno medio y tardío, de acuerdo con lo que indican los datos sedimentológicos y estratigráficos.

Palabras clave: Asociaciones fósiles, Paleógeno, turbiditas, delta, marino somero, Cuenca Surpirenaica

1. Introduction

The current biogeographic distribution of species shows the existence of hotspots characterized by high biodiversity. In marine areas the highest biodiversity is centered in the so-called Indo-Australian Archipelago hotspot. According to Renema *et al*. (2008), this hotspot was preceded by at least two other marine biodiversity hotspots during the past 50 million years: the Early Miocene hotspot, centered at the Arabian region, and the Eocene hotspot, which was located in the West Tethyan region.

Near the West Tethyan region, in the Atlantic area, the marine fauna of the middle Eocene of the Paris Basin showed an extraordinary biodiversity during Lutetian times and can be regarded as an extension of the West Tethyan hotspot (Merle, 2008; Merle *et al*., 2008; Huyghe *et al*., 2012). Merle (2008, 2009) indicates the presence of species of Tethyan origin in the Paris Basin, which contributed to enrich the biodiversity of this region. During Bartonian, the Eastern Atlantic marine biodiversity fell, but the Paris Basin and the Loire-Atlantique (Britain) still correspond to very rich areas having a mollusc richness exceeding 1000 species (Merle, 2008; 2009, Lebrun *et al*., 2013). It is during the Priabonian when the biodiversity decreased significantly in both sides of the Atlantic Ocean.

Because of its paleogeographic position, the Pyrenean area could have played an important role as an Eocene paleobiogeographical crossover between the Tethyan and Northern Atlantic domains. Although Rouault (1850), Doncieux (1908) and Cossmann and O'Gorman (1923) described rich marine faunas from the early Eocene of Pau and the Corbières, the Pyrenean marine faunas from the middle/late Eocene are still poorly documented. In the North Pyrenean area, the classical works made by d'Archiac (1846, 1850), de Bouillé (1873, 1876), Boussac (1911) about the "Nummulitic" of the Basque Coast, have hardly been updated. In Aragon and Catalonia (South Pyrenean area) the works of Villalta (1956), De Renzi (1971, 1996), Abad (2001), Pisera and Busquets (2002), among others, on fossil molluscs and sponges, can be mentioned.

The Pamplona Basin is located to the south of the Basque Coast and to the west of Aragon and Catalonia. However, from a palaeontological point of view, the Pamplona Basin is less known than its neighbouring areas. The first data were published by the French geologist Carez (1881). For this author, the Pamplona marls (Pamplona Marl Formation) were identical to the "marls of *Serpula spirulaea*", which were continuations of the La Canal de Berdún marls (Zaragoza, Aragon). Many years later, Ruiz de Gaona (1947) and Ruiz de Gaona and Colom (1950) completed a more comprehensive study of these formations, describing their foraminiferal content and concluding that they were Bartonian in age. These authors also mentioned the occurrence of important macrofossil associations near the city of Pamplona. Local micropaleontological determinations were carried out later by Puigdefábregas (1975) and Alameda *et al.* (1993). Macropalaeontological works on the bivalve *Dimya pamplonensis* (Calzada and Astibia, 1996), turtles and sirenians (Astibia *et al.*, 1999; 2005; 2006; Buffrénil *et al*., 2008), and sponges and corals (Astibia *et al.*, 2014) have been published in the latest years. Avian ichnofossils from the Gendulain Formation were cited and described in Mangin (1959-1960), Raaf *et al.* (1965), Payros *et al.* (2000), Astibia *et al.* (2007), and Astibia *et al.* (in press).

The aim of this paper is to present updated data about the fossil associations from the Pamplona Basin, which includes new information on fossil molluscs. The results will further contribute to enlarge the database for a better understanding of the evolution of global marine biodiversity throughout the Eocene.

2. Geological setting

The study area is located in the central part of Navarre (South-western Pyrenees). The current distribution and characteristics of the Eocene rocks in the area show the geometry and evolution of the original sedimentary basin (Fig. 1; see Pujalte *et al.*, 2002). In Eocene times, the South Pyrenean zone was a NW-trending foreland basin which formed adjacent to the tectonically uplifting orogen to the north. It remained as a narrow strip of sea entering from the Bay of Biscay at approximately 35°N palaeolatitude, but its palaeogeography changed in response to the increasing tectonic de-

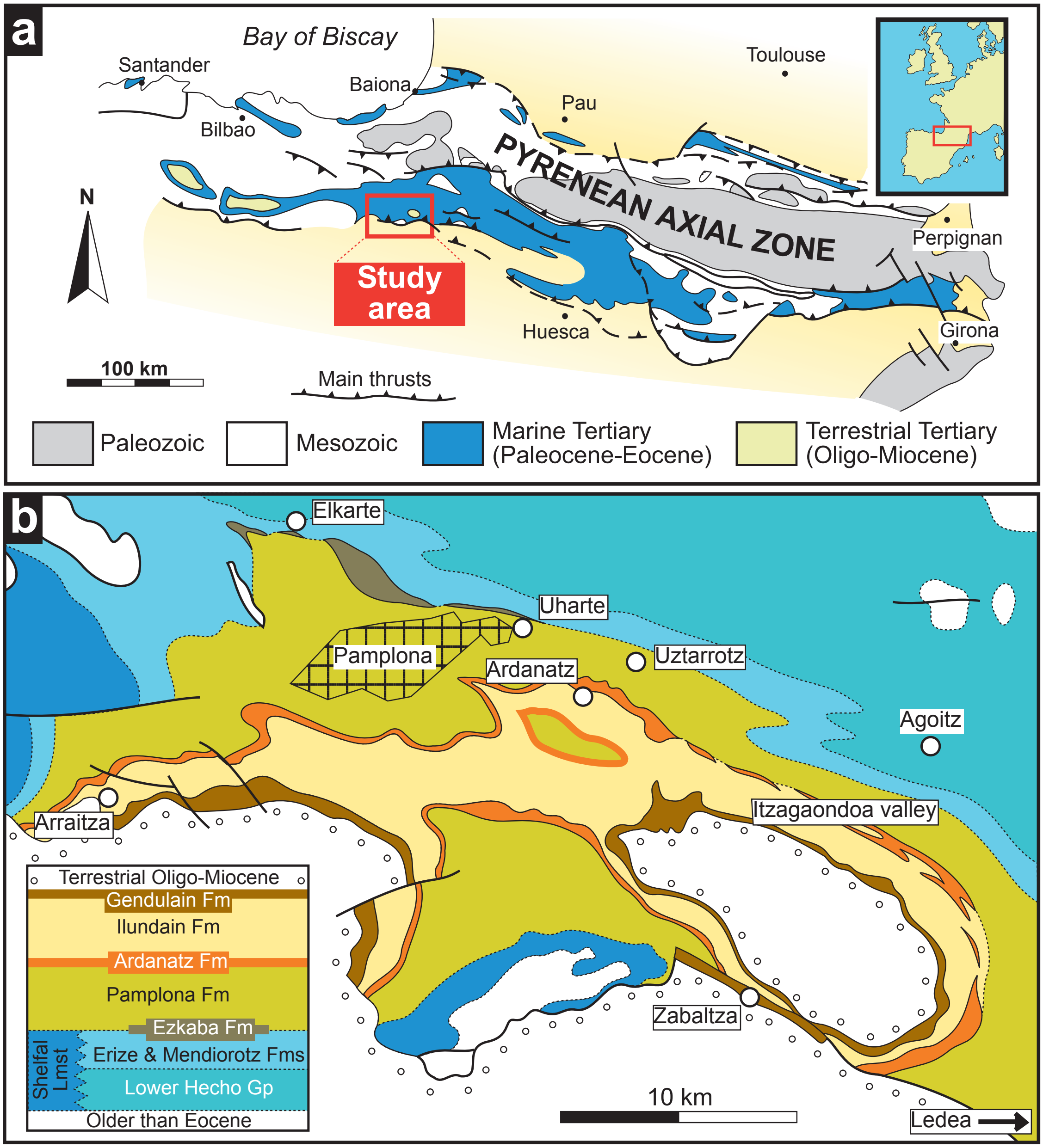

Fig. 1.- Simplified geological maps of the Pyrenees (**a**), with location of the study area in the western part of the South Pyrenean Zone (SPZ), and of the Pamplona Basin and nearby areas (**b**).

formation. During early-middle Eocene (Ypresian-Lutetian) times the basin was essentially a deep-water trough, but siliciclastic sediments derived from the uplifting and denuding Pyrenees progressively filled the basin in. The main denudation area was first located in the emergent eastern Pyrenees, where large fluviodeltaic systems developed. However, this palaeogeographic configuration progressively encroached westwards, so that by middle-late Eocene (Bartonian-Priabonian) times denudation of the orogen began in the western Pyrenees and the fluviodeltaic sedimentary context became widespread throughout the foreland basin (Plaziat, 1981; Pujalte *et al.*, 2002; Barnolas *et al.*, 2004).

The later stage is well recorded in the central part of Navarre by alternating marly and sandy lithostratigraphic units (Fig. 2). The oldest Bartonian units (Erize Marl Formation, Ezkaba Sandstone Formation and Pamplona Marl Formation) still show sedimentological and palaeontological evidence of accumulation in relatively deep waters, and they were attributed to slope (Payros *et al.*, 2010), turbiditic channel-levee (Payros *et al.*, 1997) and prodelta (Astibia *et al.*, 2005) environments, respectively. The overlying Ardanatz Sandstone Formation (also referred to as Gazolaz, Tajonar, Tabar and/or Gongolaz sandstone in the regional literature) has been thoroughly studied by Astibia *et al.* (1999, 2005, 2006, 2014). Silty marls are dominant in the locality of Ardanatz (central part of the study area), but they contain abundant tabular sandstone beds, which display sharp bases with occasional groove casts (indicating ENE palaeocurrent direction) and gradational upper boundaries; they are rich in carbonaceous plant remains, vertical and horizontal burrows (mainly Ophi-

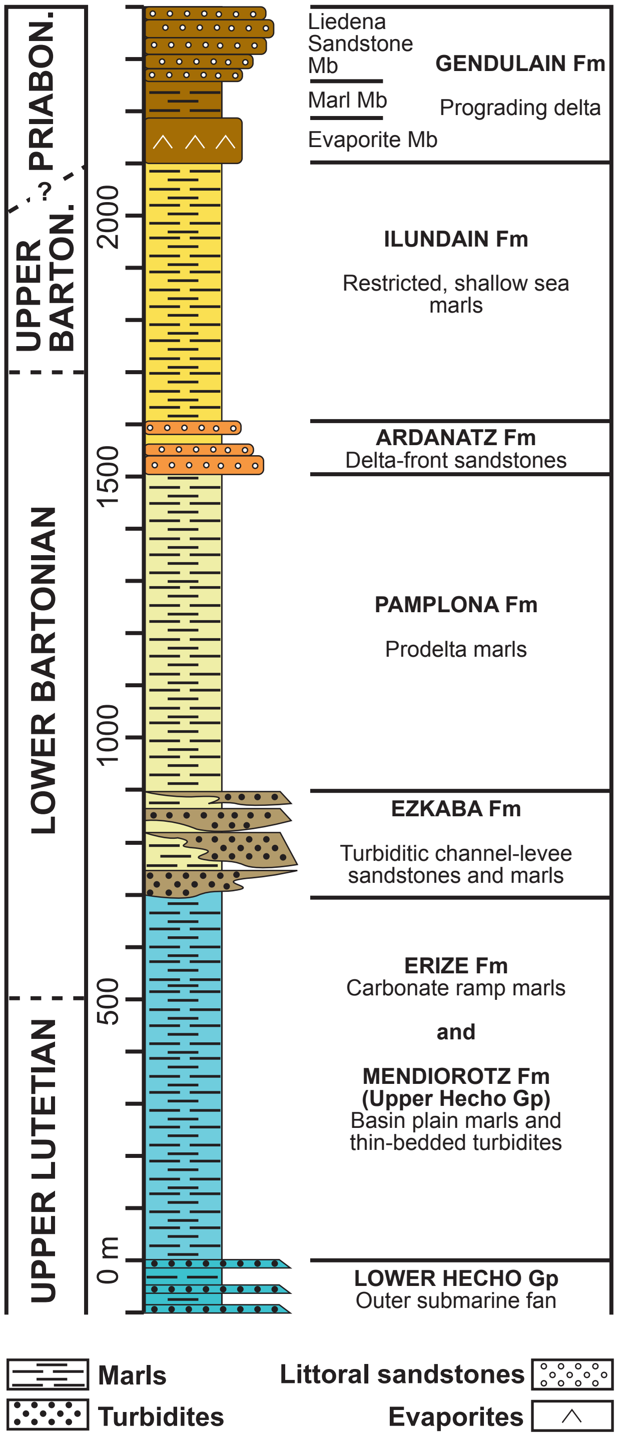

Fig. 2.- Representative columnar section of the middle and upper Eocene marly succession in the Pamplona Basin (Navarre, western Pyrenees), with its constituent lithostratigraphic units and the depositional environments so far proposed in the literature.

omorphids, *sensu* Seilacher, 2007) and bioclasts (e.g. corals and nummulitids). On the basis of their sedimentological features, the sandstone beds were interpreted as deposits from non-confined, high-concentration turbulent flows. Given that the sandstone beds are arranged in several thickening and coarsening-upward sequences, they were further interpreted as sandy hyperpycnites accumulated in flood-generated delta-front lobes (*sensu* Mutti *et al.*, 2000; 2003). In Arraitza (western part of the study area; Fig. 1b), the Ardanatz Sandstone is typified by thinner and finer-grained sandstone beds, suggesting a distal or marginal area of the Ardanatz delta front. The Ardanatz Sandstone can also be traced further to the east, bordering the Itzaga syncline, where it shows different sedimentological features (Fig. 1b). Here, laminated sandstone beds, which are normally graded and contain abundant mud clasts, are restricted to large-scale, lens-shaped lithosomes. According to these features, they were interpreted as Northwestward-directed turbiditic channels (Puigdefábregas, 1975; Leon Chirinos, 1985). However, from the general palaeogeographic layout outlined above, it is more likely that these features constituted delta-front channels across which fluvially-derived hyperpycnal flows entered the sea and eventually fed the flood-generated delta-front lobes.

The Ardanatz Sandstone Formation interfingers both laterally and vertically with the Ilundain Marl Formation (Astibia *et al.*, 2014; Fig. 2). In Arraitza, the Ilundain Marl Formation is characterized by thick tabular levels of alternating dark and light grey marls with gradational boundaries. Their siliciclastic content mainly consists of clay, whereas the carbonate content mainly derives from the abundant calcareous skeletal remains, such as bryozoans and others. The fine-grained nature of the sediment, the absence of gravity-flow deposits and the absence of light-dependant organisms suggest that the marls accumulated in a flat, aphotic seabed located below storm-wave base. This interpretation is further supported by the microforaminiferal content, similarly as common hexactinellid sponges and their preservation, which is indicative of outer-platform to upper-slope environments (Astibia *et al.*, 2014).

The Eocene succession is topped by the Priabonian Gendulain Formation (Puigdefábregas, 1975), which is composed of different types of coastal deposits, allowing its subdivision into three distinct members: lower evaporites, middle marls, and upper sandstones (Liédena Sandstone Member) (Fig. 2). Lateral variations in facies and thicknesses record the synsedimentary tectonic deformation of the study area (Cendon *et al.*, 1998; Payros *et al.*, 2000), as it progressively became a detached piggy-back basin atop of southward displacing thrust sheets. Owing to the concomitant tectonic uplift, the Gendulain Formation records the last episode of deltaic progradation from the ESE, the closure of the South Pyrenean Sea, and its definite evolution into terrestrial conditions.

3. Material and methods

The studied fossils were mainly collected from several outcrops located between the towns of Uharte and Elkarte (Ezkaba Sandstone Formation), from the localities of Uztarrotz (Eguesibar, base of the Pamplona Marl Formation), Ardanatz-Eguesibar (transition from the Ardanatz Sandstone Formation to the overlying Ilundain Marl Formation), Arraitza (approximately 100 m above the base of the Ilundain Marl Formation), from two outcrops in the Itzagaondoa Valley (in the uppermost part of the Ilundain Marl Formation), and from five outcrops between the towns of Zabaltza and Ledea-Liédena (Liédena Sandstone Member of the Gendulain Formation) (Fig. 1b). Precise locations of outcrops are not given for the protection of the fossil sites in accordance with Natural and Cultural Heritage legislation. Those who want to know further details are asked to contact the corresponding author.

A semi-quantitative study of foraminifera was carried out on two outcrops of the base of the Pamplona Marl Formation (Uztarrotz) and the uppermost part of the Ilundain Formation (Itzagaondoa Valley). These micropalaeontological data are added to those made in Arraitza (level ARR1.1), in Ardanatz (levels AD2.1 and AD3.1), and in the Liédena Sandstone (Liédena and other localities, facies B1, B3 and B4) (in Payros et al., 2000; Astibia *et al.*, 2014).

Most of the collected fossils are provisionally deposited in the Department of Stratigraphy and Palaeontology of the University of the Basque Country (Universidad del País Vasco/Euskal Herriko Unibertsitatea, UPV/EHU). A few fossils from the locality of Arraitza are housed in the Museo de Ciencias Naturales de Álava/ Arabako Natur Zientzien Museoa (MCNA) of Vitoria-Gasteiz. Most trace fossils have been photographed and studied initially in the field and only a few samples have been collected and taken to the laboratory (UPV/EHU).

4. Taphonomic remarks

The Bartonian deposits of the study area are very rich in microfossils, but not in body macrofossils, which are only locally abundant. Ichnofossils are very abundant, mainly in sandy units and marls with high terrigenous content. In Ardanatz AD3 and Arraitza ARR1 sections fossils of sponges and erected bryozoans are abundant within the silty marls (Astibia *et al.*, 2014). They usually present intense fragmentation, but often seem to correspond to complete or nearly complete specimens, without evidence of abrasion (Fig. 3a,b). From a palaeoecological point of view, they probably correspond to demic organisms, dwellers of relatively deep environments and autochthonous or parautochthonous taphonomic elements (*sensu* Fernández López, 1990; 1991), deposited during periods of reduced sedimentation in a low-energy environment. On the contrary, in several outcrops of the Ardanatz Sandstone fossils of nummulitids, corals, and many molluscs are associated mainly with levels of high terrigenous content and may have undergone taphonomic remotion processes (*sensu* Fernández López, 2000) (Fig. 3c, d).

Epibionts (small bivalves, annelid tubes and encrusting bryozoan colonies) on sponges, corals and shells of molluscs, as well as bioerosion (mainly bryozoan borings) on corals and mollusks, are frequent (Astibia *et al.*, 2014). Peripheral zone of alteration with tunnel network structures, probably made by microbial activity, are observed in thin sections of fossil sirenian ribs (Astibia *et al.*, 2005). Microfossils are often filled with pyrite. Body macrofossils are generally fragmentary, with evidence of dissolution and replacement by calcite and celestite in sponges, dissolution and aragonite-calcite neomorfism processes in corals and molluscs, and replacement by well crystallized francolite (carbonate-fluorapatite) in fossil vertebrates (Astibia *et al.*, 2005; 2014) (Fig. 3e, f). Celestite may form as a result of a rapid decomposition of organic matter in a dysoxic microenvironment that produces hydrogen sulfide. The latter can be oxidized to sulfate by subsequent bacterial sulfoxidation, and this sulfate produces celestite with the mobile strontium, the latter coming either from the aragonite-to-calcite neomorphism (Taberner *et al.*, 2002), or from other processes, such as decomposition of inherited sheet silicate mineral of continental origin with a decrease-acidification of the pH (Baker and Bloomer, 1988).

Microbial mats impressions have been identified as wrinkle marks preserved in ripple troughs and as retracted zones in the digit impressions of some bird tracks of the Liédena Sandstone (Gendulain Formation) (Fig. 3g,h) (Astibia *et al.*, in press). Microbial mats can greatly enhance the preservation of surface traces (i.e., Marty *et al.*, 2009; Carmona *et al.*, 2012). The reducing chemical conditions beneath the microbial mats may have contributed to the formation of "anoxic" minerals, such as pyrite (Schieber, 1999, 2002), which has also been observed in the surface of some slabs of the Liédena Sandstone. These anoxic conditions could explain the scarcity and low diversity of invertebrate traces in the Liédena Sandstone. According to Carmona *et al.* (2012), the microbial mats acted as taphonomic bias favouring the preservation of vertebrate tracks and conditioning the presence of endofauna.

5. Fossil assemblages

This section describes the different fossil assemblages in relation to the respective lithologic units. All the taxa and ichnotaxa recorded in the study area can be consulted in Appendix I.

5.1. Ezkaba Sandstone Formation

Only some microfossils and ichnofossils have been determined so far in this formation. Body macrofossils are scarce and fragmentary and mainly consist of tests of macroforaminifers and spines of echinoids not yet studied.

The marly deposits of the Ezkaba Formation are rich in fossils of planktic foraminifera. Among them *Orbulinoides beckmanni*, the index species that defines the biozone E12, was identified for the first time in the Pyrenean Domain (Payros *et al.*, 1997). Ichnofossils are very abundant in sandstones. The identified ichnoassemblage includes the ichnotaxa *Belorhaphe* isp., *Ophiomorpha annulata*, *Ophiomorpha rudis*, *Phymatoderma* isp., *Pilichnus dichotomus*, *Planolites* isp., *Scolizia strozzii*, and *Scolizia vertebralis* (Fig. 4a, c) (Astibia *et al.*, in press).

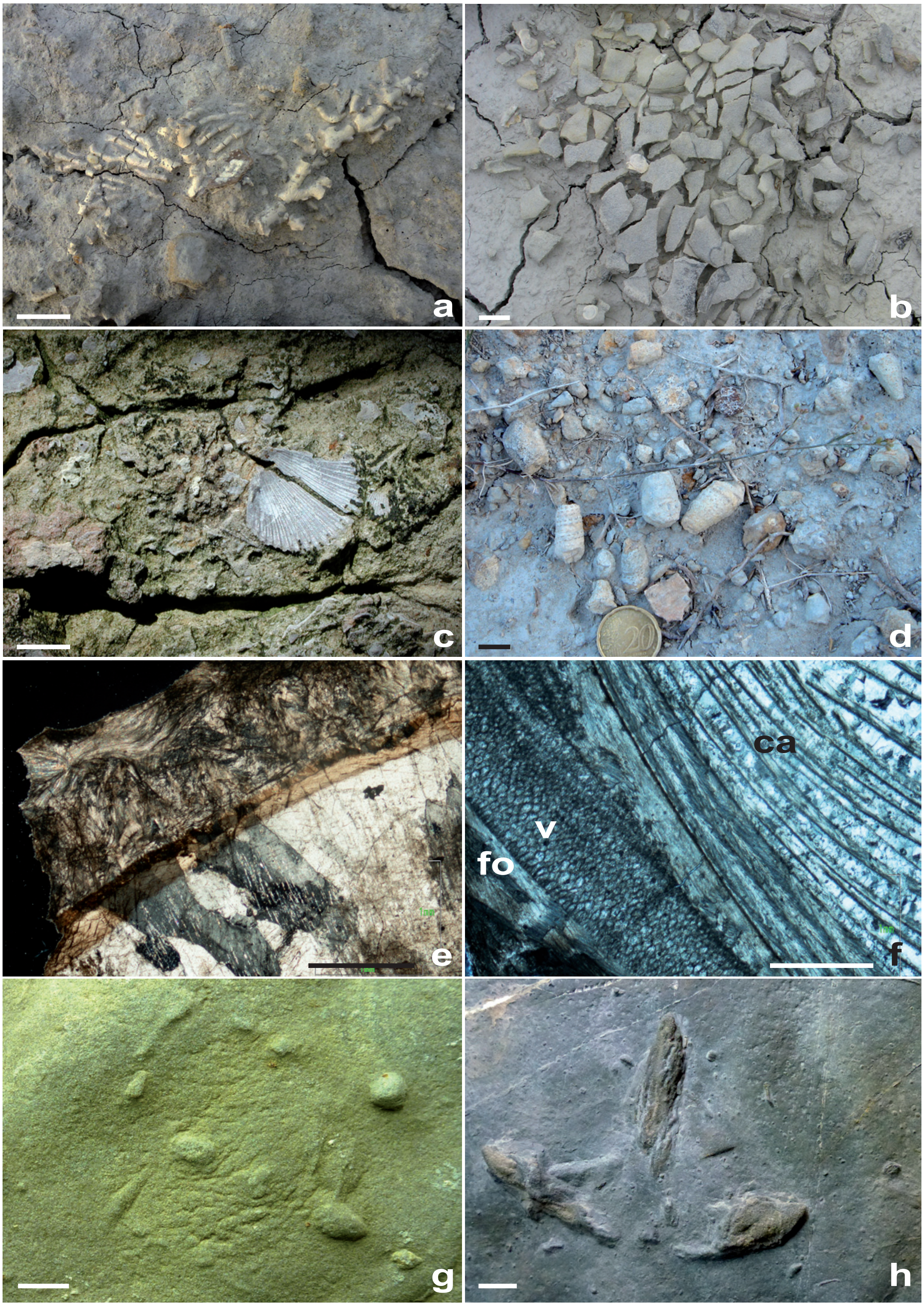

Fig. 3.- Field photographs of fossils from the middle Eocene (Bartonian) of the Ardanatz Sandstone (a, c, d) and Ilundain Marl (b) formations: **a**, colony of erect bryozoans in the silty marls showing intense fragmentation; **b**, hexactinellid sponge showing intense fragmentation (modified from Astibia *et al*., 2014); **c**, fragmentary shells of the bivalve *Chlamys* sp. (Cl) and foraminifera tests (operculiniform nummulitids of *Assilina* genus and others) in a sandstone bed; **d**, fragmentary and partially dissolved specimens of gastropods [*Ptychocerithium johannae* (Tournouër *in* Bouillé, 1873) mainly] in marls with high terrigenous content (sandy marls). Photomicrographies of fossils from Ardanatz Sandstone (e) and Ilundain Marl (f) formations: **e**, longitudinal thin-section of a specimen of *Spondylus* sp., with the original prismatic microstructure completely neomorphized by big spatic calcite crystals; **f**, tangential thin-section of a specimen of *Pycnodonte brongniarti* (Bronn, 1831), showing foliated (fo) and vesicular (v) microstructures and cementation by calcite in the empty chambers (ca). Ichnofossils from the upper Eocene (Priabonian) of the Liédena Sandstone Member (Gendulain Formation): **g**, microbial mat impression (wrinkle marks) in ripple troughs and vertical tubes; **h**, microbial mat impression as retracted zones in a bird track of cf. *Leptoptilostipus* (Liédena-Ledea section). Scale bars of **a, b, c, d**, **g**, **h** 10 mm; scale bars **e, f** 1 mm.

In the Elkarte outcrop, a marly stretch with thin interbedded turbidites, there is a predominance of ophiomorphids and graphogliptids. The determined ichnotaxa are: *Chondrites* isp., *Helminthoraphe flexuosa*, *Multina minima*, *Nereites irregularis*, *Ophiomorpha annulata*, *Ophiomorpha rudis*, *Paleodictyon strozzii*, *Planolites* isp., ?*Squamodictyon* isp., and *Taenidium crassum* (Fig. 4b) (Astibia *et al.*, in press).

5.2. Pamplona Marl Formation

Pamplona marls are rich in microfossils but the macrofauna is poor. In the Uztarrotz outcrop, an exposure in the lower part of this unit, the microassemblages are dominated by foraminifera which are associated whit common gastropods, serpulids, echinoid spines and smooth-valved ostracods. Benthic foraminifera are abundant and well preserved. Planktic foraminifera dominate the assemblages, the planktic/benthic (P/B) ratio being 75%. As for the benthic foraminiferal test composition, hyaline taxa dominate the assemblages (66%), agglutinated taxa are abundant (33%), and porcelaneous taxa are very scarce (<1%). The benthic foraminiferal assemblages are diverse (around 72 species), slightly dominated by infaunal taxa (57%). *Eponides*, *Cibicidoides*, *Lenticulina*, *Uvigerina*, *Globobulimina* species and nodosariids are the most common hyaline taxa, including *Eponides ouachitaensis*. The agglutinated taxa are dominated by trochamminids, astrorhizids (*Bathysiphon* species), *Ammobaculites* and *Marssonella* species.

Stem fragments of large isocrinid crinoids (Isselicrinidae: *Isselicrinus* sp.) are quite common throughout the lower part of the Pamplona Marl Formation. In Uztarrotz, postcranial elements of sirenian mammals have described as Dugongidae indet. (Astibia *et al.*, 2006) (Fig. 5a–g). A few spines of echinoids have also been found there. In the east of the study area ichnofossils of *Thalassinoides suevicus* are observed in the thin sandy layers interspersed in the marls. Towards the top of the Pamplona Formation trace fossils of *Ophiomorpha* and *Chondrites* among others are common.

5.3. Ardanatz Sandstone Formation

This unit and the overlying Ilundain Marl Formation have yielded the richest concentrations of body macrofossils. The fossiliferous sites occur at the transition from the Ardanatz Sandstone Formation to the overlying Ilundain Marl Formation. In the Ardanatz outcrops the micropalaeontological content is high in the intercalate marls, being dominated by foraminifera with scarce ostracods and charophyte gyrogonites (Astibia *et al.*, 2014). Benthic foraminifera strongly dominate the assemblages, the P/B ratio being 15% and 5%, respectively. Most benthic foraminifera correspond to hyaline taxa (up to 77%). Agglutinated taxa are common and porcelaneous taxa are less common. Benthic foraminiferal assemblages are moderately diverse (about 50 species), with similar proportions of epifaunal and infaunal taxa. The most common hyaline taxa are cibicidids, including *Cibicides tenuimago*, *Cibicides lobatulus* and *Cibicides refulgens*. Other benthic species present in the associations belong to *Eponides*, *Cibicidoides*, *Oridorsalis* and *Gyroidinoides* genera. Nodosariids are represented by *Anomalinoides*, *Siphonina* and *Bulimina*. The most common agglutinated taxa are calcareous-cemented taxa, including *Gaudryina abuillonensis* and *Spiroplectammina alansis*. Trochamminids and *Ammobaculites* species are common (Astibia *et al.*, 2014).

The result of the study of nummulitids provided an association formed by the species *Nummulites* aff. *cyrenaicus* (precursor form), *N.* cf. *beaumonti*, *N. ptukhiani*, *N. praegarnieri*, *Assilina schwageri*, and *Heterostegina reticulata* cf. *multifida* in the locality of Ardanatz; *N.* aff. *biedai* (precursor form), *N.* cf. *perforatus*, and *N.* aff. *cyrenaicus* in the term of Zizari-Ezkoritz; and *N.* aff. *biedai* and *N.* aff. *cyrenaicus* in the term of Lezaun (Ardanatz-Eguesibar). All these nummulitid associations characterize the top of the shallow benthic foraminiferal biozone SBZ 17 of Serra-Kiel *et al.* (1998), corresponding to the lower Bartonian (Astibia *et al.*, 1999).

In the Ardanatz outcrops body macrofossils are locally abundant. The macrofauna is mainly represented by hexactinellid and lithistid sponges, scleractinian corals, bryozoans, brachiopods, tube-dwelling polychaetes, molluscs (gastropods, bivalves, cephalopods –nautiloids– and scaphopods), arthropods (crab claw fragments), echinoderms (crinoid stalk fragments, plates –ossicles– of asteroids, and spines and test fragments of echinoids), shark teeth, turtle plates, as well as sirenian vertebrae and ribs (Figs. 5h–t, 6a–k). Sponges and corals have been described in Astibia *et al.* (2014). Among the former there are *Laocoetis samueli*, *Guettardiscyphia thiolati* and/or *Pleuroguettardia iberica*, cf. *Rhizocheton robustus*, and one indeterminate lithistid (Fig. 5h–j). Corals are represented by *Stylocoenia taurinensis*, *Astrocoenia octopartita*, *Ceratotrochus bodellei*, *Placosmiliopsis bilobatus* and *Desmophyllum castellolense* (Fig. 5k–m). Among bryozoans there are representatives of the Stenolaemata Lichenoporidae, Gymnolaemata Cupuladriidae and numerous erect forms, which are locally very abundant and well-preserved, but not yet studied (Figs. 3a, 5n). Micromorphic brachiopods (*Terebratulina tenuistriata*) are abundant in marly levels of the lower part of studied sections (Fig. 5o, p). Among the annelids, the polychaete *Rotularia spirulaea* is very abundant, being one of the most characteristic macrofossils of the middle and upper parts of the prospected sections (Fig. 5q). Scarce remains of vertebrates, including turtles and sirenians, have been assigned to indeterminate chelonians and dugongids, respectively (Astibia *et al.*, 1999; 2005; 2006; Buffrénil *et al.*, 2008) (Fig. 5t).

With the exception of a brief note on *Dimya pamplonensis* (Calzada and Astibia, 1996) nothing has been published to date about the fossil molluscs. A study on the molluscs (Gastropoda and Bivalvia) is ongoing. The gastropod association contains the following taxa: *Leptomaria peresii*, *Ptychocerithium johannae*, *Diastoma costellatum*, *Haustator*

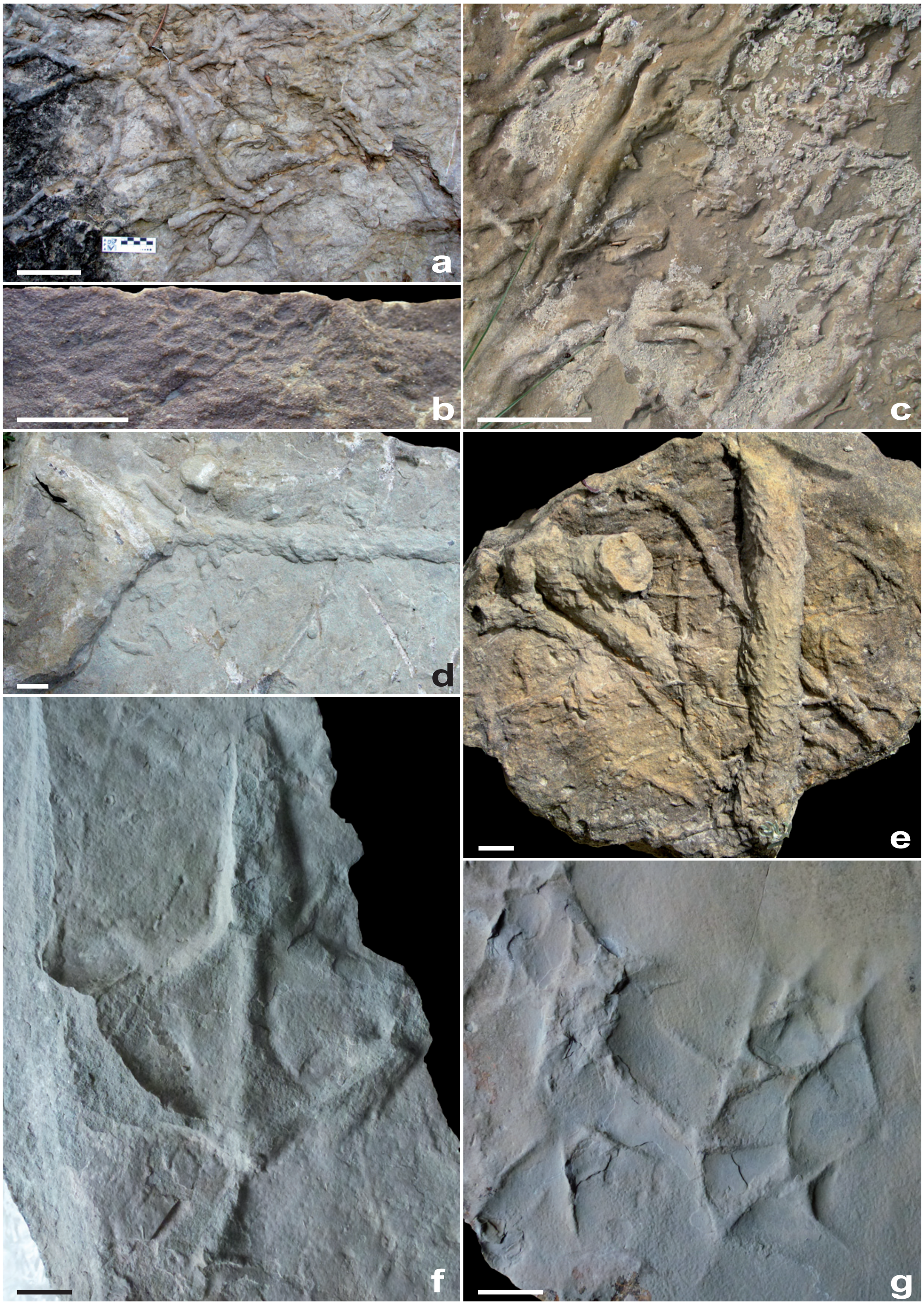

Fig. 4.- Trace fossils from the middle Eocene (Bartonian) of the Ezkaba Formation: **a**, *Ophiomorpha rudis* (Książkiewicz, 1977), epichnia; **b**, *Paleodictyon strozzii* Meneghini *in* Savi and Meneghini, 1850, hypichnion; **c**, *Scolicia strozzii* (Savi and Meneghini, 1850), hypichnion. Trace fossils from the middle Eocene (Bartonian) of Ardanatz Sandstone-Ilundain Marl formations: **d**, *Ophiomorpha* isp., hypichnion; **e**, *Spongeliomorpha* cf. *oraviense*, hypichnia. Trace fossils from the upper Eocene (Priabonian) of Liédena Sandstone (Gendulain Formation): **f**, J1, *Leptoptilostipus pyrenaicus* Payros, Astibia, Cearreta, Pereda-Suberbiola, Murelaga and Badiola, 2000, hypichnion.**g**, LH2, *Koreanaornis* isp., hypichnia. All the traces are preserved in sandstone beds. Modified from Astibia *et al.* (in press). Scale bars of **a**, **c** 100 mm; scale bars of **b**, **d, e**, **f**, **g** 10 mm.

altavillensis, *Haustator* cf. *imbricatarius conoideus, Sigmesalia* sp., Ampullinidae indet., ?*Globularia* sp., *Cirsotrema* (*Elegantiscala*) cf. *bouillei*, *Amaea* sp., *Clavilithes (Clavellofusus)* cf. *parisiensis*, Muricidae indet., *Athleta (Volutospina)* sp., Conidae indet., and *Nihonia* aff. *transversaria* (Figs. 3d, 6a–e). *Ptychocerithium johannae* is by far the most abundant species in the macrogastropod association. The provisional list of bivalves is as follows: *Hyotissa martinsi*, Ostreoidea indet., *Chlamys* cf. *biarritzensis*, *Chlamys* sp., *Spondylus* cf. *bifrons*, *Spondylus* cf. *caldesensis*, *Spondylus* sp., *Dimya* *pamplonensis*, *Chama pellati* and *Chama granulosa* (Figs. 3c,e, 6f–h). Fossil scaphopods (*Dentalium* sp.) are abundant (Fig. 6i). Finally, rare cephalopods (Nautilolidea indet.) also occur (Fig. 6j, k).

The fossil ichnoassemblages of the Ardanatz Sandstone are dominated by ophiomorphids (*sensu* Seilacher, 2007), with abundance of the ichnospecies *Ophiomorpha nodosa*. Other ichnotaxa present, decreasing in abundance, are *Ophiomorpha* isp., *Thalassinoides* isp, *Spongeliomorpha* cf. *oraviense*, and *Halopoa imbricata* (Fig. 4d, e) (Astibia *et al.*, in press).

5.4. Ilundain Marl Formation

At the west end of the study area, located approximately 100 m above the base of the Ilundain Formation, are the Arraitza outcrops (Fig. 1b). The microfossils are characterized by the abundance, good preservation and dominance of benthic foraminifera. Planktic foraminifera are scarce (P/B ratio 28%) and show low diversity; they are strongly dominated by chiloguembelinid taxa. As for the benthic foraminifera, hyaline taxa dominate the assemblages (80%), agglutinated taxa are common, and porcelaneous taxa are rare. The benthic foraminiferal assemblages are diverse (average 90 species), with similar proportions of infaunal and epifaunal taxa. *Cibicidoides*, *Eponides*, cibicidids, elongate uniserial taxa (nodosarids and stilostomellids), and buliminids are the most common hyaline taxa, and include *Cibicidoides ungerianus*, *Eponides ouachitaensis* and *Cibicides lobatulus*. The agglutinated taxa are dominated by trochamminids; the most characteristic are the tubular forms (*Bathysiphon*) (Astibia *et al.*, 2014).

The body macrofossil assemblages from Arraitza include numerous fossils of the sponges *Laocoetis samueli*, cf. *Rhizocheton robustus***,** cf. *Phlyctia expansa*, and two undeterminated lithistids (Fig. 3b). Further components of the association are undetermined corals (scarce), Lichenoporidae and other bryozoans, the brachiopods *Terebratulina tenuistriata* and ?*Gryphus* sp., the polychaete *Rotularia spirulaea* (rare), the bivalves *Spondylus* cf. *bifrons*, *Dimya pamplonensis* and indeterminate ostreoids, the barnacle *Arcoscalpellum* sp., echinoid spines and test fragments (Cidaridae and others), asteroid ossicles, and the chondrichthyans *Hexanchus agassizi*, *Macrorhizodus praecursor*, *Anomotodon* sp. and *Woellsteinia kozlovi*. Teleostean teeth (*Enchodus* sp.) and otoliths (*Chaetodipterus* sp. and others) are also common among the fossils of Arraitza (Fig. 5u–z).

In the uppermost part of the Ilundain Formation, towards the eastern part of the study area, in the Itzagaondoa Valley, the fossil association changes significantly. The microassemblage is dominated by foraminifera with common ostracods. The foraminifers are abundant and benthic foraminifera strongly dominate the assemblages, the P/B ratio being 11%. As for the benthic foraminifers, hyaline taxa dominate the assemblages (50%), agglutinated taxa are abundant (38%), and porcelaneous taxa are common (12%). Benthic foraminiferal are moderately diverse (around 41 species), with similar proportions of epifaunal and infaunal taxa. The most common hyaline taxa are *Cibicidoides* and *Planulina* species, and *Marginulina behmi*. The most common agglutinated taxa are calcareous-cemented taxa such as *Ammobaculites pyrenaicus* and *Textularia* species; rzehakinids are also common.

Macrofauna in the Itzagaondoa outcrops includes fossils of solitary corals (*Ceratotrochus bodellei* and others), bryozoans (Gymnolemata Cupuladriidae and erected forms), micromorphic brachiopods (*Argyrotheca michelottina*), tube-dwelling polychaetes (*Rotularia spirulaea* and others), and mollusc bivalves, gastropods and scaphopods. The mollusc assemblage includes the gastropods *Ptychocerithium johannae*, *Diastoma costellatum, Moniquia* sp., *Haustator altavillensis*, *Haustator* cf. *imbricatarius conoideus, Sigmesalia* sp., *Sassia* sp., *Niso* sp., *Metula (Celatoconus)* sp., *Clavilithes (Clavellofusus)* cf. *parisiensis,* Muricidae indet., *Athleta (Volutospina)* sp., Conidae indet. and *Mathilda* sp., among others (Fig. 6l–p). *Diastoma costellatum* and *Haustator* cf. *imbricatarius conoideus* are the most abundant macrogastropods. The provisional list of bivalves of the Itzagaondoa outcrops is as follow: *Glycymeris jacquoti*, *Pycnodonte brongniarti*, *Chlamys* sp., *Spondylus* sp. cf. *S. cisalpinus*-*S. nysti*, *Spondylus planicostatus*, *Venericardia junctinova* and *Chama pellati.* (Figs. 5f, 6q–v). Fossils of these taxa, except perhaps *Spondylus planicostatus*, which is common, are numerous. Scaphopods are also abundant.

As in the Ardanatz Sandstone unit, the ichnological analysis of the sandy levels intercalated in the lower part of the Ilundain marls shows abundant ophiomorphids, especially *Ophiomorpha* isp. (aff. *O. nodosa*-*O. irregulaire*). Other ichnotaxa found are *Halopoa imbricata*, *Planolites* isp., *Spongeliomorpha* cf. *oraviense*, *Spongeliomorpha* cf. *sicula*, and *Thalassinoides* isp., together with spreite burrows (?*Rhizocorallium*) (Fig. 4d,e) (Astibia *et al.*, in press).

5.5. Gendulain Formation (Liédena Sandstone Member)

The studied section culminates with the intertidal deposits of the Liédena Sandstone (Gendulain Formation) containing benthic microforaminifera of the Priabonian and abundant trace fossils of invertebrates and aquatic birds (Payros *et al.*, 2000; Astibia *et al.*, 2007). Identified invertebrate trace fossils in Liédena Sandstone are *Cochlichnus* isp., *Palaeophycus tubularis* and vertical tubes (Fig. 3g). The bird footprints are assigned to: *Gruipeda* isp., *Koreanaornis* isp., cf. *Koreanaornis*, *Leptoptilostipus pyrenaicus* and cf. *Leptoptilostipus* (Figs. 3h, 4f,g) (Astibia *et al.*, in press).

6. Discussion. Palaeoenvironments and comparisons

The palaeoenvironmental information provided by the different fossil assemblages described above (foraminifers, body macrofossils and ichnofacies) is in line with the sedimentological evolution of the Pamplona Basin. Thus, both data sets record the transition from deep-sea conditions to

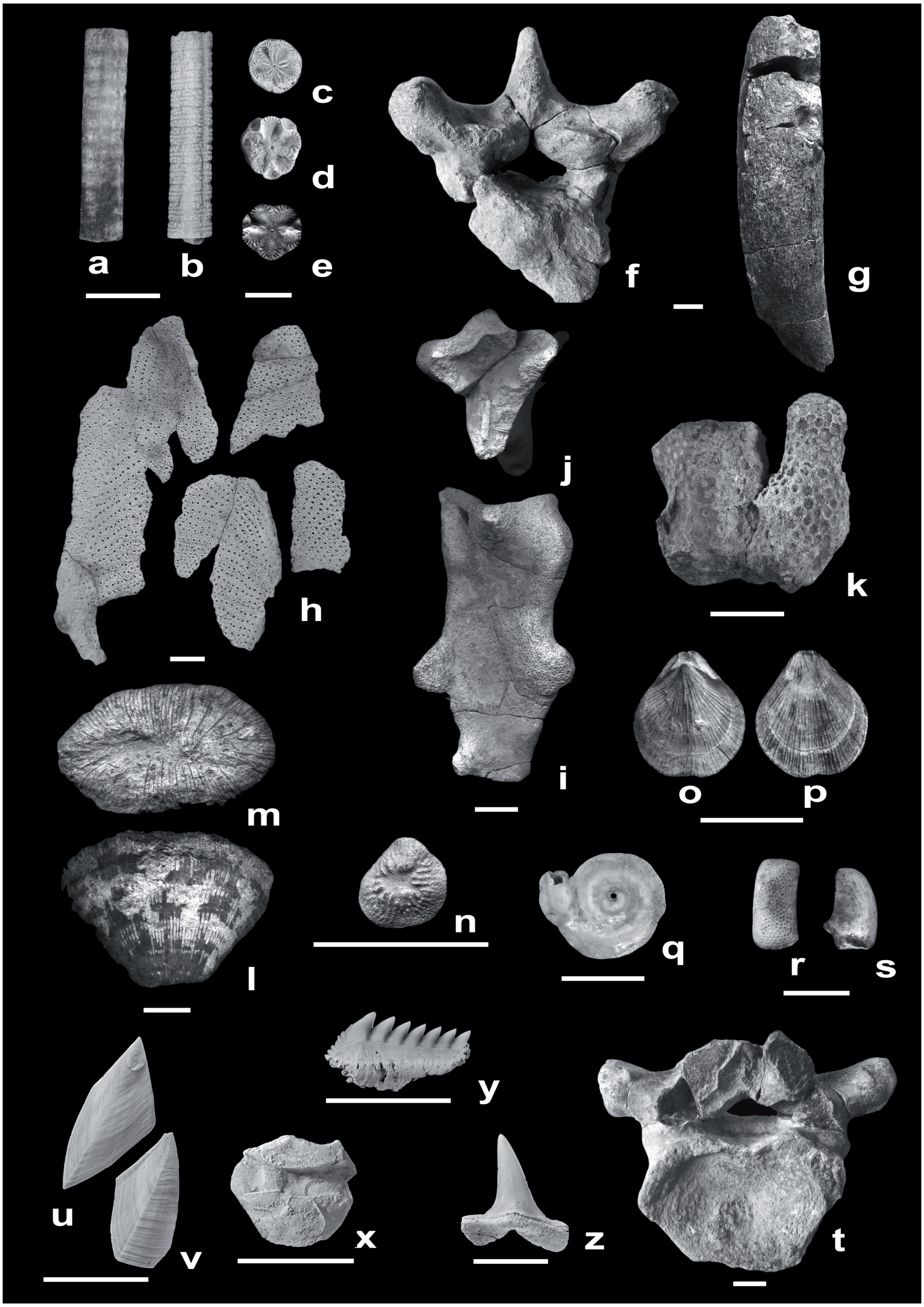

Fig. 5.- Body fossils from the middle Eocene (Bartonian) of the Pamplona Marl Formation. *Isselicrinus* sp.: **a,** UZ1.32, and **b,** UZ1.33, stem fragments in side view; **c**, UZ1.34, internodal in articular view; **d,** UZ1.35, and **e,** UZ1.36, nodals in articular view. Dugongidae indet.: **f,** UZ1.6, thoracic vertebra in anterior view; **g,** UZ1.22, rib fragment in dorsal view. Body fossils (non-molluscs) from the middle Eocene (Bartonian) of the Ardanatz Sandstone (h-t) and Ilundain Marl (u-z) formations. *Laocoetis samueli* (d'Archiac, 1850): **h**, AD3.1.3, fragments of the same specimen, outer and inner side views. *Guettardiscyphia thiolati* (d'Archiac, 1846) and/or *Pleuroguettardia iberica* Pisera and Busquets, 2002: **i–j,** AD3.1.2, lower part in lateral view and cross section respectively. *Stylocoenia taurinensis* (Michelin, 1842): **k**, AD.10, fragment of a ceroid colony. *Placosmiliopsis bilobatus* (d'Achiardi, 1868): **l–m,** AD.04, lateral and upper views. Lichenoporidae indet.: **n,** AD3.1.14, upper view. *Terebratulina tenuistriata* (Leymerie, 1846): **o–p**, AD.50, dorsal and ventral views. *Rotularia spirulaea* (Lamarck, 1818): **q**, AD2.2.6, lower (attachment) view. Asteroidea indet.: **r–s**, AD.49, marginal plate, dorsal (abradial) and lateral views. Dugongidae indet.: **t,** AR1.6, posterior thoracic vertebra in posterior view. *Arcoscalpellum* sp.: **u**, MCNA 15164, capitular plate (tergum), external left view; **v**, MCNA 13736, capitular plate, (scutum), external left view. *Chaetodipterus* sp.: **x**, MCNA, right otolith. *Hexanchus agassizi* Cappetta, 1976: **y**, MCNA 10637, lingual view. *Woellsteinia kozlovi* Adnet, 2006: **z**, MCNA 10608, lingual view. Scale bars 10 mm.

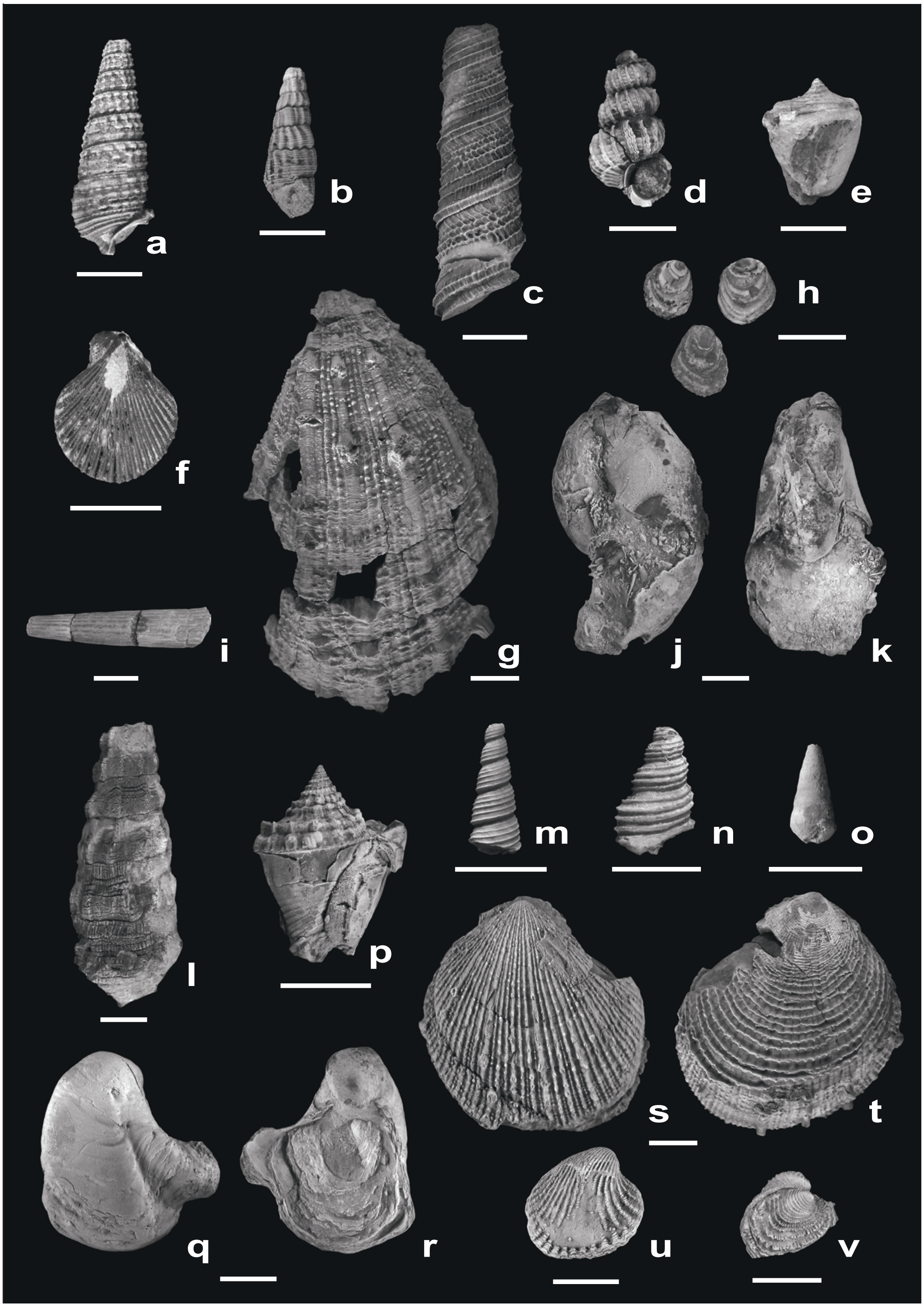

Fig. 6.- Fossil molluscs from the middle Eocene (Bartonian) of the Ardanatz Sandstone Formation. *Ptychocerithium johannae* (Tournouër *in* Bouillé, 1873): **a**, AG1.4.3, apertural view. *Diastoma costellatum* (Lamarck, 1804): **b**, AD1.3.3, apertural view. *Haustator altavillensis* (Cossmann and Pissarro, 1902): **c**, AD2.2.2. *Cirsotrema* (*Elegantiscala*) cf. *bouillei* (Tournouër *in* Bouillé, 1873): **d**, AD2.1.9, apertural view. Conidae indet.: **e**, AD.35, abapertural view. *Chlamys* sp.: **f**, AD6.1.1. *Spondylus* cf. *caldesensis* Carez 1881: **g**, AD5.1.2, right valve, external view. *Dimya pamplonensis* (Carez, 1881): **h**, TR1.1.2 (right), left valve, TR1.1.3 (left), right valve, TR1.1.4 (centre), right valve, external views. *Dentalium* sp.: **i**, AD1.3.5. Nautiloidea indet.: **j–k**, AD.48, lateral and septal views respectively. Fossil molluscs from middle-upper? Eocene (Bartonian- Priabonian?) of the uppermost part of the Ilundain Marl Formation. *Moniquia* sp.: **l**, IV.1. *Athleta (Volutospina)* sp.: **p**, IV.5, apertural view. *Haustator* cf. *imbricatarius conoideus* (Sowerby J., 1814): **m**, IV.2. *Sigmesalia* sp.: **n**, IV.3, apertural view? *Niso* sp.: **o**, IV.4, apertural view. *Pycnodonte brongniarti* (Bronn, 1831): **q–r**, IV.9, left and right valves respectively, external views. *Spondylus* sp. cf. *Spondylus cisalpinus* Brongniart, 1823 – *Spondylus nysti* d'Archiac, 1846: **s–t**, IV.6, left and right valves, external views. *Venericardia junctinova* Cossmann, 1897: **u**, IV.7, right valve, external view. *Chama pellati* Boussac, 1911: **v**, IV.8, right valve and overlapping left valve, external views. Scale bars 10 mm.

Lithological units	Outcrops	*Belorhaphe* isp.	*Chondrites* isp.	*Helminthorhaphe flexuosa*	*Multina minima*	*Nereites irregularis*	*Ophiomorpha annulata*	*Ophiomorpha rudis*	*Paleodictyon strozzii*	*Phymatoderma* isp.	*Pilichnus dichotomus*	*Planolites* isp.	*Scolizia strozzii*	*Scolizia vertebralis*	?*Squamodictyon* isp.	*Taenidium* cf. *crassum*	*Thalassinoides suevicus*	*Holopoa imbricata*	*Ophiomorpha nodosa*	*Ophiomorpha* isp. 1	*Ophiomorpha* isp. 2	*Spongeliomorpha* cf. *oraviense*	*Spongeliomorpha* cf. *sicula*	Spreite burrow indet.	*Thalassinoides* isp.	*Cochlichnus* isp.	*Paleophycus tubularis*	Vertical tubes	*Gruipeda* isp.	*Koreanaornis* isp.	Cf. *Koreanaornis*	*Leptoptilostipus pyrenaicus*	Cf. *Leptoptilostipus*
Liédena Sandstone	Zabaltza, Ledea, others																									●	●	●	●	⬤	●	⬤	●
Ilundain Fm.	Zolina, Badoztain											●						●		●		●	●	●									
Ardanatz Sandstone	Ardanatz																	●	⬤		⬤	⬤	●		●								
Pamplona Fm.	Grez, Egues		●														●																
Ezkaba Fm.	Elkarte, others	●	●	●	●	●	●	⬤	⬤	●	●	●	●	●	●	●																	

Fig. 7.- Lithostratigraphic units of the Pamplona Basin (Navarre, western Pyrenees) and vertical distribution of trace fossils. Solid dots indicate the record of different ichnotaxa in each outcrop (large dots indicate special abundance).

deltaic progradation and, eventually, a definite emersion into terrestrial conditions, which was the result of overfilling the basin as a consequence of the progressive uplift and denudation of the Pyrenees. Furthermore, the fossil assemblages allow the general paleonvironmental evolution to be analyzed more in detail and comparisons with neighbouring areas to be made.

6.1. Ezkaba Sandstone Formation (Fig. 7)

The trace-fossil assemblage of the Ezkaba Sandstone Formation, the older unit considered in this work, is characteristic of the deep-sea *Nereites* ichnofacies, as revealed by the presence of graphoglyptids (Uchman and Wetzel, 2011; Wetzel and Uchman, 2012). This agrees with the richness in planktic foraminifers of the marly deposits of this unit and the sedimentological interpretation of the Ezkaba Sandstone as channel-fill deposits of a laterally migrating channel-levee turbidite system (Payros *et al.*, 1997).

When sandstones predominate ichnoassemblages show a low diversity and are characterized by the dominance of *Ophiomorpha* (*O. rudis* and *O. annulata*) and the presence of *Scolicia* (*S. strozzii* and *S. vertebralis*), supporting the differentiation of the *Ophiomorpha rudis* ichnosubfacies of the *Nereites* ichnofacies. The *Ophiomorpha rudis* ichnosubfacies, as defined by Uchman (2009), occurs in channel and proximal lobe facies of deep-sea fans or in thick-bedded fans of deep-sea clastic ramps.

In the marly stretchs with thin interbedded turbidites (Elkarte outcrop) the presence of graphoglyptids (*Paleodictyon strozzii*, cf. *Squamodictyon* isp. and *Helminthorhaphe flexuosa*) suggests the *Paleodictyon* ichnosubfacies of the *Nereites* ichnofacies or a mixed *Paleodictyon-Ophiomorpha rudis* ichnosubfacies ichnoassemblage. The *Paleodictyon* ichnosubfacies was defined by Seilacher (1974) for more sandy and more muddy distal flysch deposits (Uchman, 2001; Uchman and Wetzel, 2011).

These ichnosubfacies are worldwide distributed and occur in geographically and geologically nearby systems of the Ezkaba Formation, such as the Early/Middle Eocene (Ypresian-Lutetian) deep-marine systems of the Hecho Group (Ainsa-Jaca Basin, Aragon, west-central South Pyrenean Area) (Uchman, 2001; Heard and Pickering, 2008) (Fig. 2). *Ophiomorpha rudis* and *Paleodictyon* ichnosubfacies are also present in the deep-marine Eocene of the Basque Basin (Rodríguez-Tovar *et al.*, 2010; Cummings and Hodgson, 2011).

6.2. Pamplona Marl Formation (Figs. 7, 8)

Upwards in the sedimentary series of the study area, in the base of the Pamplona Marl Formation, the moderately high proportion of planktic foraminifera and the high diversity and composition of benthic foraminifera, including the presence of agglutinated tubular forms (astrorhizids; Murray *et al.*, 2011), still are indicative of relatively deep-water, outer-platform to upper slope environments (Leckie and Olson, 2003; Murray, 2006). The stalked crinoid *Isselicrinus* is an extinct genus (Late Cretaceous-Miocene) of wide biogeographic distribution. Fujiwara *et al.* (2005) described the likely way of life for the individuals, which adopted a relay strategy in the muddy substrate using pre-existing upright columns as anchorage mechanism for the attachment to the sea bottom. *Isselicrinus* is regarded as a crinoid adapted to low energy muddy environments (Fujiwara *et al.*, 2005). Malubián and Olivero (2005) have indicated that the species of this genus are mostly restricted to deep-water settings in the Cenozoic. Roux *et al.* (2006) propose a bathymetric zonation of the genus *Isselicrinus* in the Eocene marls of Miretrain (Aquitaine, North-Pyrenean Basin foreland), describing four (eco)phenothypes to be indicative of depths between 200 and 1000 m

Lithological units	Outcrops	Laocoetis samueli	Cf. Rhizocheton robustus	Guettardiscyphia thiolati - P. iberica	Cf. Fhlyctia expansa	Lithistid indet. 1	Lithistid indet. 2	Stylocoenia taurinensis	Astrocoenia octopartita	Ceratotrochus bodellei	Placosmiliopsis bilobatus	Desmophyllum castellolense	Lichenoporidae indet.	Cupuladriidae indet.	Argyrotheca michelottina	?Gryphus sp.	Terebratulina tenuistriata	Rotularia spirulaea	Arcoscalpellum sp.	Isselicrinus sp.	Crinoidea indet.	Asteroidea indet.	Echinoidea indet.	Hexanchus agassizi	Macrorhizodus praecursor	Woellsteinia kozlovi	Anomotodon sp.	Enchodus sp.	Chaetodipterus sp.	Testudines indet.	Dugongidae indet.
Ilundain Fm.	Itzagaondoa									•				●	•			●				•	•								
	Arraitza	•	●		●	•	●						•			•	●	•	•			•	•	•	•	•	•	•	•		
Ardanatz Sandstone	Ardanatz	●	●	●		•		•	•	•	•	•	•	•			●	●			•	•	•		•					•	•
Pamplona Fm.	Uztarrotz																			●			•								•

Fig. 8.- Lithostratigraphic units of the Pamplona Basin (Navarre, western Pyrenees) and vertical distribution of fossil invertebrates (non-molluscs). Solid dots indicate the record of different taxa in each outcrop (large dots indicate special abundance).

or more. *Isselicrinus* (*I. didactylus*) is a common crinoid in the Eocene (Bartonian) of Biarritz / Miarritze (Basque Coast, southwestern Aquitaine Basin) (Roux, 1978).

Uztarrotz sirenian fossils consist of disarticulated vertebrae and ribs. They presumably come from the same individual. The sedimentological features of the Pamplona Marl Formation in Uztarrotz and their palaeontological content (microforaminifera and crinoids) indicate a deep marine environment. Therefore, it is likely that the sirenian remains correspond to an ademic organism (*sensu* Fernández López, 1990; 2000). Thus, the sirenian bones could have been derived from a floating carcass swept into the open sea (Astibia *et al.*, 2005).

Fossils of Sirenia are relatively abundant in the middle and late Eocene of the northern margin of the Tethys. In the Pyrenean Realm, sirenian remains have been described in a number of middle and upper Eocene localities from the Catalonian Basin (Pilleri *et al.*, 1989; Galobart *et al.*, 1992). These have generally been assigned to genus *Prototherium*. The sirenian fossil remains found in the central-western Pyrenees were still rather scarce and fragmentary (Bouillé, 1876; Pilleri *et al.*, 1989; Gómez, 1998; Astibia *et al.*, 1999; 2005; 2006), but the most complete fossil collection of the oldest sea cow from Western Europe have been recently found in deltaic deposits of the Sobrarbe Formation (Ainsa Basin, Aragon) (Badiola *et al.*, 2011; Díaz-Berenguer *et al.*, 2014).

6.3. Ardanatz Sandstone and Ilundain Marl formations (Figs. 8, 9)

As noted above, the Ardanatz Sandstone and Ilundain Marl formations are the richest units with body macrofossils in the study area. In Ardanatz outcrops (Ardanatz Sandstone Formation) the low proportion of planktic foraminifera and the high abundance of benthic foraminifera, their composition (including common porcelaneous foraminifera) and moderate diversity suggest a shelfal depth of deposition (Murray, 2006).

By contrast, the palaeontological and stratigraphic data indicate that the Arraitza outcrop (Ilundain Marl Formation) may correspond to somewhat deeper environments (Astibia *et al.*, 2014). The scarcity of planktic foraminifera in Arraitza, which is slightly higher than in Ardanatz, and the diversity and composition of benthic foraminifera, including the presence of agglutinated tubular forms (Jones and Charnock, 1985; Murray *et al.*, 2011), are indicative of outer-platform to upper-slope environments. The peak in chiloguembelinid abundance and the high abundance of benthic foraminifera may be indicative of increased local productivity in this area.

There are clear differences between the faunal compositions of the Arraitza and Ardanatz outcrops. Among the sponges *Guettardiscyphia/ Pleuroguettardia* have been found only in the Ardanatz AD3 section, and cf. *Phlyctia expansa* and indetermined lithistid sp. 2 only occur in Arraitza (Astibia *et al.*, 2014). Corals and molluscs are less abundant and diverse in Arraitza, unlike what happens with shark teeth fossils.

Eastward in the study area and in the uppermost part of the Ilundain Marl Formation, the scarcity of planktic foraminifera and the composition of the moderately diverse benthic foraminifera (including common porcelaneous foraminifera) suggest an inner shelfal depth of deposition (Leckie and Olson, 2003; Murray, 2006).

The comparison between fossil-invertebrate associations of Ardanatz and Itzagaondoa valley outcrops highlights the existence of notable differences wetween them. In the Itzagaondoa outcrops no sponges have been found. In Ardanatz (and Arraitza) hexactinellid and lithistid sponges occur. Most hexactinellids live in rather deep waters on soft substrates (Vacelet, 1988; Tabachnik, 1991; Charbonnier *et al.,* 2007; Pisera *et al.,* 2006). Accordingly, the shallower sedimentary environment of the Itzagaondoa outcrops could explain their

Lithological units	Outcrops	*Leptomaria peresii*	*Ptychocerithium johannae*	*Diastoma costellatum*	*Moniquia* sp.	*Haustator altavillensis*	*Haustator* cf. *imbricatarius conoideus*	*Sigmesalia* sp.	Ampullinidae indet.	?*Globularia* sp.	*Sassia* sp.	*Cirsotrema* (*Elegantiscala*) cf. *bouillei*	*Amaea* sp.	*Niso* sp.	*Metula* (*Celatoconus*) sp.	*Clavilithes* (*Clavellofusus*) cf. *parisiensis*	Muricidae indet.	*Athleta* sp.	Conidae indet.	*Nihonia* aff. *transversaria*	*Mathilda* sp.	*Glycymeris jacquoti*	*Pycnodonte brongniarti*	*Hyotissa martinsi*	Ostreoidea indet.	*Chlamys* cf. *biarritzensis*	*Chlamys* sp.	*Spondylus* cf. *bifrons*	*Spondylus* cf. *caldesensis*	*Spondylus* sp. cf. *S. cisalpinus* - *S. nysty*	*Spondylus planicostatus*	*Spondylus* sp.	*Dimya pamplonensis*	*Venericardia junctinova*	*Chama pellati*	*Chama granulosa*	*Dentalium* sp.	Nautiloidea indet.
Ilundain Fm.	Itzagaondoa		●	⬤	●	●	⬤	●			●			●	●	●	●	●	●		●	⬤	⬤		●		●			⬤	●			⬤	⬤		⬤	
	Arraitza																								●			●					●					
Ardanatz Sandstone	Ardanatz	●	⬤	●		●	●	●	●	●		●	●			●	●	●	●	●				●	●	●	●	●	⬤			●	●		●	●	⬤	●

Fig. 9.- Lithostratigraphic units of the Pamplona Basin (Navarre, western Pyrenees) and vertical distribution of fossil molluscs. Solid dots indicate the record of different taxa in each outcrop (large dots indicate special abundance).

absence. Regarding the mollusc associations, the most notable differences between fossil-invertebrate associations of Ardanatz and Itzagaondoa valley outcrops are: (1) the abundance of phytophagous gastropod *Ptychocerithium joahannae* in Ardanatz sections and its scarcity in the Itzagaondoa valley; (2) the presence in the Ardanatz sections of Ampullinidae indet., ?*Globularia* sp., *Cirsotrema* (*Elegantiscala*) cf. *bouillei*, *Amaea* sp., *Clavilithes* (*Clavellofusus*) cf. *parisiensis*, *Nihonia* aff. *transversaria*, *Spondylus* cf. *caldesensis*, *Dimya pamplonensis* and *Chama granulosa*, among others and its absence in the Itzagaondoa localities; on the contrary (3) the abundance of phytophagous gastropod *Diastoma costellatum* in the Itzagaondoa outcrops and its scarcity in the Ardanatz outcrops; and (4) the presence of *Moniquia* sp., *Sassia* sp., *Niso* sp., *Metula* (*Celatoconus*) sp., *Mathilda* sp., *Pycnodonte brongniarti*, *Spondylus planicostatus*, *Spondylus* sp. cf. *Spondylus cisalpinus-S. nysti* and *Venericardia junctinova* in the Itzagaondoa outcrops, which are absent in the Ardanatz sections. Although differences between the composition of these associations can be observed, they share numerous phytophagous gastropods (*Ptychocerithium*, *Diastoma*, *Globularia* and Ampullinidae indet) reflecting shallow waters in the euphotic zone.

Trace fossil assemblages at the Ardanatz Sandstone and Ilundain Marl formations, with dominance of *Thalassinoides* and *Ophiomorpha*, could be related to the *Cruziana* ichnofacies. The archetypal *Cruziana* ichnofacies occurs from just slightly above the fair-weather base to the storm wave base, from the lower shoreface to the lower offshore, under moderate- to low-energy conditions (i.e., MacEachern *et al.*, 1999; 2007).

Palaeoichnological data of the Ardanatz Sandstone and the lower part of the Ilundain marls fit well with the shallowing processes that throughout the middle and late Eocene occur in the area, according to the sedimentological and stratigraphic data and the other palaeontological data (body fossils) (Pujalte *et al.*, 2002; Barnolas *et al.*, 2004; Astibia *et al.*, 2014; Astibia *et al.*, in press).

6.3.1. Comparisons with other areas

Globally considered, the body fossil assemblages of the Ardanatz Sandstone and Ilundain Marl formations are comparable with the Eocene associations of the Basque Coast, in the southwestern Aquitaine Basin (Nord Pyrenean area), studied since the nineteenth century (d' Archiac, 1846; 1850; Bouillé, 1876; Boussac, 1911) and also with those of the Eocene (Bartonian) age of the west-central and eastern part of the South Pyrenean area, in Aragon (Jaca Basin) (Villalta, 1956; Puigdefábregas, 1975; Barnolas and Gil-Peña, 2001; Oms *et al.*, 2003) and Catalonia (Igualada and Vic regions) (Abad, 2001; Busquets *et al.*, 1994; Carrasco, 1994; Pisera and Busquets, 2002).

However, the studied associations of the Pamplona Basin seem to be less diverse than those from the above-mentioned areas. The lower palaeontological diversity may be due to the still preliminary nature of the studies carried out so far, which involves sampling biases (e.g. field collection of specimens which are only visible to the naked eye, the need to screen-wash sediment to study the microgastropods and micromorphic brachiopods), taphonomic biases and/or palaeoecological differences (more restricted environments).

The sponge associations seem similar to those of the Eocene of Biarritz/Miarritze (Basque Coast, Aquitanian Basin) described by d'Archiac (1846, 1850), where *Laocoetis samueli* and stellate forms such as *Guettardiscyphia thiolati* and *Pleuroguettardia iberica* are the most representative sponges of the fossil assemblage.

The gastropods *Ptychocerithium johannae*, *Diastoma costellatum*, *Haustator imbricatarius*, and the bivalves *Spondylus bifrons*, *Spondylus nysti*, *Spondylus planicostatus* and *Chama pellati*, among other molluscs, are present in the Paleogene series of the Basque Coast, in the surroundings of the town of Biarritz, specifically in the outcrops of Villa Marbella and of the upper part of the Côte des Basques (Bartonian-Priabonian, Côte des Basques Marls Formation, Mathelin and Sztràkos, 1993; Sztràkos *et al.*, 1998) (Boussac, 1908, 1911). *Spondylus nysti* d'Archiac, 1846, *Spondylus planicostatus* d'Archiac, 1850, *Chama granulosa* d'Archiac, 1850 and *Chama pellati* Boussac, 1911 were defined in the Paleogene of Biarritz. *Hyotissa martinsi* was also erected by d'Archiac (1847) as "*Ostrea Martinsii*" in the "Nummulitique" of Biarritz. *Pycnodonte brongniarti* is present in the upper part (lower Oligocene?) of the Paleogene series of Anglet/Angelu and Biarritz (Chambre d'Amour and other sites) ("*Ostrea vesicularis*" in d'Archiac, 1846; "*Ostrea Brongniarti*" in Bouillé, 1876 and Boussac, 1908, 1911).

The Villa Marbella outcrop, in the lower part of the Côte des Basques blue marls, is the same site that Bouillé (1876) named "Lady Bruce" (Boussac, 1911). Tournouër (in Bouillé, 1876) described the "Cérites –Cerithiidae– des couches à *Serpula spirulaea*" in Lady Bruce. Bouillé (1876) cited the presence of "*Serpula spirulaea*" (*Rotularia spirulaea*) in Lady Bruce and Côte des Basques outcrops. The presence of "*Serpula spirulaea*" had already been reported in Biarritz by d'Archiac (1846, 1850).

Other faunal assemblages, partially comparable, are the mollusc fossil assemblages from the Eocene (Bartonian) marls of the Basa Valley (Ballibasa) (Sobás, Yebra de Basa, San Román de Basa and Isún sites, Pamplona marls *sensu lato,* Jaca Basin, west-central Pyrenean area, Puigdefábregas, 1975; Oms *et al.*, 2003), situated in the neighbouring territory of Huesca (Aragon), about 120 km to southwest from our studied area. The fossil gastropods from these localities were studied by Villalta (1956). The faunal associations of the Pamplona and Jaca basins share close if not the same species of the genera *Niso*, *Globularia*, *Clavilithes*, *Sassia*, *Moniquia* (as *Faunus* in Villalta, 1956), some Epitoniidae and, at least, the species *Haustator altavillensis* and *Diastoma costellatum.* The Ballibasa levels are probably somewhat older that those of the Ardanatz Sandstone and Ilundain Marl Formation and their faunas (at least the molluscs) seem to be more diverse than those of Navarre. Fish otoliths of Yebra de Basa have recently been studied by Brzobohatý and Nolf (2011). The assemblage reflects a very shallow neritic environment, different of the one from the Villa Marbella in Biarritz, with a deep neritic-upper slope otolith association (Brzobohatý and Nolf, 2011).

Regarding to the Eocene of Catalonia, the Ardanatz AD3 level outcrops, with the stellate and conical siliceous sponges and erected bryozoan colonies, could be compared to the Bartonian shelf deposits from the Vic Marls Formation in the northeastern part of the Ebro Basin (Busquets *et al.*, 1994; Pisera and Busquets, 2002; Astibia *et al.*, 2014). Farrés (1961) cited the presence of *"Cerithium Johannes"* in the Bartonian marls from Gurb (Vich region). *Spondylus caldesensis*, *Spondylus bifrons* and *Spondylus nysti* are present in several sites of Igualada, Manresa and Vic regions, in the Igualada Formation (late Bartonian, most likely Priabonian in age, Taberner *et al.*, 1999; Costa *et al.*, 2013) (Carrasco, 1994; Abad, 2001). *Pycnodonte brongniarti* has a wide biostratigraphic and palaeobiogeographic distribution (Paleocene-Miocene, through northern Africa and southern Eurasia) and is abundant in numerous Eocene localities of Igualada and Vic regions (Igualada Formation) (Abad, 2001).

Regarding the biogeographic relationships with the Western Europe, the mollusc associations found in the Pamplona basin share two elements found in the middle Eocene (Lutetian) of San Giovanni Ilarione (Verona basin, Italy): *Clavilithes parisiensis* and *Diastoma costellatum* (Quaggiotto and Mellini, 2008). These two faunal elements correspond to cosmopolitan species and have been also found in the Middle Eocene of the Paris Basin. Another species found in the Tethys is *Leptomaria peresii* occurring in the Priabonian of Alps (France). Species found in the North-West Atlantic are *Haustator imbricatarius*, *Nihonia transversaria* from the Paris Basin and *Haustator altavillensis*, originally described from the Middle Eocene of Normandy. As seen above, the rest of this association seems restricted of the Pyrenean area, so the existence of an endemic fauna or/and the beginning of a faunal differentiation between the Northern (Paris Basin, Normandy) and the southern faunas (Pyrenean and Aquitaine basins), which is observed since the Rupelian (Lozouet and Maestrati, 1986; Merle *et al*., 2002), can be proposed as a hypothesis. However, further research on this mollusc association is necessary.

6.4. Gendulain Formation (Liédena Sandstone Member) (Fig. 7)

Sedimentological evidence (synaeresis cracks, flat-topped wave ripples, halite moulds, etc.) indicates a relatively confined marginal marine environment for these deposits (Payros *et al.*, 2000).

The Liédena Sandstone ichnofauna presents a low ichnodiversity. The vertebrate tracks are exclusively composed of bird ichnotaxa and two of them, *Koreanaornis* and *Leptoptilostipus*, have been related with shorebird trackmakers (i.e., Lockley and Harris, 2010). Lockley *et al.* (1994) proposed the shorebird ichnofacies, which comprises ichnocoenoses of shorebirds attributable to Charadriiformes, Anseriiformes and Ciconiiformes. Gibert and Sáez (2009) considered the shorebird ichnofacies to be a subset of the *Scoyenia* ichnofacies (an ichnosubfacies *sensu* Melchor *et al.*, 2006) that characterizes the subaerial part of low-energy shore areas. On the other hand, the presence of *Cochlichnus* in a non-marine setting is typical of the *Mermia* ichnofacies and suggests a low energy perennial freshwater environment (Hasiotis, 2002; Buatois and Mángano, 2002). The occurrence of characteristic ichnotaxa of more than one ichnofacies in a single ichnofauna, as the occurrence in Liédena deposits, could be interpreted as a consequence of the trace-fossil producers being environmentally tolerant animals that could inhabit and behave similarly in either setting. Overall, the palaeohydrological and palaeoenvironment scenario deduced from the bioturbation and other organic and sedimentary structures is consistent with extremely sensitive to water table oscillations, causing cyclic exposure and submersion of large areas, and to variations in salinity throughout the tidal cycle.

7. Conclusions

Fossil associations from the middle and late Eocene (Bartonian and Priabonian) sedimentary succession of the Pamplona Basin are described. This succession accumulated in the western part of the South Pyrenean peripheral foreland basin and extends from deep-marine turbiditic (Ezkaba Sandstone Formation) to deltaic (Pamplona Marl, Ardanatz Sandstone and Ilundain Marl formations) and marginal marine deposits (Liédena Sandstone Member, Gendulain Formation).

Palaeontological data of the studied sedimentary units fit well with shallowing processes that throughout the middle and late Eocene occur in the area, in accordance with the results obtained from sedimentological and stratigraphic data.

The studied units are very rich in microfossils and ichnofossils, but not in body macrofossils, which are only locally abundant. In some outcrops of the Ardanatz Sandstone and Ilundain Marl formations fossils of sponges and erected bryozoans seem to correspond to complete or nearly complete specimens, without evidence of abrasion. They probably correspond to demic organisms. In other outcrops fossils are fragmentary and associated mainly with levels of high terrigenous content and may have undergone some taphonomic remotion processes.

Epibiontic activity and bioerosion on fossil invertebrates and sirenian ribs are frequent. The fossil invertebrates are generally fragmentary, showing dissolution, replacement by calcite and celestite, and aragonite-calcite neomorfism processes. Replacement by francolite occurs in fossil vertebrates. Microbial mats impressions have been identified in the digit impressions of some bird tracks of the Liédena Sandstone. The microbial mats may have acted as taphonomic bias favouring the preservation of vertebrate tracks and conditioning the presence of endofauna.

At least 23 ichnogenera and 28 ichnospecies have been identified in the study area. Among the body macrofossils, 78 taxa of macroforaminifers, sponges, corals, bryozoans, brachiopods, annelids, molluscs, arthropods, echinoderms and vertebrates have been reliably identified. However, both the number of ichnotaxa and invertebrate species (e. g. bryozoans and molluscs) may be considerably higher.

In the older unit, the Ezkaba Sandstone Formation, only some microfossils and ichnofossils have been determined. There, body macrofossils are scarce and fragmentary. The trace-fossil assemblage is characteristic of the deep-sea *Nereite*s ichnofacies. The *Ophiomorpha rudis* and the *Paleodictyon* ichnosubfacies can be differentiated in this unit, which are typical of channel axis and off-axis environments. They agree with the richness of planktic foraminifera of the marly deposits of this unit and the sedimentological interpretation of the Ezkaba Sandstone as channel-fill deposits of a laterally migrating channel-levee turbidite system.

The Pamplona marls are rich in microfossils but macrofossils are rare. In the base of this unit microfossils, with moderately high proportion of planktic foraminifera and high diversity and composition of benthic foraminifera, are indicative of relatively deep waters, outer-platform to upper slope environments. Stalk fragments of crinoids (*Isselicrinus* sp.) are quite common throughout the lower part of the Pamplona Formation. Postcranial elements of sirenian mammals (Dugongidae indet.) have also been described.

The Ardanatz Sandstone and Ilundain Marl formations are the richest sources of body macrofossils in the study area. In the Ardanatz outcrops (Ardanatz Sandstone Formation), the low proportion of planktic foraminifera and the high abundance of benthic foraminifera, their composition (including common porcelaneous foraminifera) and moderate diversity suggest a shelfal depth of deposition. Eastward, in the study area and in the uppermost part of the Ilundain Marl Formation, the scarcity of planktic foraminifera and the composition of the moderately diverse benthic foraminifera (including common porcelaneous foraminifera) suggest an inner shelfal depth of deposition.

The comparison of fossil-invertebrate associations of the locality of Ardanatz and the Itzagaondoa valley outcrops shows notable differences. In Itzagaondoa outcrops no fossil sponges have been found, and this can be explained because the Itzagaondoa outcrops represent a shallower sedimentary environment. Trace fossil assemblage at the Ardanatz Sandstone and Ilundain Marl formations could be related to the *Cruziana* ichnofacies.

Body fossil assemblages of Ardanatz Sandstone and Ilundain Marl formations are comparable with the Eocene (Bartonian-Priabonian) age associations of the Basque Coast (southwestern Aquitaine Basin, North Pyrenean area), specifically in the outcrops of the Côte des Basques Marls Formation. They are also comparable with those of Eocene (Bartonian-Priabonian) from the west-central and eastern part of the South Pyrenean area, in Aragon (Ballibasa, Jaca Basin) and Catalonia (Vic Marls and Igualada formations). At the Western Europe scale, the mollusc assemblages seem endemic for the Pyrenean area, although they share several cosmopolitan species with the Middle Eocene of the Tethys (Italy and France, Alps) and of the Nort-West Atlantic (Paris Basin and Normandy).

The studied associations seem to be less diverse than those from the above-mentioned areas. The lower palaeontological diversity of the Pamplona Basin may be due to the still preliminary nature of the studies carried out so far, which involves sampling and taphonomic biases and/or palaeoecological differences.

The ichnofauna of the Liédena Sandstone, in the upper part of the sedimentary succession, is composed of bird tracks, and both invertebrate horizontal and vertical structures. The assignation of this ichnofauna to a specific ichnofacies is tentative, and we regard it as showing a combination of the characteristics of the *Mermia* and *Scoyenia* ichnofacies.

In conclusion, the fossil associations found in the middle-upper Eocene succession of the Pamplona Basin were found to be rich and diverse enough to allow an integrated palaeoenvironmental analyses to be carried out herein for the first time. The fossil associations show similarities, but also differences, with coeval associations from neighbouring areas, such as the long-known, classic outcrops in the southwestern Aquitaine Basin, in Aragon and in Catalonia, and even in more distant areas, such as the Paris Basin. Such differences provide the Pamplona Basin a distinctive character and increase its interest for palaeobiodiversity studies. Consequently, future studies will focus on specific fossil groups.

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Appendix I

Ichnotaxa and macrofossil taxa recorded so far in the Eocene of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees)

Ezkaba Sandstone Formation

Ichnotaxa

Belorhaphe isp.
Chondrites isp.
Helminthoraphe flexuosa Uchman, 1995
Multina minima (Uchman, 2001)
Nereites irregularis (Schafhäutl, 1851)
Ophiomorpha annulata (Książkiewicz, 1977)
Ophiomorpha rudis (Książkiewicz, 1977)
Paleodictyon strozzii Meneghini in Savi and Meneghini, 1850
Phymatoderma isp.
Pilichnus dichotomus Uchman, 1999
Planolites isp.
Scolizia strozzii (Savi and Meneghini, 1850)
Scolizia vertebralis Książkiewicz, 1977
?*Squamodictyon* isp.
Taenidium crassum Bromley, Ekdale and Richter, 1999

Pamplona Marl Formation

Ichnotaxa
Chondrites isp.
Ophiomorpha isp.
Thalassinoides suevicus (Rieth, 1932)

Taxa
Echinodermata Klein, 1734
Crinoidea Miller, 1821
Isselicrinus sp.

Chordata Haeckel, 1874
Mammalia Linnaeus, 1758
Dugongidae indet.

Ardanatz Sandstone-Ilundain Marl formations

Ichnotaxa
Halopoa imbricate Torell, 1870
Ophiomorpha isp.
Ophiomorpha isp. (aff. *O. nodosa-O. irregulaire*)
Ophiomorpha nodosa Lundgren, 1891
Planolites isp.
Spongeliomorpha cf. *oraviense*
Spongeliomorpha cf. *sicula*
Spreite burrows (?*Rhizocorallium*)
Thalassinoides isp.

Taxa
Rhizaria Cavalier-Smith, 2002
Foraminifera d'Orbigny, 1826
Assilina schwageri (Silvestri, 1928)
Heterostegina reticulata cf. *multifida* (Bieda, 1950)
Nummulites cf. *beaumonti* d'Archiac and Haime, 1853
Nummulites aff. *biedai* Schaub, 1962
Nummulites aff. *cyrenaicus* Schaub, 1981
Nummulites cf. *perforatus* (de Montfort, 1808)
Nummulites ptukhiani Kacharava, 1969
Nummulites praegarnieri Schaub, 1981

Porifera Grant, 1836
Hexactinellida Schmidt, 1870
Laocoetis samueli (d'Archiac, 1850)
cf. *Rhizocheton robustus* Pisera and Busquets, 2002
Guettardiscyphia thiolati (d'Archiac, 1846) and/or *Pleuroguettardia iberica* Pisera and Busquets, 2002

Demospongia Sollas, 1875
Cf. *Phlyctia expansa* Pomel, 1872
Lithistid indet. 1
Lithistid indet. 2

Coelenterata Frey and Leuckart, 1847
Anthozoa Ehrenberg, 1834
Stylocoenia taurinensis (Michelin, 1842)
Astrocoenia octopartita (Oppenheim, 1901)
Ceratotrochus bodellei Barta-Calmus, 1973
Placosmiliopsis bilobatus (d'Achiardi, 1868)
Desmophyllum castellolense Álvarez-Pérez, 1997

Bryozoa Ehrenberg, 1831
Stenolaemata Borg, 1926
Lichenoporidae indet.

Gymnolaemata Allman, 1856
Cupuladriidae indet.

Brachiopoda Duméril, 1806
Rhynchonellata Williams, Carlson, Brunton, Holmer and Popov, 1996
Argyrotheca michelottina (Davidson, 1870)
?Gryphus sp.
Terebratulina tenuistriata (Leymerie, 1846)

Annelida Lamarck, 1809
Polychaeta Grube, 1850
Rotularia spirulaea (Lamarck, 1818)
Polychaeta indet. 1
Polychaeta indet. 2

Mollusca Linnaeus, 1758
Gastropoda Cuvier, 1795
Leptomaria peresii (d'Orbigny, 1850)
Ptychocerithium johannae (Tournouër *in* Bouillé, 1873)
Diastoma costellatum (Lamarck, 1804)
Moniquia sp.
Haustator altavillensis (Cossmann and Pissarro, 1902)
Haustator cf. *imbricatarius conoideus* (Sowerby J., 1814)
Sigmesalia sp.
Ampullinidae indet.
? *Globularia* sp.
Sassia sp.
Cirsotrema (*Elegantiscala*) cf. *bouillei* (Tournouër *in* Bouillé, 1873)
Epitonium sp.
Amaea sp.
Niso sp.
Metula (Celatoconus) sp.
Clavilithes (Clavellofusus) cf. *parisiensis* Mayer-Eymar, 1876
Muricidae indet.
Athleta (Volutospina) sp.
Conus sp.
Nihonia aff. *transversaria* (Lamarck, 1804)
Mathilda sp.

Bivalvia Linnaeus, 1758
Glycymeris jacquoti (Tournouër *in* Bouillé, 1873)
Pycnodonte brongniarti (Bronn, 1831)
Hyotissa martinsi (d'Archiac, 1850)
Ostreiodea indet.
Chlamys cf. *biarritzensis* (d'Archiac, 1846)
Chlamys sp.
Spondylus cf. *bifrons* Münster *in* Goldfuss, 1840
Spondylus cf. *caldesensis* Carez 1881
Spondylus planicostatus d'Archiac, 1850
Spondylus sp. cf. *Spondylus cisalpinus* Brongniart, 1823 − *S. nysti* d'Archiac, 1846
Spondylus sp.
Dimya pamplonensis (Carez, 1881)
Venericardia junctinova Cossmann, 1897
Chama pellati Boussac, 1911
Chama granulosa d'Archiac, 1850

Scaphopoda Bronn, 1862
Dentalium sp.

Cephalopoda Cuvier, 1797
Nautiloidea indet.

Arthropoda von Siebold, 1848
Maxillopoda Dahl, 1956
Arcoscalpellum sp.

Malacostraca Latreille, 1802
Decapoda indet.

Echinodermata Bruguière, 1791 (ex Klein, 1734)
Crinoidea Miller, 1821
Crinoidea indet.

Echinoidea Leske, 1778
Asteroidea indet.
Echinoidea indet.

Chordata Haeckel, 1874
Chondrichthyes Huxley, 1880
Hexanchus agassizi Cappetta, 1976
Macrorhizodus praecursor (Leriche, 1905)
Woellsteinia kozlovi Adnet, 2006
Anomotodon sp.

Actinopterygii Klein, 1885
Enchodus sp.
Chaetodipterus sp.

Reptilia Laurenti, 1768
Testudines indet.

Mammalia Linnaeus, 1758
Dugongidae indet.

Gendulain Formation (Liédena Sandstone Member)

Ichnotaxa
Cochlichnus isp.
Palaeophycus tubularis Hall, 1847
Vertical tubes
Gruipeda isp.
Koreanaornis isp.
cf. *Koreanaornis*
Leptoptilostipus pyrenaicus Payros, Astibia, Cearreta, Pereda-Suberbiola, Murelaga and Badiola, 2000
cf. *Leptoptilostipus*