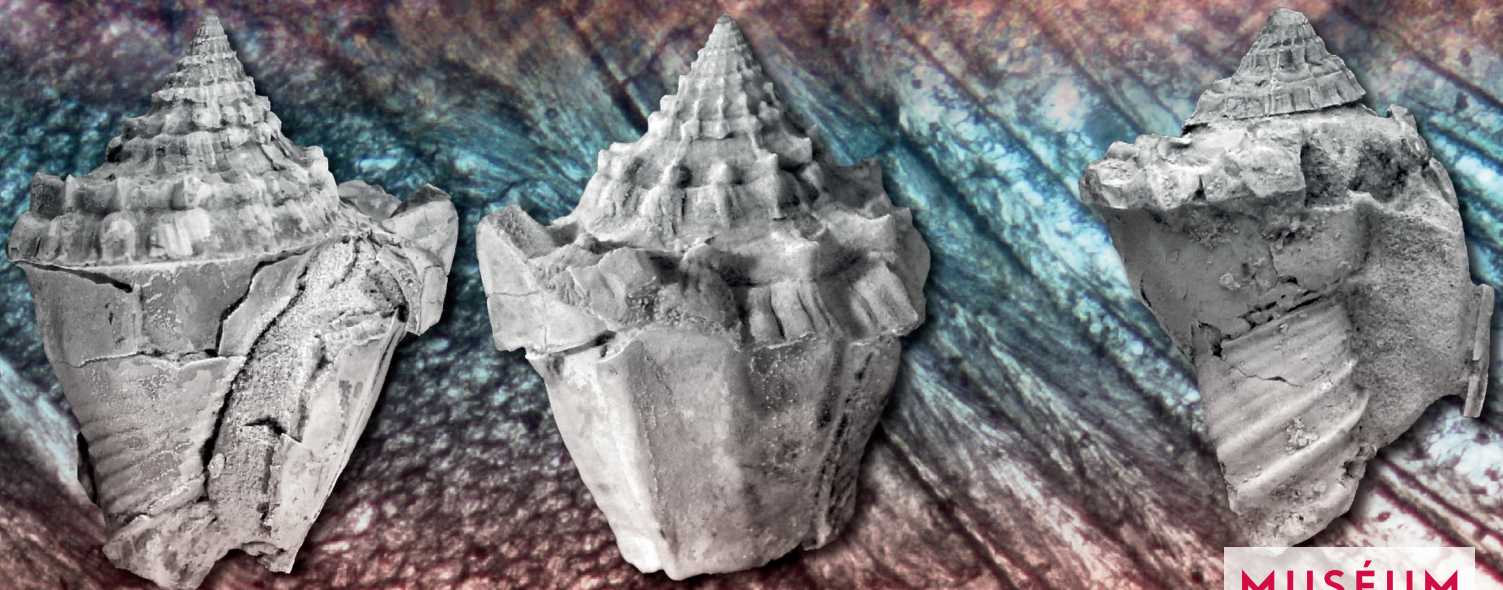


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the Eocene marly formations of the Pamplona Basin
and surrounding areas (Navarre, western Pyrenees)

Humberto ASTIBIA, Didier MERLE, Jean-Michel PACAUD,
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Gastropods and bivalves from the Eocene marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees)

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ABSTRACT

Gastropods and bivalve 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). Fossils are generally fragmentary and many correspond to remains that have undergone taphonomic reworking. Significant effects of diagenesis are also detected, with evidence of compression or deformation, dissolution, aragonite-calcite neomorphism and cementation by celestite. Bioerosion traces and fossil encrusters are common. Fossils of 37 taxa, 25 gastropods and 12 bivalves, have been identified confidently. The number of species is probably considerably higher, as the study of some fossils, mainly the most small-sized

KEY WORDS

Gastropods,
bivalves,
Paleogene,
shallow-marine
sediments,
Pyrenean area,
new combinations,
new species.

species, is pending. One new species, *Athleta (Volutospina) delvallei* Astibia, Merle & Pacaud, n. sp. (Gastropoda, Volutidae), is described herein. Fossil assemblages are comparable to those from the Eocene of the Basque Coast (North Pyrenean area) and Aragon and Catalonia (west-central and eastern part of South Pyrenean area). Most of the mollusc taxa seem to be endemic to the Pyrenean area, but several Tethyan and Northern elements have also been recorded. These results enlarge the database for a better understanding of the evolution of global marine biodiversity throughout the Eocene.

RÉSUMÉ

Gastéropodes et bivalves des formations marneuses de l'Éocène du Bassin de Pampelune et de ses environs (Navarre, Pyrénées occidentales).

Les associations de gastéropodes et de bivalves de la succession sédimentaire de l'Éocène moyen et ?supérieur (Bartonien et ?Priabonien) du Bassin de Pampelune sont décrites. Cette succession s'est accumulée dans la partie occidentale du bassin d'avant-pays périphérique sud-pyrénéen et comprend des dépôts marins turbiditiques profonds (Formation des Grès d'Ezkaba) des dépôts deltaïques (formations des Marnes de Pampelune, des Grès d'Ardatz et des Marnes d'Ilundain) et des dépôts marins marginaux (Formation Gendulain). Les fossiles sont généralement fragmentaires et beaucoup d'entre eux correspondent à des restes remaniés. Des effets significatifs de la diagénèse sont également détectés, avec des signes de compression ou de déformation, de dissolution, de néomorphisme aragonite-calcite et de cimentation par célestine. Les traces de bioérosion et les fossiles d'organismes incrustants sont fréquents. Les restes fossiles de 37 espèces, dont 25 correspondant à des gastéropodes et 12 à des bivalves, ont été identifiés. Ce nombre pourrait être considérablement plus élevé, grâce à l'étude de très petites espèces (micro-mollusques) qui reste à faire. Une nouvelle espèce, *Athleta (Volutospina) delvallei* Astibia, Merle & Pacaud, n. sp. (Gastropoda, Volutidae), est décrite ici. Les associations fossiles sont comparables à celles de l'Éocène de la côte basque (Région nord-pyrénéenne), d'Aragon et de la Catalogne (parties centre-ouest et est de la Région sud-pyrénéenne). La plupart des taxons de mollusques semble être endémique à la Région pyrénéenne, mais plusieurs éléments téthysiens et du Nord de l'Europe ont également été enregistrés. Ces résultats élargissent la base de données au vu d'une meilleure compréhension de l'évolution de la biodiversité marine mondiale tout au long de l'Éocène.

MOTS CLÉS
Gastéropodes,
bivalves,
Paléogène,
sédiments marins peu
profonds,
Pyrénées,
combinaisons nouvelles,
espèce nouvelle.

INTRODUCTION

During the Eocene the West Tethyan region was a marine biodiversity hotspot (Renema *et al.* 2008). In the Northern Atlantic area, the middle Eocene (particularly during the Lutetian) marine fauna of the Paris Basin showed an extraordinary biodiversity, particularly regarding the molluscs, and can consequently be regarded as an extension of the West Tethyan hotspot (Merle 2008; Merle *et al.* 2008; Huyghe *et al.* 2012). In fact, Merle (2008, 2009) indicated the presence of species of Tethyan origin in the Paris Basin, which contributed to enrich the biodiversity of this region. During the Priabonian the biodiversity decreased significantly in both sides of the Atlantic Ocean (Hansen 1988; Lozouet 1997; Huyghe *et al.* 2012).

During the Eocene, the Pyrenean area constituted a transitional zone between the Tethyan and Northern Atlantic domains. However, the Pyrenean middle/late Eocene mollusc faunas are still relatively poorly documented. In the North Pyrenean area, the classic works by d'Archiac (1846, 1850), Bouillé (1873, 1876), Boussac (1911) and Cossmann (1921) on the molluscs from the "Nummulitic" of the Basque coast and Aquitaine have hardly been updated. More recent studies on Eocene molluscs have been carried out in Aragon and Catalonia (South Pyrenean area), such as those by Villalta

Comella (1956), De Renzi (1971, 1996), Abad (2001), Pisera & Busquets (2002), Dominici & Kowalke (2007, 2014) and Tomašových *et al.* (2014), among others.

Regarding the western Pyrenees, the first palaeontological data from the Pamplona Basin and surrounding areas came from French geologist Carez (1881). He reported the occurrence of extensive marl units, which he referred to as "marls of *Serpula spirulaea*", and mentioned the abundance of a small bivalve, which he named *Plicatula pamplonensis* (*Dimya pamplonensis* (Carez, 1881) n. comb., Calzada & Astibia 1996). Marquina (1908) worked on Eocene strata in Navarre, presented the demarcation of the nummulitic zones and cited the presence of fossil stems of "*Pentacrinus*" and *Plicatula pamplonensis* in the marls of the Pamplona Basin. Later, Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949), and Ruiz de Gaona & Colom (1950) described the foraminiferal content of these marls, suggested a Bartonian age, and mentioned the occurrence of rich macrofossil associations in some localities around the city of Pamplona. Local micropaleontological determinations were provided later by Puigdefábregas (1975) and Alameda *et al.* (1993). More recently, macropaleontological works on the bivalve *Dimya pamplonensis* n. comb. (Calzada & Astibia 1996), turtles and sirenians (Astibia *et al.* 1999, 2005, 2006), sponges and corals (Astibia *et al.* 2014), brachiopods (Bitner *et al.* 2016), and trace fossils (Payros *et al.* 2000; Astibia *et al.*

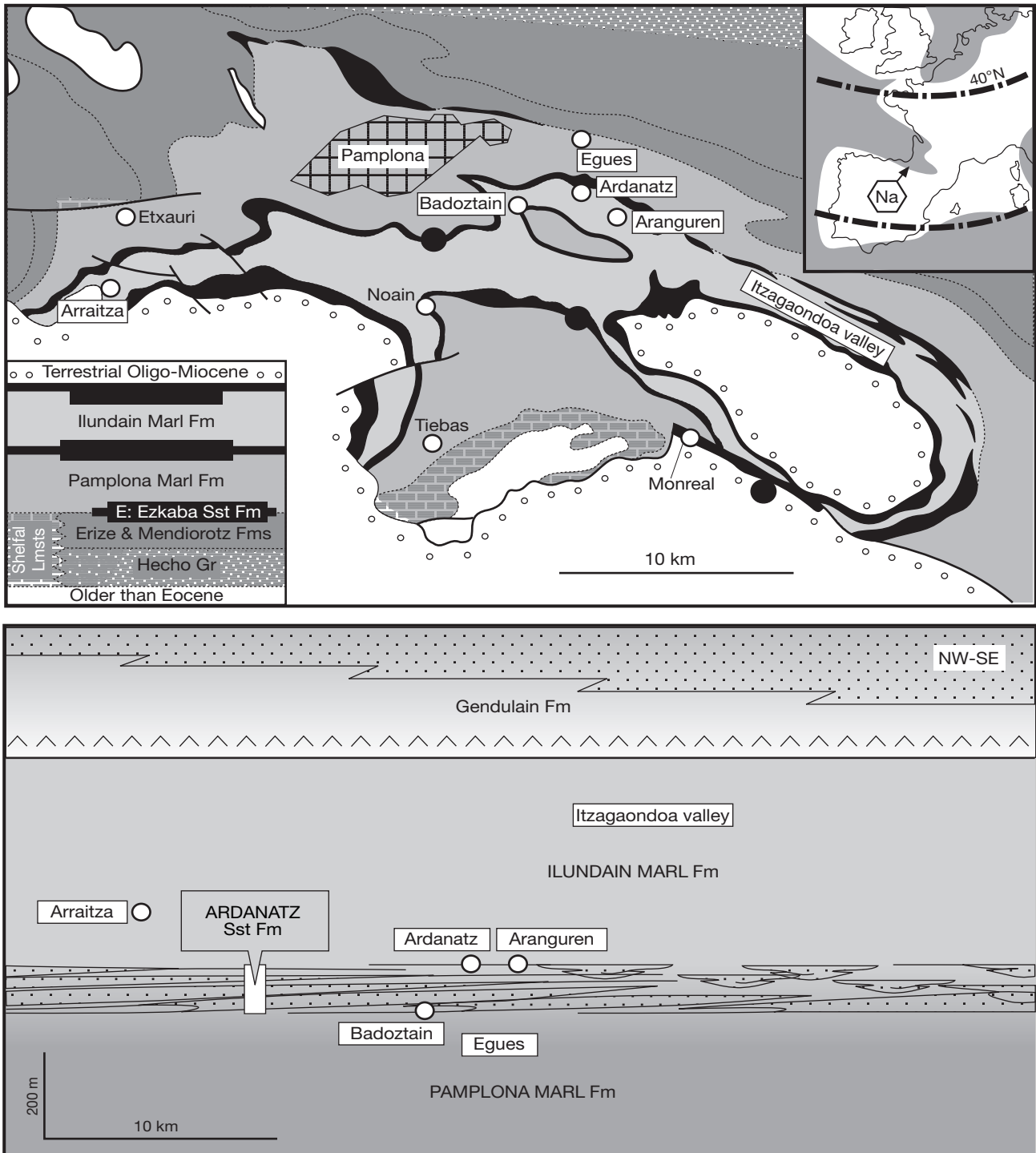


FIG. 1. — Above, simplified geological map of the study area in the central part of Navarre (western Pyrenees). The studied paleontological localities are in *italics* and framed. The Eocene western European paleogeography is shown in inset (**Na**, Navarre). Below, synthetic NW-SE cross section of the study area, showing the overall stratigraphy, sedimentary architecture and (projected) location of the studied sites.

2007, 2017) have been published. In this paper we present our first results on the gastropods and bivalves represented in the fossil associations of the Pamplona basin and neighbouring areas. Medium and large-sized species, alongside some smaller species, are herein reported, whereas the study of most small-sized species is pending. Most of the molluscs seem to be endemic to the Pyrenean area, although several species

from the Tethyan (Italy and Alps) and Northern (Paris Basin and Normandy) domains have also been recorded (Astibia *et al.* 2016), thus confirming the role of the Pyrenean area in connecting the two domains. The results exposed herein will further contribute to enlarge the database for a better understanding of faunal gradients and the evolution of global marine biodiversity throughout the Eocene.

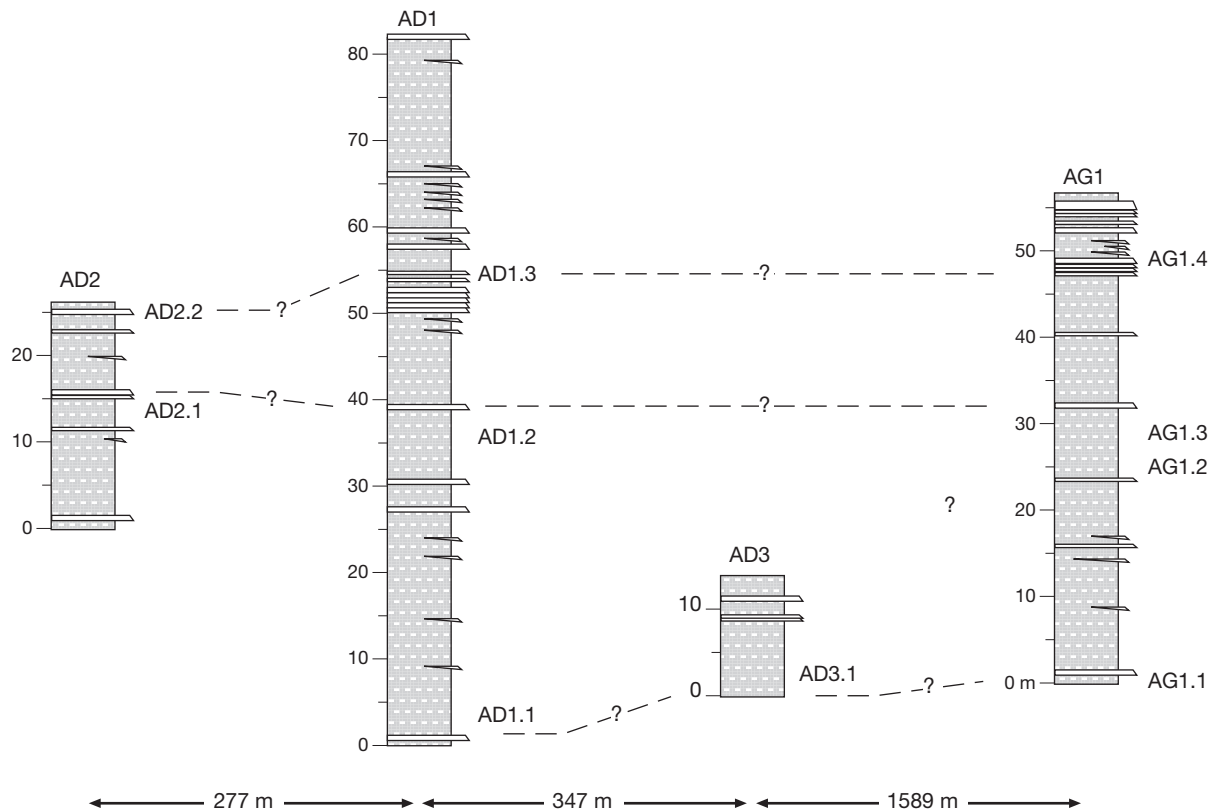


FIG. 2. — Tentative correlation of some sections across the transition between the Ardanatz Sandstone and the Ilundain Marls in the Ardanatz-Araguren area (see Fig. 1 for location), showing the stratigraphic position of the studied fossiliferous levels (sandstone beds are not to scale; modified from Astibia *et al.* 2014).

LOCATION, MATERIAL AND METHODS

The study area is located in the central part of Navarre, in the South-western Pyrenees (Fig. 1). During the Eocene, the South Pyrenean zone was a NW-trending foreland basin, located adjacent to the south of an uplifting orogen. For most of the Eocene it constituted a narrow gulf entering from the Bay of Biscay at approximately 35°N palaeolatitude. Eventually, sediments derived from the uplifting and denuding Pyrenees filled the basin. By middle-late Eocene (Bartonian-Priabonian) times fluviodeltaic sedimentary systems were widespread throughout the foreland basin (Plaziat 1981; Pujalte *et al.* 2002; Barnolas *et al.* 2004).

This evolution is well recorded in the central part of Navarre by alternating marly and sandy lithostratigraphic units (Fig. 1). The lower part of this succession is represented by the Bartonian Ezkaba Sandstone Formation, a channel-levee turbidite system fed directly from the uplifting orogen to the north (Payros *et al.* 1997). The overlying Pamplona Marl, Ardanatz Sandstone and Ilundain Marl formations mainly represent prodelta, delta front and restricted platform paleoenvironments, respectively (Astibia *et al.* 2005, 2014). Finally, the Late Eocene (Priabonian) Gendulain Formation is composed of coastal deposits (Puigdefábregas 1975; Payros *et al.* 2000). The latter unit contains the youngest deposits with marine influence in the region.

The abundant micropaleontological content of these deposits is dominated by foraminifera, but ostracods are also common. Body macrofossils are locally abundant in the Ardanatz Sandstone and

Ilundain Marl formations. The macrofauna is mainly represented by macroforaminifera, hexactinellid and lithistid sponges, scleractinian corals, bryozoans, brachiopods, tube-dwelling polychaetes, molluscs (gastropods, bivalves, cephalopods and scaphopods), arthropods (crustaceans), 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 (Calzada & Astibia 1996; Astibia *et al.* 1999, 2005, 2006, 2014, 2016; Buffrénil *et al.* 2008; Bitner *et al.* 2016).

The mollusc fossils studied herein were collected from several outcrops, few kilometers from the city of Pamplona, which expose: 1) the upper part of the Pamplona Marl Formation (mainly in the surroundings of Egues; EG1, AZ1, IZ1 sections); 2) the transition between the Pamplona Marl Formation and the Ardanatz Sandstone Formation (near the town of Badoztain; BD1 section); 3) the Ardanatz Sandstone Formation or, more precisely, its transition into the overlying Ilundain Marl Formation (Ardanatz-Eguesibar, Aranguren and other localities; TR1, ZB1, AD1-AD6, AG1 sections); 4) the lower part of the Ilundain Marl Formation, approximately 100 m above its base (near the town of Arraitza; ARR1 section); and 5) the uppermost part of the Ilundain Marl Formation (three localities of the Itzagaondoia Valley; IV section) (Figs 1, 2). Precise location of the outcrops is deliberately omitted with the aim of protecting the fossil sites, in accordance with Natural and Cultural Heritage legislation. However, further details can be obtained from the corresponding author.

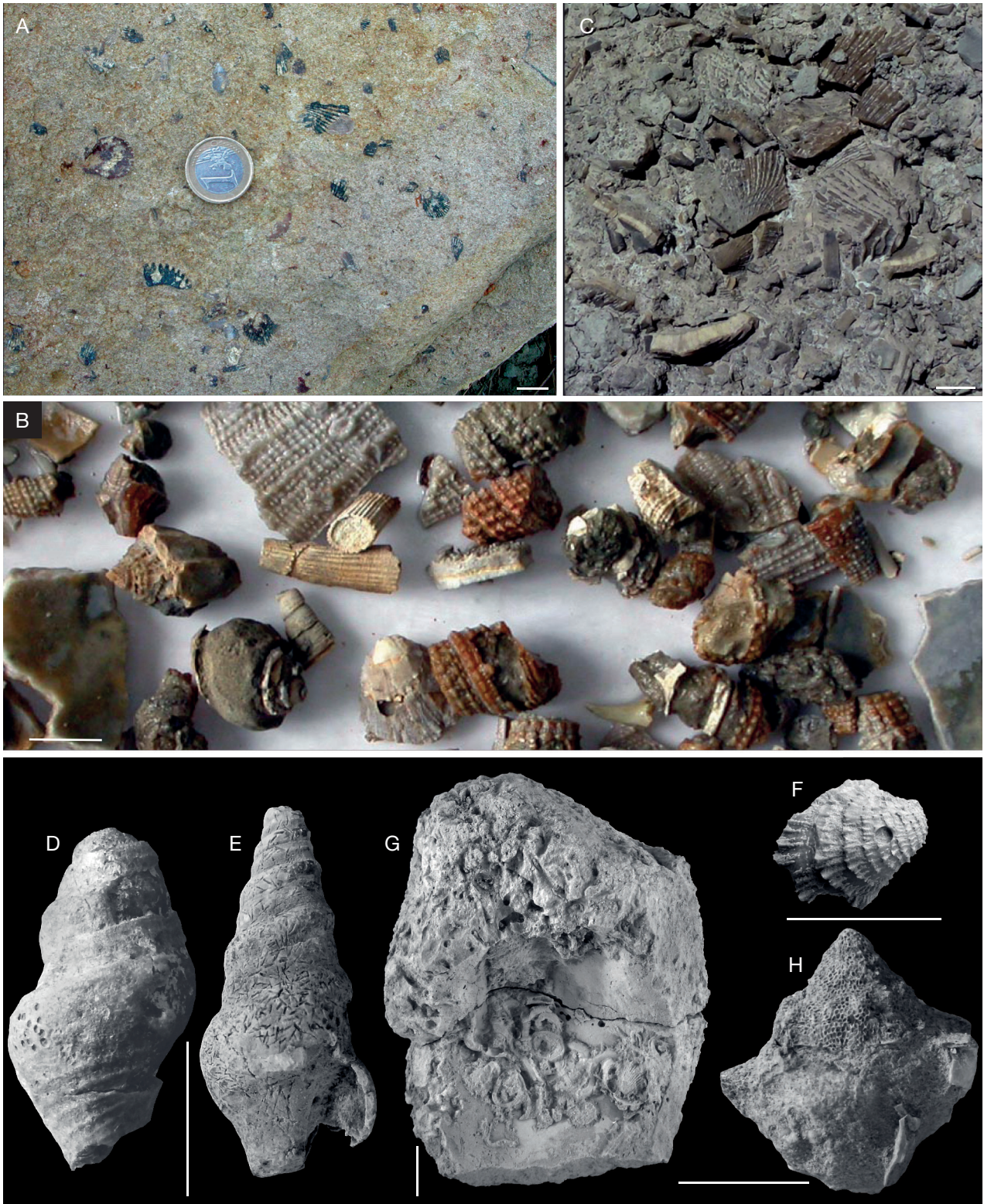


FIG. 3. — Taphonomic features, bioerosion borings and encrusters on fossil molluscs from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A**, field image of reworked fragmentary specimens of the bivalve *Chlamys* Röding, 1798 in a sandstone bed of the Ardanatz-Eguesibar AD3 section; **B**, evidence of taphonomic smoothing, fragmentation and dissolution in a sample from the Ardanatz-Eguesibar AD2 section; **C**, field image showing fragmentation in a specimen of *Spondylus* cf. *caldesensis* Carez, 1881 in the Ardanatz-Eguesibar AD5 section; **D**, probably clionid sponge borings (*Entobia* Bronn, 1838) on a specimen (AD.17) of *Nihonia* aff. *transversaria* (Lamarck, 1804) n. comb. from the Ardanatz-Eguesibar AD sections (section and level unknown); **E**, bryozoan borings (*Pinaceocladichnus* Mayoral, 1988) on a specimen (AD2.2.1) of *Nihonia* aff. *transversaria* (Lamarck, 1804) n. comb. from the Ardanatz-Eguesibar AD2 section; **F**, boring, probably made by predatory gastropods (*Oichnus* Bromley, 1981), on a shell (IV.14) of *Chama pellati* Boussac, 1911 from the Itzagaondo Valley IV section; **G**, Borings, probably made by polychaetes (?*Caulostrepsis* Clarke, 1908), and encrusting bryozoans, polychaetes and bivalves on a valve (AD.18) of *Spondylus cisalpinus* Brongniart, 1823 (ecomorph *bifrons*) from the Ardanatz-Eguesibar AD section (precise section and level unknown); **H**, Encrusting bryozoans on a specimen of *Athleta* (*Volutospina*) *delvallei* Astibia, Merle & Pacaud, n. sp. (AD2.1.5) from the Ardanatz-Eguesibar AD2 section. Scale bars: 10 mm.

All fossils were cleaned with potassium hydroxide (90%, flakes QP) and photographed after being covered with ammonium chloride. A selection of 17 thin sections of fossil gastropods and bivalves was prepared for standard transmitted light petrography, cathodoluminescence (CL) and carbonate staining with alizarin red S and potassium ferricyanide (following Dickson 1965). The mineralogy of 5 samples was analyzed by X-ray diffraction (XRD).

The classification and nomenclator of Gastropoda families of Bouchet *et al.* (2005) has been followed for taxonomy. The classification of Carter *et al.* (2011) and the glossary of Carter *et al.* (2012) were used for the Bivalvia. The taxonomy of the studied specimens is detailed below in the Systematic Palaeontology section. All 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).

ABBREVIATIONS

Institutions

UPV/EHU Universidad del País Vasco/Euskal Herriko Unibertsitatea;
 MNHN.F Muséum national d’Histoire naturelle, Collection de Paléontologie, Paris.

Gastropods

H height;
 W width.

Bivalves

H height, umbo-pallial diameter;
 L length, antero-posterior diameter;
 W thickness;
 min minimum value;
 \bar{x} mean value;
 max maximum value;
 n number of measured specimens.

All measurements are in millimeters. Numbers in parentheses indicate approximate measures, due to the fragmentary nature of many of fossils.

TAPHONOMY

BIOSTRATINOMIC AND REWORKING PROCESSES

The Bartonian succession of the study area is very rich in microfossils, but generally lacks macrofossils, only locally abundant. Macrofossils associated with siliciclastics, i.e., sandstone beds and silty and sandy marls, generally have poor preservation and correspond to remains that underwent taphonomic reworking (resedimentation and/or reelaboration, *sensu* Fernández López 2000). Such is the case of many disjointed and fragmentary

specimens of the bivalve *Chlamys* found in sandstone beds (Fig. 3A), as well as of Cerithioidea and other gastropods in sandy marls from Ardanatz-Eguesibar and Aranguren (Ardanatz Sandstone), which commonly lost their protoconch, aperture and early whorls, or are broken (disarticulation, smoothing and fragmentation processes) (Fig. 3B).

Fossils included in marls, such as the silty marls of the Ardanatz Sandstone and Ilundain Marl formations, despite generally being fractured (fossil diagenetic fragmentation), frequently correspond to entire specimens and hardly show signs of abrasion. Examples include sponges and erected bryozoans (Astibia *et al.* 2014), along with probably reclined, semi-infaunal bivalves, such as *Spondylus* and *Pycnodonte* (Fig. 3C). We can assume that they corresponded to demic organisms whose remains suffered little, if any, taphonomic reworking.

In addition, many fossil shells show signs of bioerosion, especially borings of sponges (*Entobia* isp.), bryozoans (*Pinnaceoeladichnus* isp.) and polychaetes (*Caulostrepsis?*) (Fig. 3D, E, G) and holes (praedichnia of gastropods, *Oichnus* isp.) (Figs 3F; 13N). Sessile encrusters (mainly bryozoans and polychaetes) epizoozoans (*sensu* Taylor & Wilson 2003), both in living and in dead hosts, are common (Figs 3G, H; 11C).

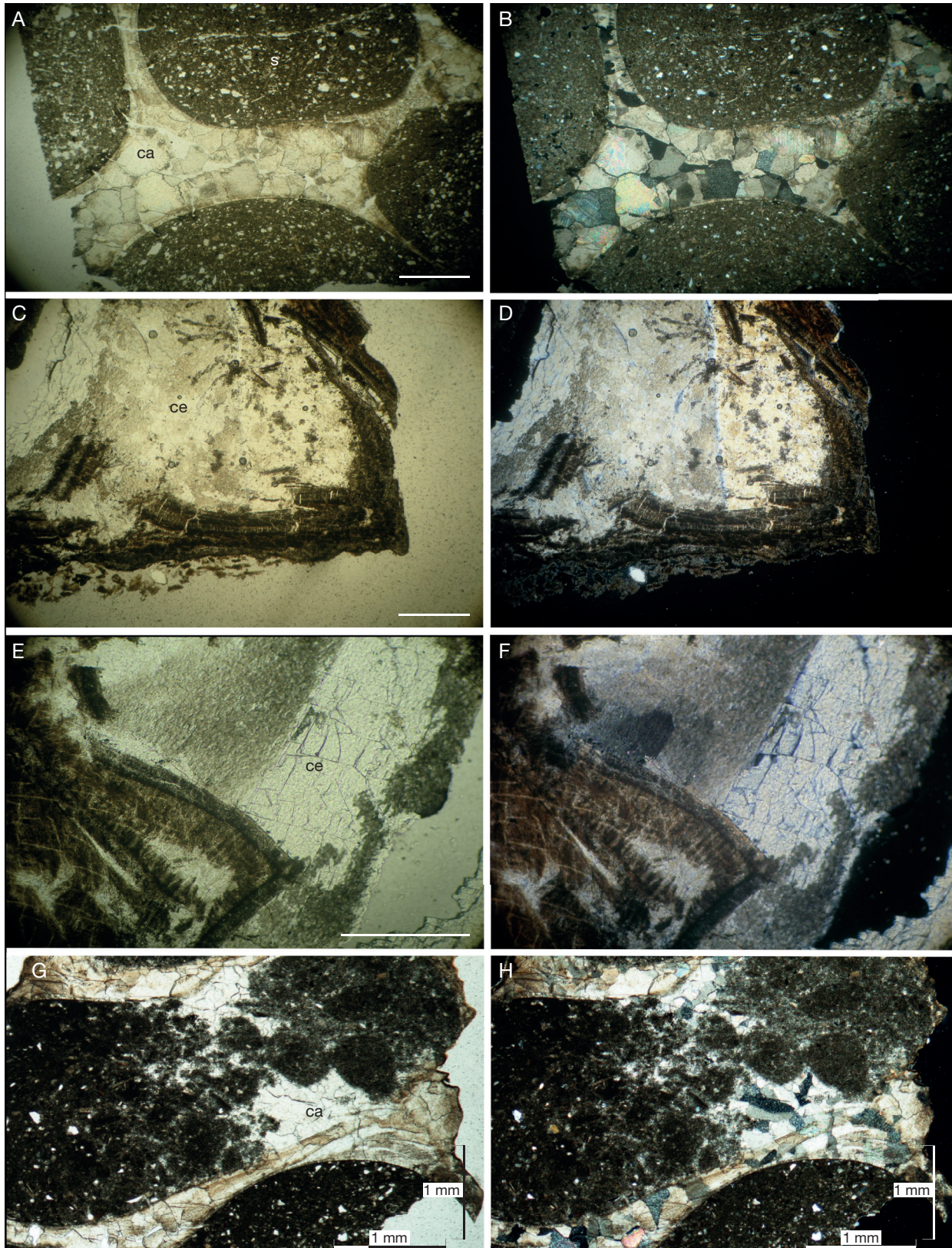
MICROSTRUCTURE AND FOSSIL-DIAGENETIC PROCESSES

Fossil-diagenetic processes in gastropod and bivalves shells here under study included compression or deformation, fragmentation, dissolution (e.g. Figs 3A-C; 7; 8G), aragonite-calcite neomorphism or, in some cases, cementation by celestite. Fossil gastropods belonging to the species *Ptychocerithium baylei* (Tournouër, 1874) n. comb. collected in the Ardanatz Sandstone (AD1 section, levels AD1.3 and AD1.4; AG1 section, level AG1.3, Figs 1; 2) were studied in thin section and show the original structures affected by diagenesis.

The longitudinal sections of *Ptychocerithium* shells show evidence of neomorphism processes with an intense development of large crystals of equant calcite (ca). However, trace-ghost remains of the original aragonitic crossed lamellar structure are still preserved with a brown pseudo-pleochroism (Fig. 4A, B). A strong early compression, which fragmented the shells into large pieces, with a greater presence of the original aragonitic microstructure, is also evident. Early cementation by large crystals of celestite (ce) in the body cavity is dominant (Fig. 4C, D), filling all the empty spaces, as shown by the absence of sediment. In detail, celestite crystals display straight exfoliation planes, without bending, but are broken as a consequence of their fragility (Fig. 4E, F). When the gastropod body spaces were occupied by detrital sediment and peloidal micrite, neomorphic processes also advanced into the sediment, affecting the structure of the shell, with a strong development of equant calcite crystals (Fig. 4G, H).

Celestite commonly forms as a result of rapid decomposition of organic matter in a dysoxic microenvironment, which pro-

FIG. 4. — Photomicrographs of thin-sections of *Ptychocerithium baylei* (Tournouër, 1874) n. comb. fossil shells from the transition between the Eocene (Bartonian?Priabonian) Ardanatz Sandstone and Ilundain Marl formations (Navarre, AD1 and AG1 sections), showing different structures affected by diagenesis: **A**, longitudinal thin-section of specimen AG1.4.5 (parallel nicols), showing traces-ghosts of the original aragonitic crossed lamellar structure preserved as dark traces inside the neofomed big crystals of equant calcite (ca). The shell cavity is filled with fine sediment (s) containing abundant terrigenous fragments, the distribution of which adapts to the curvature of the shell; **B**, same as **A** with crossed nicols, showing a very thin generation of small crystals and neofomed big crystals of calcite in the inner shell layer; **C**, specimen AD1.3.1 (parallel nicols), illustrating the area of shell compaction and breakage of the structure organized in different layers;



independent fragments are supported by big celestite crystals (**ce**) with no deformation, which shows that celestite cementation was after compaction; **D**, same as **C** with crossed nicols. Full cementation of the shell cavity by celestite crystals, no sediment being involved; **E**, specimen AD1.3.2 (parallel nicols), detail of the shell cavity cemented by big celestite crystals (**ce**); shell fragments with a foliated structure are supported by celestite crystals; **F**, same as **E** with crossed nicols. Celestite exfoliation (cleavage) planes present right angles, without bending, but are broken; **G**, general view of specimen AD1.4.1 (parallel nicols). Traces-ghosts of the original aragonitic crossed lamellar structure are preserved as dark traces within neoformed, big equant calcite crystals (**ca**), showing pseudo-pleochroism from colourless to brownish; **H**, same as **G** with crossed nicols. Scale bars: A-D, F-H: 1 mm; E, 0.5 mm.

duces hydrogen sulfide. The latter can be oxidized to sulphate by subsequent bacterial sulfoxidation. This sulphate produces celestite when combined with mobile strontium, which is released either from aragonite-to-calcite neomorphism (Taberner *et al.* 2002) or from other processes, such as decomposition of inherited sheet silicate minerals of continental origin with a decrease-acidification of the pH (Baker & Bloomer 1988).

Diagenetic processes affecting fossil bivalves of the species *Spondylus cisalpinus* Brongniart, 1823 (Ardanatz Sandstone, AG1 section, level AG1.4; Ilundain Marl Formation, IV section, Figs 1; 2), and *Pycnodonte brongniarti* (Bronn, 1831) (Ilundain Marl Formation, IV section, Fig. 1) were also studied in thin section.

Longitudinal sections of *Spondylus* observed with parallel nicols show an inner shell layer characterized by a fibrous prismatic structure (FP) with a great development of thin and elongated prisms, initially composed of aragonite according to Bøggild (1930: 269), slightly bent (Fig. 5A). The calcitic crossed foliated structure (CF) is visible as the outer shell layer, but it is less developed and lacks apparent continuity with the FP structure. Spines protrude from the outer shell layer in all *Spondylus*, consisting of pillars with crossed foliated (CF) structure. The original structure of the middle layer, belonging to the miostracum (?), was partially masked by the FP structure. Finally, the CF structure is commonly covered with a thin layer of micritic carbonate residues (cr) (Fig. 5A). When observed under crossed nicols, evidence of diagenetic alteration is clear, as the original aragonite prisms of the FP structure are neomorphized and generate large calcite crystals with different orientations (Fig. 5B).

In some samples, the middle shell layer (miostracum?), initially with aragonitic nacreous structure (n) and characterized by its brown tones, has been well preserved, despite being neomorphized during diagenesis (Fig. 5C). The FP structure presents large calcite crystals and preserves small remnants of modified thin prisms. However, the CF structure seems to have been less sensitive to diagenetic alteration and shows signs of non-transformation (Fig. 5D).

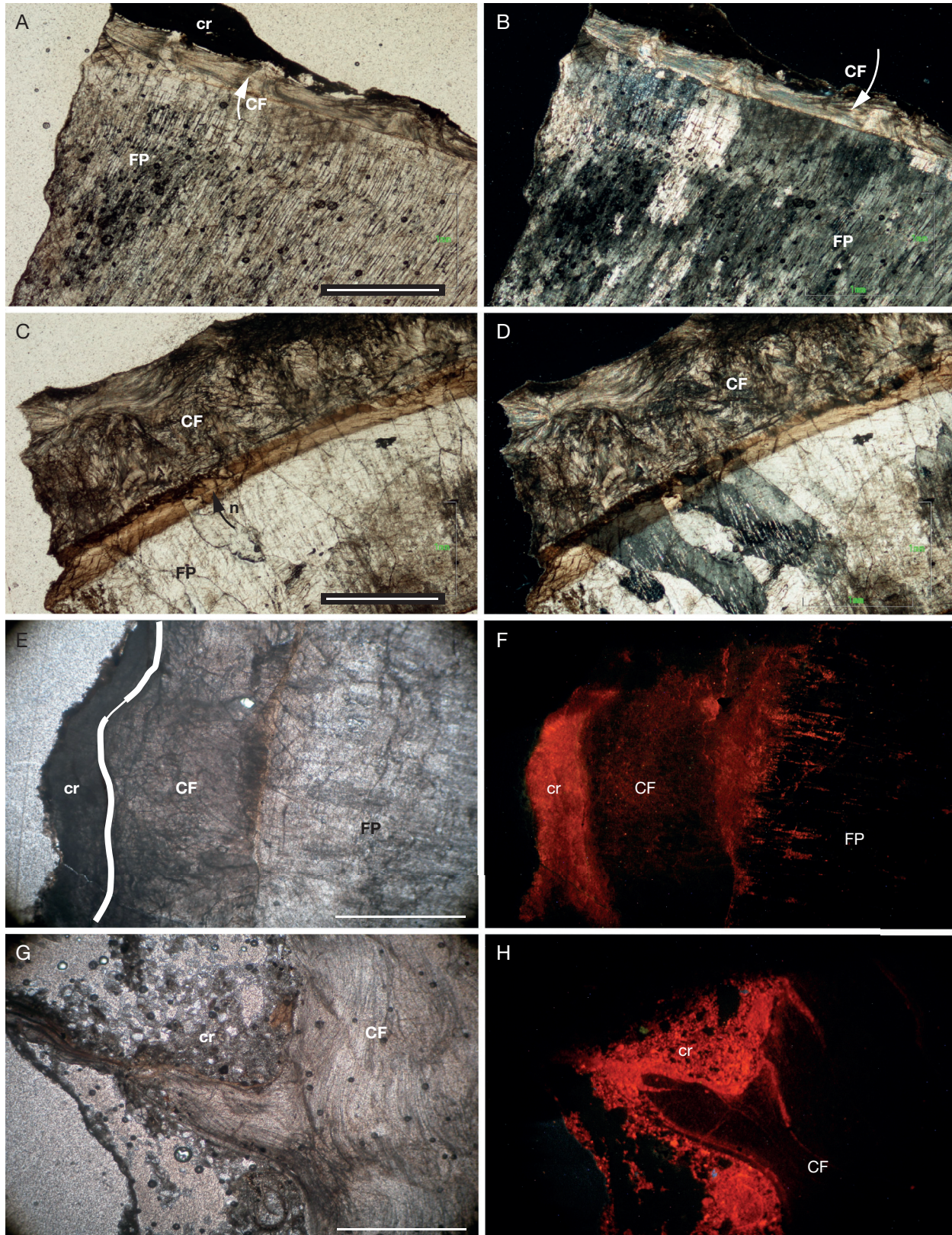
Under cathodoluminescence, both CF and FP structures respond with dull luminescence, whereas micritic carbonate residues (cr), show more intense red luminescence. The lack of luminescent response of the CF and FP structures, despite the evidence of intense neomorphism observed in FP, may be indicative of early neomorphism in an oxidizing phreatic

environment, which did not permit incorporation of manganese and iron cations to the calcite network (Fig. 5E-H).

Fossils of *Pycnodonte brongniarti* (Bronn, 1831) collected from the Ilundain Marl Formation, when observed in thin section, present a dominant complex crossed lamellar structure (CL), with less developed vesicular (V) structure in transverse sections (Fig. 6). In addition, repetitive thin and very long cells (ec), initially empty, limited between thin layers of the complex crossed lamellar structure (CL) have been observed in the more bended areas (Fig. 6A). In these areas empty cells (ec) are numerous and fractured, with evidence of small wall movements which facilitated a full early cementation by equant ferroan calcite crystals. Etching with Stained Alizarin Red S and potassium ferricyanide permits distinction of equant cement with mauve colour from the CL structure with red colour (Fig. 6B) (Adams & MacKenzie 1998). In detail, two stages of cementation can be determined, the first with early development of small acicular crystals, characteristic of meteoric and marine water mixing (a), and the second cementation stage (b) with big equant ferroan calcite crystals. The last cementation type (b), having ruled out its origin in meteoric phreatic environments, is more characteristic of a phreatic burial environment (Fig. 6C, D) (Tucker & Wright 1992; Tucker 1994). The CL structure is dominant and can evolve to vesicular structure (V) in the bended areas, probably as adaptive strategy used by *Pycnodonte brongniarti* to economize metabolic energy during growth of the shell.

At higher magnifications continuity seems to be continuity between the lamellae of the CL structure to the V walls, with the same optical behaviour in both the stained and equant cements. Interestingly, the walls of the V microstructure remain preserved, despite their thinness, as emphasized by darker traces of micrite with organic remains, opaque ores and fluid inclusions (Fig. 6E). Full cementation involves large calcite crystals with a preferred orientation and exceeds the limits of the vesicles. This strongly suggests a general phreatic cementation (Fig. 6F) (Tucker & Wright 1992; Tucker 1994). However, diagenetic intensity was higher in some samples, with partial destruction of the walls. It should also be noted that when the transverse sections are bigger, the formation of the structure (V) is visible through the partitioning lines indicative of growth band separation and disruption of the largest net vesicles, and then continues with the growth of smaller vesicles. In addition, the fill-

FIG. 5. — Photomicrographs of thin-sections of *Spondylus cf. caldesensis* Carez, 1881 and *Spondylus cisalpinus* Brongniart, 1823 (ecomorph *bifrons*) fossil shells from the transition between the Eocene (Bartonian–Priabonian) Ardanatz Sandstone and Ilundain Marl formations (Navarre, AD5 and AG1 sections), and of *Spondylus cisalpinus* Brongniart, 1823 fossil shells from the uppermost part of the Ilundain Marl Formation (Navarre, IV section), showing different structures affected by diagenesis: **A**, Specimen IV.15, longitudinal thin-section (parallel nicols) of *Spondylus cisalpinus* fossil shell showing an inner shell layer with fibrous prismatic structure (FP) characterized by fine and long prisms. The original aragonite layer (according to Bøggild 1930: 269) was replaced by calcite. Above the inner shell layer is the calcitic crossed foliated microstructure (CF), much less developed, which corresponds to the shell's outer layer. The middle layer, corresponding to the miostracum (?), has been obliterated by the FP structure. Micritic carbonate residues (cr) are observed along with the CF; **B**, same as **A**, with crossed nicols. The strong neomorphism suffered by the fibrous prismatic structure (FP) can be seen, with big calcite crystals showing different extinctions; however, the CF structure is less affected by diagenesis; **C**, specimen AG1.4.1, longitudinal thin-section (parallel nicols) of *Spondylus cisalpinus* (ecomorph *bifrons*) with a strongly modified fibrous prismatic structure (FP), originally aragonitic, where prisms are hardly preserved. The thin brownish area with aragonitic nacreous structure (n) corresponds to the middle shell layer (miostracum?), which is covered with an outer shell layer with calcitic crossed foliated microstructure (CF); **D**, same as **C** with crossed nicols. The neomorphic big calcite crystals extend to the thin brownish area of the middle shell layer (miostracum?). The crossed foliated structure (CF) suffered a lesser degree of neomorphism; **E**, specimen AG1.4.2, longitudinal thin-section (parallel nicols) of *Spondylus cisalpinus* (ecomorph *bifrons*). View of the fibrous prismatic structure (FP), the crossed foliated microstructure (CF) and micritic carbonate residues (cr); **F**, same as **E** under cathodoluminescence.



The different layers show different effects of fossil-diagenetic alteration. The red luminescence of the micritic carbonate residues (**cr**) indicates that they have been more strongly affected by diagenesis than the shell layers, as the crossed foliated structure (**CF**) is non-luminescent and the prismatic structure (**FP**) is only partially luminescent (dull luminescence). The advance of diagenesis towards the shell interior is shown by the luminescent red colour extending along interprismatic paths; **G**, specimen AD5.1.1, thin-section (parallel nicols) of *Spondylus cf. caldesensis*. View of the crossed foliated structure (**CF**), with its spines/radial ribs coated by micritic carbonate residues (**cr**); **H**, same as **G** under cathodoluminescence, showing non-luminescent crossed foliated structure (**CF**) along with luminescent micritic carbonate residues (**cr**) and fractures affecting locally the CF structure. Scale bars: 1 mm.

ing is produced by smaller crystals (polycrystalline in each vesicle), involving a change in environmental conditions.

Regarding behaviour under cathodoluminescence, the CL structure shows dull luminescence, indicating that this type of structure was capable of enduring the diagenetic alteration that undoubtedly affected all the shell. Conversely, the acicular crystals, that were formed during the early infilling of the empty cells (a), respond with weak luminescence, as they were possibly generated in an oxidizing and mixing aqueous environment. The subsequent filling with equant calcite cement (b), much more luminescent in bright red, suggests a reducing environment and incorporation of iron and manganese into the calcite network (Fig. 6G). A similar behaviour can be deduced to have occurred between the CL structure and the walls of the V structure, which show very low luminescence in comparison to the cement that filled the vesicles, which produces generally intense red colours (Fig. 6H).

In summary, significant effects of diagenesis were observed in the fossils studied. In the gastropods, neomorphism processes with formation of large crystals of equant calcite occurred when the body cavity was filled with early detrital sediment. In other specimens lacking intrashell sediment, broken trace-ghosts of the original aragonitic crossed lamellar structure are still preserved and early cementation by precipitation of large celestite crystals within the body cavity can be observed.

Different diagenetic behaviours can also be deduced for *Spondylus* fossil shells depending on their structure. The CF structure is more resistant than the FP structure, in which original aragonite prisms are neomorphized and generate large calcite crystals with different orientations. This observation is supported by cathodoluminescence.

Pycnodonte fossil structures are more complex and allow the diagenetic evolution to be better established. The CL and V structures are dominant and resistant to diagenesis. The cements incorporated into empty cells and V structures allow the identification of two diagenetic stages. The first cement (a) was in all likelihood generated in an oxidizing and mixing aqueous environment, whereas the second (b) is considered as characteristic of a phreatic burial environment. This observation agrees with stratigraphic and micropaleontological data (see below: Fossil associations and palaeoenvironments), which indicate that the fossiliferous strata of the uppermost Ilundain Marl Formation in the Itzagaondo valley, where fossils of *Pycnodonte brongniarti* are abundant, were deposited in a shallow inner shelf environment.

SYSTEMATIC PALAEOONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758
 Class GASTROPODA Cuvier, 1795
 Clade (Superorder) VETIGASTROPODA
 Salvini-Plawen, 1980
 Superfamily PLEUROTOMARIOIDEA Swainson, 1840
 Family PLEUROTOMARIIDAE Swainson, 1840

Genus *Leptomaria* Eudes-Deslongchamps, 1864

TYPE SPECIES. — *Pleurotomaria amonea* Eudes-Deslongchamps, 1849 by original designation.

Leptomaria peresii (d'Orbigny, 1850)
 (Fig. 7A-D)

Pleurotomaria peresii d'Orbigny, 1850: 313.

Pleurotomaria nicacensis Bayan, 1870: 12.

Conotomaria peresii – Benfrika 1994: 99.

Leptomaria peresii – Pacaud 2004: 620.

MATERIAL. — Ardanatz Sandstone. AD4 section: 2 incomplete and somewhat laterally compressed specimens from level AD4.1 (c. equivalent to AD3.1). 2 fragmentary specimens from AD sections (section and level unknown). AG1 section: 2 fragments from level AG1.2.

DIMENSIONS. — H = (>25.0)-42.0; W = (>32.0)-(>39.0).

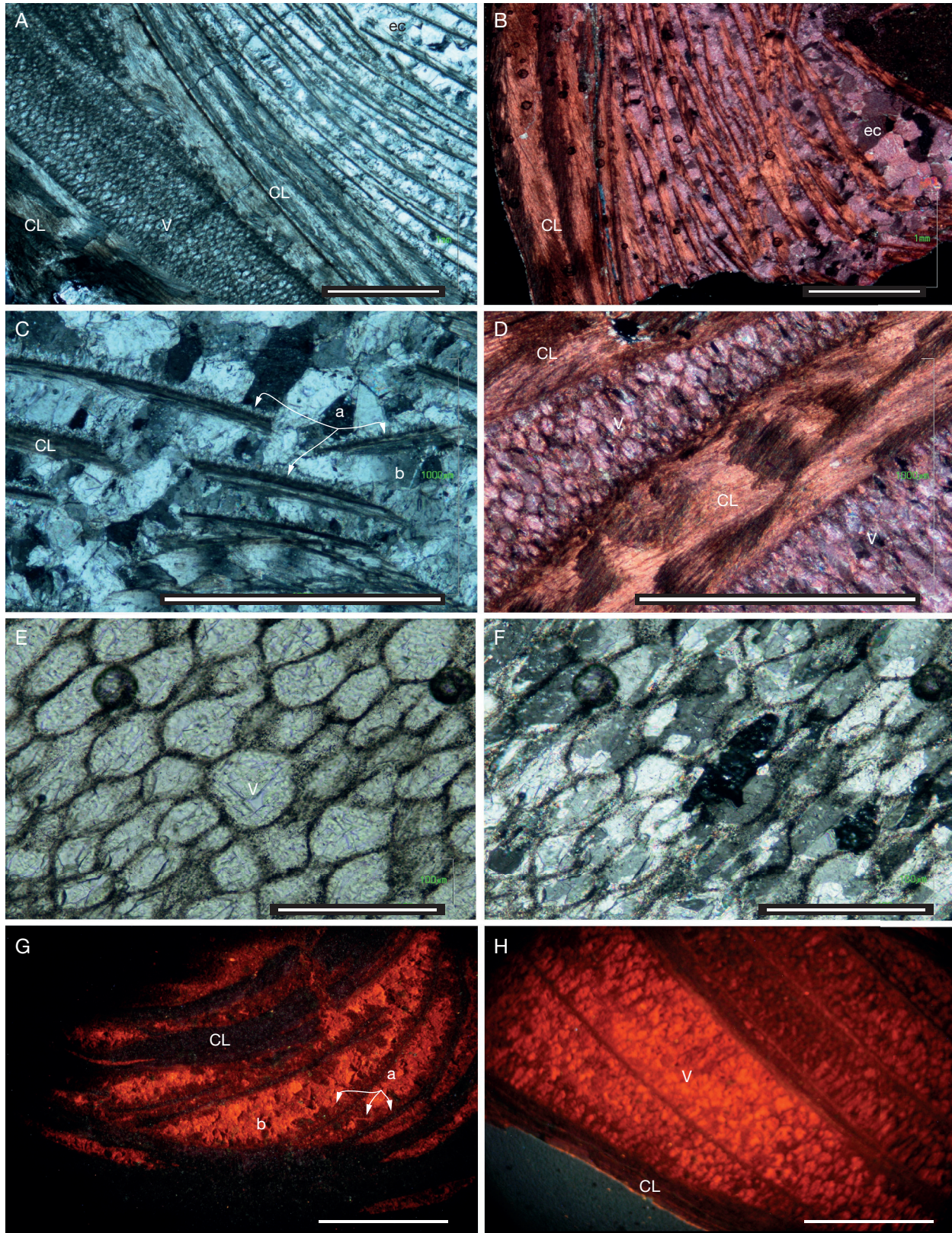
DESCRIPTION

High and thick trochiform (trochoid) shell; protoconch pausispiral, homostrophic, smooth, preserved in one of the specimens; base convex; umbilicus present, preserved in one specimen (?); granular surface sculpture, with spiral cords and wavy and weak axial ribs; ornamentation of the adapical part of adult whorls above seleniarea more marked, with procline (tri-) nodular axial ribs (spiral cords acquire granular appearance); abapical part below seleniarea with thin spiral cords and ortocline-opisthocline axial ribs. Aperture mixing, U-shaped slit unpreserved, but seleniarea visible below shoulder (in the apical part of the whorls), narrow, marked by scaly, regularly spaced and opistocytic scars.

REMARKS

The high conispiral shell and the presence of seleniarea allow assignation of these remains to the family Pleuro-

FIG. 6. — Photomicrographs of thin-sections of *Pycnodonte brongniarti* (Bronn, 1831) fossil shells, from the uppermost part of the Eocene (Bartonian-?Priabonian) Ilundain Marl Formation (Navarre, IV section), showing different structures affected by diagenesis: **A**, longitudinal thin-section of specimen IV.16 (crossed nicols), showing the complex crossed lamellar structure (**CL**), along with the vesicular structure (**V**) and empty cells (**ec**) delimited by CL thin walls, later filled by spatic cement with equant crystals; **B**, specimen IV.17 (crossed nicols), curvature area where the thin layers with crossed lamellar structure (**CL**) generate empty cells (**ec**), later broken and filled with equant calcite cement. Staining with Alizarin Red S and potassium ferricyanide allows distinction of carbonate minerals containing Fe⁺² (ferroan minerals) from those with little or no iron (non-ferroan minerals). The CL structure has an intense red colour (non-ferroan calcite) whereas the calcite cement shows mauve colour (ferroan calcite); **C**, specimen IV.16 (crossed nicols), detail of (originally) empty cells, whose thin walls with crossed lamellar structure (**CL**) were broken and slightly displaced. Two cementation stages are observed: **a**, early acicular growth only on one side of the wall fragments (typical of the phreatic marine area); and **b**, later equant calcite cementation, infilling completely the original empty spaces; **D**, specimen IV.18 (crossed nicols), detail of alternating crossed lamellar structure (**CL**), stained in red colour, and vesicular structure (**V**), generally displaying a lenticular arrangement; **E**, specimen IV.16



(parallel nicols), detail of the vesicular structure (V), where the thin walls show organic matter remains and evidence of iron ores; F, same as E, with crossed nicols. The equant cementation involves big calcite crystals which are not deformed and cross the vesicle walls, typical evidence of cementation in phreatic environments; G, specimen IV.19 under cathodoluminescence. The thin layer with crossed lamellar structure (CL) hardly shows luminescence (non-luminescence), while the equant calcite cement infilling the cells is composed of red luminescent big crystals. In detail, some cement crystals (a) associated with the walls are non-luminescent and suggest oxidizing environments, whereas the subsequent filling of the central area, in red colour (b), shows evidence of a reducing environment; H, specimen IV.19, showing the complex crossed lamellar (CL) and vesicular (V) structures under cathodoluminescence. The CL structure and the vesicle walls show weak (dull) luminescence, while the equant calcite cement infilling the vesicles shows intense red colour. Scale bars: A-D, G, H, 1 mm; E, F, 0.3 mm.

tomariidae. The second feature excludes these from Trochoidea. The narrow seleniarea, its location in the apical part of the whorls and the rather granular sculpture of the shell, are all indicatives of the genus *Leptomaria* (see Pacaud 2004, 2007).

Leptomaria peresii (d'Orbigny, 1850) was defined in the Priabonian of the Fontaine du Jarrier (Alpes-Maritimes) (MNHN.F.R64076, d'Orbigny collection). It exhibits similar proportions to those of the Danian species *Leptomaria penultima* (d'Orbigny, 1850), but its spiral ornamentation is more marked, with thicker and wider cords (see Pacaud 2004, 2007).

The occurrence of Pleurotomariidae has previously been mentioned in Eocene strata of neighbouring geological regions. Boussac (1911: pl. 4, fig. 6) figured and assigned a fossil from the Eocene of La Gourèpe, in the Paleogene series of the Basque Coast (southwestern Aquitaine Basin), in the surroundings of the town of Biarritz/Miarritze, to "*Pleurotomaria*" *lamarcki* Mayer, 1876. Farrés (1961) and Farrés & Staid-Staad (1964) cited, but did not illustrate, two species as *Pleurotomaria deshayesi* Bellardi, 1852 (a junior subjective synonym of *L. peresii*, see Pacaud 2007) and as *Pleurotomaria cf. concavata* [sic] Deshayes, 1832 (a species attributed to the genus *Chelotia*) in the Bartonian-Priabonian of Gurb (Vic region, Catalonia).

Clade (Superorder) CAENOGASTROPODA Cox, 1960
 Clade (Order) SORBEOCONCHA
 Ponder & Lindberg, 1997
 Superfamily CERITHIOIDEA Fleming, 1822
 Family CERITHIIDAE Fleming, 1822

 Genus *Ptychocerithium* Sacco, 1895

TYPE SPECIES. — *Cerithium granulinum* Bonelli in Michelotti, 1840 by original designation.

Ptychocerithium baylei (Tournouër, 1874) n. comb.
 (Fig. 7E-J)

Cerithium baylei Tournouër, 1874: 528.

Cerithium suessi Tournouër in Bouillé, 1873: 463, pl. 5, fig. 12 (*non* Gemmellaro, 1868).

Cerithium sp. – Tournouër in Bouillé 1876: 250.

Ptychocerithium johannae – Boussac 1911: 34, pl. 7, fig. 16. — Astibia *et al.* 2016: 13, fig. 6a.

MATERIAL. — Ardanatz Sandstone. AD1 and AD2 sections: 1 specimen from level AD1.2; 2 specimens from level AD1.3; 13 specimen from level AD2.1; 1 specimens from level AD2.2. AG1 section: 12 specimens from level AG1.3; 1 specimen from level AG1.4. Ilundain Marl Formation, IV section: 13 specimens. All are fragmentary specimens, lacking the apical part and the aperture (or most of it).

DIMENSIONS. — Largest specimen: H > 34.0; W = 13.0 (incomplete specimen, about 42.0 high complete?).

DESCRIPTION

Shell medium-sized; cerithiform; multi-whorled (about 12 whorls in adult specimens); protoconch not preserved; teleoconch long, turruculate, abapical half straight or slightly convex; apical angle about (17)-22 degrees; spire whorls flat sided; spiral sculpture consists of three well developed primary or major beaded, granulated, cords (spiral ribs P1, P2, P3), four beaded secondary cords (adapically to P1, between P1 and P2 and P3, abapically to P3), tertiary cords occurring between other cords; P1 more developed than the others in the last two whorls of the spire and in the body whorl. Morphological variability occurs, with specimens with the second secondary beaded cord almost as developed as the two first primary cords (P1 and P2), but others (IV section) with P3 very poorly developed (Fig. 7I); growth lines opisthocyrtos-ortoclines; primary beads or nodules situated at the intersection (cross-over points) with generally not very prominent axial ribs; the number of primary beads of the last five whorls of the spire ranges from 14 or 13, 16 more frequently, to 18; body or last whorl with three major beaded cords, beads considerably more elongated, no less than eight cords (four "primary" and four "secondary" intercalated) below the three major granulated ones, strong varix opposite aperture (abapertural side); aperture always broken, relatively small, about 16-20% of the total shell length (?), with remains of well developed (?) inner lip, posterior (anal) canal and moderately extended (?) anterior siphonal canal.

REMARKS

This species is the most abundant gastropod in the fossil associations of the Ardanatz Sandstone. The presence of Cerithiidae (*Cerithium* sp.) in the Bartonian of Ardanatz-Eguesibar was already mentioned by Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949) and Ruiz de Gaona & Colom (1950).

The studied specimens are similar to those first described as "*Cerithium* sp. indéterminé." by Tournouër (1864) and later as "*Cerithium suessi*" (Tournouër in Bouillé 1873: 463, pl. 5, fig. 12) in the marls with *Serpula spirulaea* (*Rotularia spirulaea* (Lamarck, 1818)) in the north of Peyrehorade (Landes, Aquitaine Basin). Later Tournouër (1874) renamed *C. suessi* (correction for primary homonymy, pro *Cerithium suessi* Tournouër, 1873 non Gemmellaro, 1868) as *Cerithium baylei*. Our specimens are comparable to the syntypes of *Cerithium baylei* from the Priabonian of Peyrehorade in the Tournouër collection (MNHN.F.B21040).

A species closely related to *Ptychocerithium baylei* n. comb. is *P. johannae* (Tournouër in Bouillé, 1873), from the Paleogene series of the Basque Coast, outcrop of Villa Lady Bruce, in the surroundings of Biarritz/Miarritze (Bartonian-Priabonian, Côte des Basques Marls Formation, southwestern Aquitaine Basin, Jacquot 1864; Mathelin & Sztrákos 1993; Sztrákos *et al.* 1998, 2010). Described as "*Cerithium johannae*" by Tournouër (in Bouillé 1873: 446, pl. 5, fig. 11), this species was also described by Boussac (1911: pl.7, fig.16) from the outcrop of Villa Marbella, the same as Lady Bruce according to this author. However, *P. baylei* n. comb. and *P. johannae* present a somewhat different morphology. In *P. baylei* n. comb. the



FIG. 7. — Fossils of gastropods from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A-D**, Pleurotomaridae indet.: **A, B**, AD4.1.1, apertural and oblique apical views; **C**, AD.19, lateral view; **D**, AG1.2.1, oblique apical view; **E-J**, *Ptychocerithium baylei* (Tournouër, 1874) n. comb.: **E**, AG1.4.3, apertural view; **F**, AG1.3.1, apertural view; **G**, AD2.1.6, apertural view; **H**, AG1.3.2; **I**, IV.20; **J**, IV.14; **K-O**, *Diastoma costellatum* (Lamarck, 1804): **K**, IV.22, dorsal view; **L**, AD1.3.3, apertural view; **M**, IV.24; **N**, IV.23, apertural view; **O**, IV.25, apertural view? **P, Q**, *Benoistia* sp.: IV.33, dorsal and ventral views; **R**, *Jponsia* sp., IV.1, dorsal view. Scale bars: 5 mm.

primary spiral sculpture consists of well developed beaded or granulated cords. On the contrary, in *P. johannae*, as pointed out by Tournouër (see Bouillé 1873: 446), the granulations are only well developed in the first teleoconchal whorls, being significantly attenuated in the next whorls and resulting in smoother spiral cords.

The morphology of our specimens coincides with that of two specimens of *P. johannae* included in the Cossmann collection from the Bartonian of Biarritz (MNHN.FJ12641). However, due to the presence of well-developed beaded or granulated cords, in our opinion these two specimens should be better assigned to *P. baylei* n. comb.

The morphology is also quite similar to that described by Tournouër for “*Cerithium biarritzense*” (in Bouillé 1876: 62, pl. 3, fig. 5), another of the “Cérites des couches à *Serpula spirulaea*” (in denomination of Boussac 1911) from the site of Lady Bruce. It is very likely that *P. baylei* n. comb. and *C. biarritzense* are synonymous.

P. baylei n. comb. differs from *P. sublamellosum* (d’Archiac, 1846) by having flat and not slightly convex spire whorl profiles (see d’Archiac 1846: pl. 9, fig. 8). Furthermore, one specimen of *P. sublamellosum* illustrated – as *Cerithium sublamellosum* – by Boussac (1911: 11, fig. 11) and another four fossils assigned to the same species in the Cossmann collection (MNHN.FJ12761) from Biarritz, exhibit four spiral cords, and not three as in *P. baylei* n. comb., with less developed beads but more marked axial ribs than in *P. baylei* n. comb. *Ptychocerithium gentili* (Boussac, 1911), also present in the Bartonian of Biarritz (Villa Marbella site), has four spiral cords (see Boussac 1911: 22, fig. 5).

Gastropods are abundant in the Eocene of Catalonia, in the eastern part of the South Pyrenean area (Carez 1881; Cossmann 1898a, 1906; Farrés 1961; Farrés & Staid-Staadt 1964; De Renzi 1971; Dominici & Kowalke 2014). Cossmann (1898a, 1906) discusses and defines many gastropod species from the Eocene of Catalonia, but *P. baylei* n. comb. was not cited.

Family DIASTOMATIDAE Cossmann, 1894

Genus *Diastoma* Deshayes, 1861

TYPE SPECIES. — *Melania costellata* Lamarck, 1804 by monotypy.

Diastoma costellatum (Lamarck, 1804)
(Fig. 7K-O)

Diastoma costellatum Lamarck, 1804b: 430.

Diastoma hispanicum Cossmann, 1906: 442, pl. C, figs 15-17.

Diastoma biarritzense Oppenheim, 1906: 82, 83, pl. 9, fig. 18. — Boussac 1911: 48, pl. 11, fig. 10.

MATERIAL. — Ardanatz Sandstone. 3 specimens from AD sections (levels unknown). AD1 and AD2 sections: 1 specimen from level AD1.3; 1 specimen from level AD2.1; 1 specimen from level

AD2.2. AG1 section: 3 fragments from level AG1.4. Ilundain Marl Formation, IV section: 37 specimens. All incomplete specimens, aperture not preserved.

DIMENSIONS. — Largest specimen: H > 25.0; W = 8.5 (incomplete specimen, about 30.0 high complete?).

DESCRIPTON

Shell medium-sized; slender, turriculate; whorls convex-sided, incised sutures; main ornamentation consist of 13-19 regularly spaced axial ribs, with one or two varices on each whorl, in general not very strong, crossed by 4-5 equally spaced primary cords (spiral ribs) in early whorls, 7-10 in adult spire, 14 or more in the last whorl; intercalated secondary and even some tertiary spiral ribs; variability in the development of the axial sculpture is observed, especially in the varices, from very marked to virtually absent; in some specimens adapical third spirals and axial ribs are coarse, thicker, with granulose and elongated intersections.

REMARKS

This species is the most abundant gastropod in the fossil associations from the outcrops of the Itzagaondoa Valley (IV section), in the uppermost part of the Ilundain Marl Formation. The morphology of the shells is quite similar to *Diastoma costellatum* (Lamarck, 1804), a species defined in the Lutetian strata of the Paris Basin. However, the ornamentation of our fossils is more marked than in the specimens of *D. costellatum* from the Lutetian strata of Damery (Marne) (see in Courville *et al.* 2012), Chaussy (Val-d’Oise, MNHN.FJ02476, J12812, Cossmann coll.) or Grignon (Yvelines, MNHN.FJ03710, Cossmann coll.) of the Paris Basin, and markedly more pronounced than in the holotype of *Diastoma imbricatum* Cossmann, 1898 from the Bartonian of Bois-Gouët (Loire-Atlantique, MNHN.FJ04722, Cossmann coll.) (Cossmann 1898b). In this sense, it bears greater resemblance with the species *Diastoma hispanicum* Cossmann, 1906 from the Early Eocene of Perauba (Catalonia), but in our opinion the differences between *D. costellatum* and *D. hispanicum* are not significant. Farrés & Staid-Staadt (1964) cite the occurrence of *D. costellatum* in the “Biarritzian” (Bartonian-Priabonian, Cascella & Dinarès-Turell 2009; Costa *et al.* 2013) from the Comarca de Vic (Catalonia). *Diastoma costellatum* is also mentioned and figured by Boussac (1911: pl. 8, fig. 7; pl. 11, fig. 9) in the “Nummulitique” of Biarritz, from the Auversian (Bartonian) of Villa Marbella and from the Bartonian or early Priabonian of the Côte des Basques Marls Formation (south-western Aquitaine Basin). The Cossmann collection includes three specimens of *D. costellatum* (MNHN.FJ12818) and three specimens of *Diastoma costellatum elongatum* (Brongniart, 1823) (MNHN.FJ12822) from Biarritz, and they are fully comparable to those of Navarre. Oppenheim (1906: 82, pl. 9, fig. 18) described a new species, *Diastoma biarritzense*, from the marls of the Côte des Basques. Boussac (1911: pl. 11, fig. 10) described a shell fragment from the Côte des Basques, which he also assigned to the species *Diastoma biarritzense* Oppenheim, 1906, due to its lower number and less development axial ribs – similar to the specimen AD1.3.3 from

Ardanatz sandstone (Fig. 7L). However, in our opinion the morphological features of *D. biarritzense* fit within the variability of *D. costellatum*. Puigdefàbregas (1975, determinations by Villalta Comella) mentioned the presence of *D. costellatum elongatum* and *D. costellatum biarritzense* in the Eocene marls of Binacua and San Román de Basa (Pamplona Marls *sensu lato*, Jaca Basin, west-central part of the South Pyrenean area), which are all situated in the neighbouring territory of Huesca (Aragon), about 120 km to the southeast of our study area.

Family BRACHYTREMATIDAE Cossmann, 1906

Genus *Benoistia* Cossmann, 1900

TYPE SPECIES. — *Cerithium muricoides* Lamarck, 1804 par monotypy.

Benoistia sp. (Fig. 7P, Q)

MATERIAL. — Ilundain Marl Formation, IV section: 1 incomplete specimen.

DIMENSIONS. — H > 18.0; W = (12.0) (incomplete specimen, about 22 mm high complete).

DESCRIPTION

Shell medium sized. Four last whorls preserved. Conical and slightly elongated teleoconch. Suture moderately deep. Axial sculpture of 5-8 low ribs becoming less and less marked during the growth. On the spire, one strong primary cord on the sutural ramp and two other primary cords on the convex part of the whorl. On the last whorl, one strong primary cord on the sutural ramp and around four other primary cords on the convex part of the whorl. On the two last whorls, appearance of secondary cords and threads. Numerous granules on the primary cords and major secondary cords. Aperture not visible.

REMARKS

The elongated shape of *Benoistia vidali* Cossmann, 1906 from the Early Eocene of Catalonia (Perauba) strongly resembles *Benoistia* sp. However, since the early teleoconch whorls, the axial ribs are well defined and strongly nodulose, whereas *Benoistia* sp. bear only small nodules. On the last whorl, *Benoistia vidali* displays subspinose nodules on the shoulder, whereas they are developed in *Benoistia* sp. *Benoistia bofilli* Cossmann, 1906, from the Early Eocene of Catalonia (Perauba), differs by a shorter shape, more marked axial ribs and a less granulose surface. *Benoistia muricoides* (Lamarck, 1804), from the Middle Eocene of the Paris Basin, differs by a shorter shape and by nodulose and subpinose ribs, but it shares a granulose surface with *Benoistia* sp. *B. acutidens* (Deshayes, 1833) from the Lutetian of the Paris Basin shares an elevated spire, but is easily distinguishing by its sculpture in which the first spiral cord of the convex part of the whorl forms a strong keel. In addition, the surface of the shell is not granulose. The Rupelian species *B. boblayi* (Deshayes, 1833)

possesses a more conical shell and its axial ribs are almost not marked. Finally this species of *Benoistia* seems to be new, but more material is needed to complete its shell description and particularly the aperture.

Family PACHYCHILIDAE Fischer & Crosse, 1892

Genus *Jponsia* Pacaud & Harzhauser, 2012

TYPE SPECIES. — *Melania cuvieri* Deshayes, 1825 by original designation.

Jponsia sp. (Figs 7R; 8A, B)

MATERIAL. — Ilundain Marl Formation, four fragmentary specimens from IV section.

DIMENSIONS. — Largest specimen: H > 50.0; W = (22.0) (incomplete specimen, about 70 mm high complete?).

DESCRIPTION

Shell medium-large sized; cerithiform, robust, long spire; strong axial sculpture with coarse ribs (varices), slightly spiny and opisthocline, especially developed in the middle and abapical parts, about 11 (preserved young spire)-9(10) (adult spire) per whorl; adapical third of whorls depressed and rather flat, forming a fringe or band with thin axial ribs (growth lines?) and two separate upper and lower grooves (furrows) in the larger specimens. Spiral sculpture marked by furrows giving the axial ribs an imbricated-staggered outline. Last whorl small, less than a third of the total height of the shell, with net spiral ornamentation down to the base.

REMARKS

In a recent work Pacaud & Harzhauser (2012) reviewed the Pachychilidae of the European Paleogene, suggesting the creation of three new genera: *Jponsia*, *Moniquia* and *Eginaea*. These authors included in the new genera some Cretaceous and Paleogene species, previously assigned to genera such as *Faunus* De Montfort, 1810, *Melanatria* Bowdich, 1822, *Pirena* Lamarck, 1822 or *Tinnyea* Hantken, 1887.

Although the material available in this study is very limited, in principle, the genus *Jponsia* seem to be more appropriate than *Moniquia*, because the development of the spiral sculpture is greater; unlike the development of the spiny sculpture, which is smaller and adapically not abaxially oriented.

The morphology of our specimens is quite similar to that of the fossils which Villalta Comella (1956: 152-154, pl. 4, fig. 1) assigned to *Faunus (Melanatria) undosus* (Brongniart, 1823), from the Bartonian marls of San Román de Basa (Huesca, Jaca Basin, South Pyrenean area). It is also comparable to a specimen of *Jponsia undosa* (Brongniart, 1823) figured by Pacaud & Harzhauser (2012: pl. 2, fig. 4) from the Bartonian of Roncà (Italy), although the fragmentary state of both the Italian and our specimens does not allow further insight.

Family TURRITELLIDAE Lovén, 1847

Genus *Haustator* Montfort, 1810

TYPE SPECIES. — *Haustator gallicus* Montfort, 1810 by monotypy.

Haustator altavillensis (Cossmann & Pissarro, 1900)
(Fig. 8C-G)

Turritella altavillensis Cossmann & Pissarro, 1900: 196, pl. 20, figs 6-7.

Turritella (*Haustator*) *altavillensis* – Villalta Comella 1956: 143, 144, pl. 3, figs 1a-1e.

MATERIAL. — Ardanatz Sandstone. 4 specimens from AD sections (levels unknown). AD1 and AD2 sections: 1 specimen from level AD1.2; 1 specimen from level AD2.1; 2 specimens from level AD2.2. Ilundain Marl Formation, IV section: 4 fragments. All incomplete specimens, protoconch, early teleoconchal whorls and aperture not preserved.

DIMENSIONS. — Largest specimen: H > 47.0; W = 15.0 (incomplete specimen, about 80 mm high complete?).

DESCRIPTION

Shell large-sized, turriculate, sharply conical; protoconch and aperture are missing in all specimens; apical angle about 10-11 degrees (?); adult whorls flat-sided, basally carinate, sculptured with 7-8 fine spiral keeled cords, sharps, more tightly packed the first three or four cords, more separate and developed the following, being the 7th (the penultimate cord, spiral C? of Marwick 1957) the most prominent; the last two cords may form a basal carination, variable in development, and sometimes seem to protrude slightly above the next whorl; space between cords (spiral grooves) concave; adult growth lines between the sutures (outer lip trace) opistocirces-prosoclines, with moderately oblique lateral sinus; growth lines develop a fine axial costulation, pointed by partial dissolution of the fossil shells. The intersection between the thin axial ornamentation and the spiral cords gives them a finely and irregularly toothed, granulated appearance.

REMARKS

The presence of Turritellidae among the gastropods from the Eocene of marly formations of Navarre was already mentioned by Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949) and Ruiz de Gaona & Colom (1950), who cited the species “*Turritella duvali*” in the Bartonian of Ardanatz-Eguesibar.

The genus *Turritella* Lamarck, 1799 is widely used for many turritelline species. Turritelline genus-level systematics remains unclear (Allmon 1996). According to Marwick (1957) and Tracey & Todd (1996), the flat-sided adult whorls and prominent primary spirals C forming a basal carination allow the studied fossils to be tentatively assigned to *Haustator*, but unfortunately the protoconch and the early teleoconch, which are important to reliably identify this genus, are missing in our material.

During the past, several species of the genus *Turritella* have been described in the Paleogene series of Bearn and the

Basque Coast (southwestern Aquitaine Basin) and Catalonia (eastern margin of the Ebro Basin). D’Archiac (1850: pl. 13, fig. 19) described and figured a fossil of *Turritella inscripta* d’Archiac, 1850 (synonym of ?*Haustator inscripta* (d’Archiac, 1850)), a species established from perhaps too fragmentary specimens. Three specimens of ?*H. inscripta* from the Eocene of Biarritz (Villa Marbella, Côte des Basques Marls Formation; MNHN.F.J12239, Cossmann coll.) present, as diagnosed by d’Archiac (1850), two carina on every whorl, a morphology distinctively different to that in our fossils. D’Archiac (1850) also cited *Turritella carinifera* Deshayes, 1832 (synonym of *Haustator contractus* (Sowerby J. de C. in Dixon, 1850)) in the Eocene of Biarritz and Pau (Bosdarros/Lo Bòsc d’Arròs). Rouault (1850: pl. 15, figs. 13, 14) described and figured two specimens of *T. carinifera* from the Early Eocene of Bosdarros (synonym of *Haustator pseudoelegans* (Cossmann, 1923)). Bouillé (1876) also cited *T. carinifera* from the sites of Lady Bruce and Phare (Roche d’Haïtzar) near Biarritz. Our specimens exhibit flat sides and basal carina, but they are more elongate than those figured by Rouault (1850). They are in fact more alike a specimen of *T. carinifera*, figured by Cossmann & Pissarro (1910: pl. 20, fig. 125-4) from the Lutetian of Chaumont-en-Vexin (Paris Basin), although spiral cords of the latter seem to be more numerous and more regularly distributed on every whorl than in fossils from Navarre. On the other hand, Newton (1912) suggested *T. oppenheimi* as a replacement name for *T. carinifera* Deshayes, 1832 (non Lamarck, 1822, a recent species) (Tracey & Todd 1996), but *T. oppenheimi* is a subjective synonym of *Haustator contractus* (Sowerby J. de C. in Dixon, 1850).

The overall morphology of the studied fossils is quite similar to specimens of *Turritella asperula* Brongniart, 1823 from the “Rupelian” (Oligocene) of the Chambre d’Amour, in the “Nummulitique” of Biarritz (southwestern Aquitaine Basin), described and figured by Boussac (1911: 82, 83, pl. 21, fig. 15 and pl. 22, figs 3, 4). However, the arrangement of spiral ribs looks quite different. In our specimens the ribs are stronger and more separate in the medium-abapical part of the whorls, while in *Haustator asperulus* the ribs are more regularly distributed over the entire surface of each whorl. The differences with *H. asperulus* from the Oligocene of Iran and Greece, as published in Harzhauser (2004), are even more marked. Unlike our specimens, *H. asperulus* does not have adult whorls with sharp, keeled, spiral ribs. Similar differences can be established with respect to two specimens of *H. asperulus* from the Rupelian of Saint-Hilaire (Pierrefitte, Essonne, France, MNHN.F.A42164 and A42165), figured by Lozouet & Maestrati (2012).

Our fossils are, however, very similar to those which Villalta Comella (1956: 143, 144, pl. 3, figs 1a-1e) assigned to the species *Turritella* (*Haustator*) *altavillensis* Cossmann & Pissarro (1900), from the Bartonian of San Román de Basa and Isún de Basa (Huesca, Jaca Basin, South Pyrenean area). According to Villalta Comella (1956), *H. altavillensis* could be a variety of *H. contractus*, which, like our specimens, would differ by having finer and more granular and irregularly distributed spiral cords, among other distinctive features. However, Villalta



FIG. 8. — Fossils of gastropods from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A, B**, *Jponisia* sp.: **A**, IV.26; **B**, IV.27; **C-G**, *Haustator altavillensis* (Cossmann & Pissarro, 1900): **C**, AD1.2.3; **D**, AD.21; **E**, IV.28; **F**, AD2.2.3; **G**, AD2.2.2. **H-L**, *Haustator* cf. *imbricarius conoideus* (Sowerby J., 1814): **H**, AD2.1.7; **I**, IV.29; **J**, IV.2; **K**, IV.30; **L**, AG1.3.5; **M-P**, *Sigmesalia* sp.: **M**, IV.3, apertural view?; **N**, AD.25; **O**, AD1.3.4; **P**, AD2.1.8; **Q-S**, Ampullinidae indet.: **Q, R**, AD.26, apertural and oblique apical views; **S**, AD.27; **T**, ?*Globularia* sp., AD.28, apertural view. Scale bars: 5 mm.

Comella (1956) indicated that, despite the large number of specimens available, there is a great homogeneity of characters with no intermediate forms, a fact that could point to the validity of the species *Haustator altavillensis* (Cossmann & Pissarro, 1900). Years later, Puigdefàbregas (1975, determinations by Villalta Comella) also mentioned the presence of *H. altavillensis* in the Eocene marls of Yebra de Basa, a locality situated near San Román de Basa and Isún de Basa.

Haustator cf. imbricatarius conoideus (Sowerby J., 1814)
(Fig. 8H-L)

Turritella conoidea Sowerby J., 1814: 109, pl. 51, figs 1-2, 4.

MATERIAL. — Ardanatz Sandstone. 4 specimens from AD sections (levels unknown). AD2 section: 1 specimen from level AD2.1. AG1 section: 1 specimen from level AG1.2; 1 specimen from AG1.3; 6 specimens from AG1.4. Ilundain Marl Formation, IV section: 33 specimens. All fossils are fragmentary; aperture not preserved.

DIMENSIONS. — Largest specimen (incomplete, somewhat crushed): H > 22.0; W = (9.0).

DESCRIPTION

Shell medium to large-sized, turretlike, sharply conical; protoconch and aperture unknown in the whole sample available; apical angle of about 16-22 degrees (?); teleoconch with deep sutures, spire whorls convex-sided and pseudo-imbricated aspect (abapical part of the whorls protruding with respect to the adapical part of the next whorl); adult ornamentation consists of regularly spaced finely granulose spiral cords of at least three orders; growth-lines opisthocirces. Some morphological variability in the convexity of the whorls and in the development of the first abapical rib, generally slightly more prominent than in other “primary” spirals, was observed.

REMARKS

The morphology of the specimens from the study area resembles that of *Haustator imbricatarius* (Lamarck, 1804), a species present in the basins of Paris and London, among other areas. In *H. imbricatarius* (specimens from the Lutetian of Damery [Marne] [Courville *et al.* (2012), Chaussy [Val-d’Oise] and Chaumont-en-Vexin [Oise] [MNHN.F.J03715 and J12228, Cossmann coll.]) considerable variability can be observed, but the outline of the whorls is generally quite straight, sometimes even slightly concave, whereas in our fossils it is slightly convex. D’Archiac (1846) cited an incomplete material of *Turritella imbricataria* Lamarck, 1804 from the Eocene of the Port des Basques, near Biarritz (southwestern Aquitaine Basin). Later Boussac (1911) also cited *T. imbricataria* in the “Auversien” from the same area, at the site of Villa Marbella, in the southern part of the Côte des Basques (Côte des Basques Marls Formation), and *Turritella trempina* Carez, 1881 in the “Bartonian inférieur ou Priabonien” from the northern part of the Côte des Basques. Likewise, two specimens of the Cossmann collection (MNHN.F.J12119) collected from the Priabonian of Biarritz and classified as *H. imbricatarius* have flat-sided spire whorls, not convex as in the specimens from Navarre.

According to Carez (1881), *H. trempinus* is distinguished from *H. imbricatarius* especially by its narrower shape. The four specimens of *H. trempinus* figured by Carez (1881: pl. 4, figs 8-11) have an apical angle of about 10 degrees. Similarly, one single fossil figured by Boussac (1911: 51, pl. 11, fig. 17) from Cote des Basques also appears to have an apical angle of about 10 degrees. By contrast, the apical angle of seven specimens of *Haustator imbricatarius* figured by Courville *et al.* (2012) from the Lutetian of Damery (Marne, Paris Basin) is, like in the Eocene fossils of Navarre, greater, about (14) 16-19 degrees. Cossmann regarded *Turritella trempina* Carez, 1881 as synonymous with *Turritella ataciana* d’Orbigny, 1850. According to De Renzi (1971), the species *T. trempina* created by Carez in the Eocene (Ilerdian) from the Conca de Tremp (Catalonia), would be a junior synonymous of *Turritella dixonii* Deshayes, 1861.

The fossils from Navarre bear greater similarities to several specimens of *Haustator imbricatarius conoideus* (J. Sowerby, 1814) from the Bartonian of Bracklesham Bay and, especially, of Barton-on-Sea (England) included in the Cossmann collection (MNHN.F.J12173 and J12227). The spiral ornamentation is similar in all cases and, although the spire of the specimens from Bracklesham Bay is less imbricated, the slightly convex profile of whorls is also similar. *Haustator elongatus* (J. Sowerby, 1814) from the Bartonian of Barton-on-Sea (MNHN.F.J12188, Cossmann coll.) also has “imbricated” whorls and a somewhat convex silhouette, but the shell is narrower, with a smaller apical angle than in *H. imbricatarius conoideus* and in our fossils.

Subfamily PAREORINAE Finlay & Marwick, 1937

Genus *Sigmesalia* Finlay & Marwick, 1937

TYPE SPECIES. — *Turritella sulcata* Lamarck, 1804 (non Bosc, 1801) by original designation (synonym of *Sigmesalia koeneni* Le Renard, 1994).

Sigmesalia sp.
(Fig. 8M-P)

MATERIAL. — Ardanatz Sandstone. 1 fragmentary specimen from AD sections (section and level unknown). AD1 and AD2 sections: 6 fragments from level AD1.3; 1 fragmentary specimen from level AD2.1. Ilundain Marl Formation, IV section: 3 fragmentary specimens. In all fossils protoconch and aperture not preserved.

DIMENSIONS. — Largest specimen: H > 15.9; W = 7.8 (incomplete specimen, about 19.0 high complete?).

DESCRIPTION

Medium-sized, turretlike, conical; protoconch unknown; apical angle about 32 degree; adult sculpture with 4 (5) prominent and smooth spiral cords; spire whorl sides convex, angled, shouldered, and more flattish abapically from the second spiral cord; last whorl with about a dozen ribs down to the base of the shell; aperture broken, but it expands (effuse) over the columella.

REMARKS

The assignation of fossils to Pareorinae is difficult when the aperture is not intact (see Marwick 1957). However, the general shape of the studied fossils is suggestive of the genera *Mesalia* Gray, 1847 and *Sigmesalia* Finlay & Marwick, 1937. Squires & Saul (2007) regarded both as congeneric forms.

The studied specimens can be compared to the species *Sigmesalia variabilis* Defrance, 1828 from the Bartonian of Jaignes (Seine-et-Marne, Paris Basin), which also exhibits four spiral cords (Cossmann & Pissarro 1910: pl. 21, fig. 126-5). However, in *S. variabilis*, spire whorl sides are less convex and cords are weaker (?) than in our specimens. Therefore, the latter are more similar to specimens of *S. fasciata* (Lamarck, 1804) figured by Cossmann & Pissarro (1910: pl. 21, fig. 126-9) from the Lutetian of Villiers-Saint-Frédéric (Yvelines, Paris Basin), with spiral cords stronger (?) than in *S. variabilis*. The resemblance to *S. fasciata* (Lamarck, 1804) from the Bartonian of Vendrest (Seine-et-Marne; MNHN.F.J12322, Cossmann coll.) and to *S. variabilis* (Defrance, 1828) from the Bartonian of Le Fayel (Oise; MNHN.F.J12325, Cossmann coll.) is also remarkable. However, in the latter two species the shape of whorls is frustoconical, whereas in our material the shape, abapically the shoulder (the second rib), is more angular, having more convex-cylindrical appearance. *Sigmesalia koeneni* Le Renard, 1994 from the Lutetian of Damery (Marne, Paris Basin) (Courville *et al.* 2012: pl. 3, figs 8, 16, 19) and *S. solida* (Deshayes, 1861) from the Bartonian of Le Guépelle, Saint-Witz (Val-d'Oise; MNHN.F.J12353, Cossmann coll.) have more and finer ribs, and less angular and convex whorl sides. On the other hand, the strong development of the spiral cords in our fossils bears a great resemblance to *S. pyrenaica* (d'Orbigny, 1850) from the Ypresian of Arañonet (Catalonia) (MNHN.F.J12189, Cossmann coll.) and from Fabrezan (Aude), but in both cases the number of prominent ribs is lower (two or three) than in our fossils. The small size of the available samples prevents greater accuracy.

Superfamily CAMPANOLOIDEA Douvillé, 1904
Family AMPULLINIDAE Cossmann, 1918

Ampullinidae indet.
(Fig. 8 Q-S)

MATERIAL. — Ardanatz Sandstone. 3 specimens from AD sections (section and level unknown). AG1 section: 1 specimen from AG1.3. MD1 section: 1 specimen. All specimens fragmentary, protoconch not preserved, aperture absent or very incomplete.

DIMENSIONS. — Largest specimen: H > 22.0; W = 19.0.

DESCRIPTION

Shell medium-sized; globose shape; spire relatively high, with more than three whorls; shouldered whorls, tabulate and grooved (shoulder sharpened) last whorl; last whorl inflated, specially in its middle part; shell surface rather smooth, only growth lines stand out slightly.

REMARKS

Ampullinidae includes gastropods that historically many authors (Cossmann 1888; Glibert 1963, among others) included in the family Naticidae. Later, Kase (1990) and Kase & Ishikawa (2003a, b) separated Ampullinidae and Naticidae using both their soft anatomies and shell morphologies. Recently, Caze *et al.* (2011) included coloured pattern features to discriminate between both families. According to the criteria by Kase & Ishikawa (2003a, b), the relatively high spire and shouldered and tabulate whorls suggest our fossils may be closer to the family Ampullinidae. Both families can generally be readily distinguished on the basis of their different opening and umbilical region morphology. Unfortunately, however, the poor preservation of the studied specimens does not allow further assessment.

The outline of the adapical part of the last whorl of the studied fossil shells is angular, like in *Ampullina* Bowdich, 1822, a genus in which 41 Paleogene species have been described (see Caze *et al.* 2011), and, in a lesser extent, like in *Crommium* Cossmann, 1888, which includes six exclusively Paleogene species. In *Globularia* Swainson, 1840 (Danian-Recent) the adapical shape of the whorls is generally more rounded.

The presence of Ampullinids in the Eocene of the South Pyrenean area was early reported by Cossmann (1898a: 10, pl. 8, figs 23, 24), who described and figured the species *Ampullina vidali* Cossmann, 1898 from the “middle Nummulitic” of Ager (South Pyrenean area). Farrés (1961) cited in the Bartonian-Priabonian of Vic numerous species that he assigned to the genus *Natica*, today mostly included in Ampullinidae. Martinius (1995) mentioned the abundance of *Amaurellina* (*Crommium*) *intermedia* Deshayes, 1833, cf. *Amaurellina* sp. and *Natica* sp. in some biofacies of the Early Eocene of Roda (Aragon). In the North Pyrenean area, Rouault (1850: pl. 16, figs 2, 3) described and figured two fossils from the Early Eocene of Bosdarros that assigned to *Ampullaria* indet and *Natica baylei* Rouault, 1850 (synonym of *Ampullina baylei* (Rouault, 1850)). The shape of the columellar lip and the high and acute spire points to the family Ampullinidae in both cases.

Genus *Globularia* Swainson, 1840

TYPE SPECIES. — *Ampullaria sigaretina* Lamarck, 1804 by subsequent designation (Herrmannsen, 1847).

?*Globularia* sp.
(Fig. 8T)

MATERIAL. — Ardanatz Sandstone. One fragmentary specimen from AD sections (section and level unknown). Protoconch and aperture not preserved.

DIMENSIONS. — H = (21.3); W = (18.0).

DESCRIPTION AND REMARKS

Shell medium-sized; globose shape (spherical outline); spire with more than three whorls; whorls tabulate; huge last whorl of semicircular shape, shell surface smooth, only growth lines stand out slightly.

The shape of the last whorl is semicircular, like in the genus *Globularia* Swainson, 1840, for example in the species *Globularia sigaretina* (Lamarck, 1804) from the Lutetian of Damery (Marne, Paris Basin) (Courville *et al.* 2012) and the Bartonian of Antilly (Oise; MNHN.F.J10972, Cossmann coll.). In the North Pyrenean area, Cossmann (1923: 35, pl. 3, figs 35-36) cited *Ampullina* cf. *splendida* (Deshayes, 1834) (synonym of *Globularia splendida* (Deshayes, 1834)) from the Early Eocene of Gan, a locality close to Bosdarros (southwestern Aquitaine Basin). Villalta Comella (1956) described two Ampullinidae, *Globularia grossa* (Deshayes, 1864) and a new species *Amauropsina thomasii* in the Bartonian marls of Basa Valley (Huesca, Jaca Basin, South Pyrenean area). *Amauropsina thomasii* Villalta Comella, 1956 exhibits a more compressed shell than the fossil from Ardanatz. Farrés (1961) cited, among other species, *Natica sigaretina* Lamarck, 1804 and *Natica acuta* Lamarck, 1804 in the Eocene of the Region of Vic (Catalonia), which are now assigned to the genera *Globularia* and *Crommium*, respectively. Our sample is too small and fragmentary for an accurate specific assignment.

Clade (Order) HYSOGASTROPODA

Ponder & Lindberg, 1997

Informal group PTENOGLOSSA Gray, 1853

Superfamily EPITONIOIDEA Berry, 1910

Family EPITONIIDAE Berry, 1910

Genus *Cirsotrema* Mörch, 1852

TYPE SPECIES. — *Turbo scalaris* Linnaeus, 1758 by original designation.

Subgenus *Elegantiscala* de Boury, 1911.

TYPE SPECIES. — *Scalaria elegantissima* Deshayes, 1861 by original designation.

Cirsotrema (*Elegantiscala*) cf. *bouillei*

(Tournouër *in* Bouillé, 1873) n. comb.

(Fig. 9A)

Scalaria bouillei Tournouër *in* Bouillé, 1873: pl. 6, fig. 1. — Bous-sac 1911: 35, pl. 3, fig. 5.

MATERIAL. — Ardanatz Sandstone. AD2 section: 1 specimen from level AD2.1. Protoconch not preserved, aperture broken.

DIMENSIONS. — H > 23.0; W = 12.0.

DESCRIPTION

Shell medium to large, turriculate; whorls convex-sided with strong spiral and axial sculpture; 6-7 well marked spiral cords; raised axial ribs, 15-17 per whorl, foliated, with wavy lamellations and a little spiny, angular shoulder expansion (slightly hooked at shoulder). Aperture sub-circular.

REMARKS

The presence of Epitoniidae (= Sculariidae) among the gastropods of the Bartonian marly formations of Navarre was early mentioned by Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949) and Ruiz de Gaona & Colom (1950), who reported *Scalaria* sp. from the localities of Ardanatz-Eguesibar, Tejería (Mendillorri), Altos de Badoztain and Pamplona-Beloso.

This fossil is quite similar to an incomplete specimen from the Priabonian of Biarritz (MNHN.F.J10160, Cossmann coll.) assigned to *Cirsotrema* (*Elegantiscala*) *bouillei* (Tournouër *in* Bouillé, 1873) n. comb. and three fossils assigned to *Scalaria bouillei*, which were described and figured by Bous-sac (1911: 35, pl. 7, figs 13, 14) from the Auversian (Bartonian) of the site of Villa Marbella (Côte des Basques Marls Formation, southwestern Aquitaine Basin), also near the city of Biarritz. Our specimen also looks like *Cirsotrema acuta* (Sowerby, 1812) (Sowerby 1812: 50, pl. 16) from Barton Beds (Barton, Highcliffe, England). Morton (2018, <http://www.dmap.co.uk/fossils/>) figured a specimen of this species as *Elegantiscala acuta*. Taking the original figure by Sowerby (1812) and Morton's photos, *C. acuta* has a straight profile, not convex, and a more spiny angular shoulder expansion in the whorls than our specimen AD2.1.9. In comparison with the fossils from Biarritz, AD2.1.9 seems to have more developed and perhaps less numerous axial ribs. Unfortunately, further precision is not possible with the available material.

Genus *Epitonium* Röding, 1798

Subgenus *Crisposcala* de Boury, 1886

TYPE SPECIES. — *Scalaria crispa* Lamarck, 1804 by original designation.

Epitonium (*Crisposcala*) aff. *subpyrenaicum*

(Tournouër *in* Bouillé, 1873)

(Fig. 9B-E)

Scalaria subpyrenaica Tournouër *in* Bouillé, 1873: pl. 3, fig. 2.

Scala (*Crisposcala*) *acuminensis* [sic] – Villalta Comella (1956: 132, 133, pl. 2, fig. 1 (non *Scalaria acuminensis* de Boury, 1883).

MATERIAL. — Pamplona Marl Formation: two specimens from EG1 section; one fragmentary specimen from AZ1 section; one incomplete specimen from IZ1 section. Transition between the Pamplona Marl Formation and the Ardanatz Sandstone Formation (or Ilundain Marl Formation): three specimens from BD1 section. Aperture is either incomplete or not preserved at all in all specimens.

DIMENSIONS. — H = (11.1); W = 9.0-17.0.

DESCRIPTION

Turriculate shell with shouldered whorls; numerous, thin and scarcely developed spiral cords; thick, coarse, poly-lamellar axial ribs, folded back (adapturally) except in the shoulder, where a spiny and angular-hooked structure, more marked in some especially thick axial ribs (varices?), is generated; surface of axial ribs with a rhomboidal reticular pattern as a result of wavy lamellations composite structure; deep sutures; slightly marked umbilical depression; holostomate, sub-circular aperture.

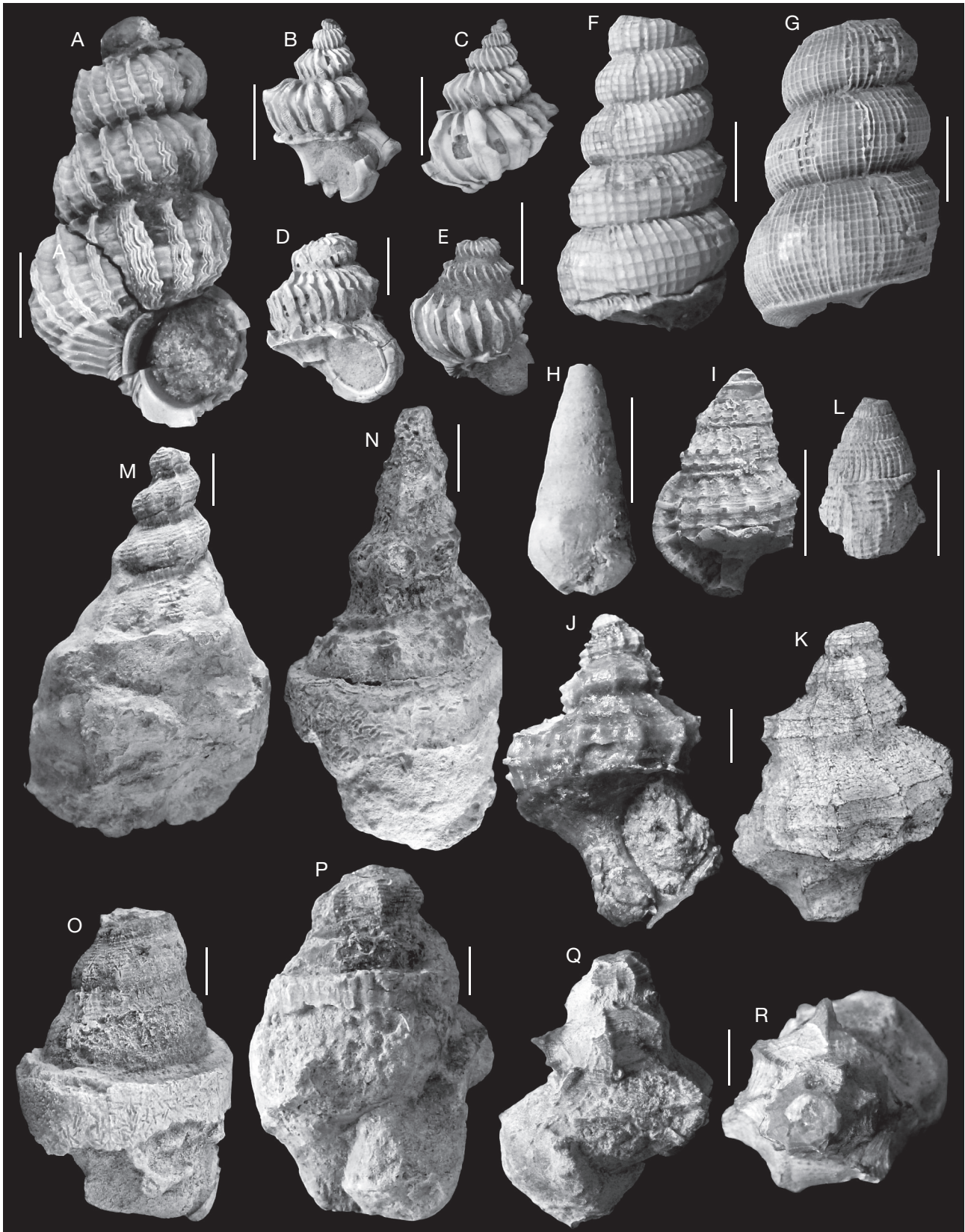


FIG. 9. — Fossils of gastropods from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A**, *Cirsotrema (Elegantiscala) cf. bouillei* (Tournouër in Bouillé, 1873) n. comb.: AD2.1.9, apertural view; **B-E**, *Epitonium aff. subpyrenaica* (Tournouër in Bouillé, 1873): **B**, EG1.1.2; **C**, EG1.1.1; **D**, BA1.2.4, apertural view; **E**, BA1.2.3; **F**, *Amaea (Acrilla) pellati* De Raincourt & Munier-Chalmas, 1863 n. comb., AZ1.1.1; **G**, *Amaea (Acrilla) sp.*: AD.29; **H**, *Niso sp.*: IV.4; **I**, *Sassia (sensu lato) sp. 1*, IV.31; **J, K**, *Sassia (sensu lato) sp. 2*, AD.33, dorsal and ventral views; **L**, *Metula (Cela-toconus) sp.*: IV.32; **M-P**, *Clavilithes (Clavellofus) cf. parisiensis* Mayer-Eimar, 1876: **M**, AD2.1.10; **N**, AD.30; **O**, AD.31; **P**, AD2.1.11; **Q, R**, *Paziella (Flexopteron) sp.*, AD2.1.12, dorsal and apical views. Scale bars: 5 mm.

REMARKS

Our fossils are quite similar to *Epitonium (Crisposcala) acumiense* (de Boury, 1886) from the Bartonian marls of Isún de Basa (Huesca, Jaca Basin, South Pyrenean area) (Villalta Comella (1956: pl. 2, fig. 1). They also bear a great resemblance to *E. (Crisposcala) acumiense* from the Bartonian of Acy-en-Multien (Paris Basin) (Cossmann & Pissarro 1907) and to *E. (Crisposcala) subpyrenaicum* (Tournouër in Bouillé, 1873) (Bouillé 1876: pl. 3, fig. 2) from the Bartonian marls of Côte des Basques (Biarritz, Côte des Basques Marls Formation, southwestern Aquitaine Basin). However, both *E. (Crisposcala) acumiense* from Acy-en-Multien and *E. (Crisposcala) subpyrenaicum* from Biarritz (figured in Boussac 1911: pl. 21, fig. 5) have thinner axial ribs than the fossils from Huesca and Navarre.

Genus *Amaea* H. Adams & A. Adams, 1853

Subgenus *Acrilla* H. Adams, 1860

TYPE SPECIES. — *Scalaria acuminata* Sowerby G.B. II, 1844 by original designation.

Amaea (Acrilla) pellati

(De Raincourt & Munier-Chalmas, 1863) n. comb.
(Fig. 9F)

Scalaria pellati De Raincourt & Munier-Chalmas, 1863: 203, 204, pl. 7, fig. 6a, b.

MATERIAL. — Pamplona Marl Formation: 1 fragmentary specimen from AZ1 section. Protoconch and aperture not preserved.

DIMENSIONS. — H = (20.0); W = (11.5).

DESCRIPTION AND REMARKS

Turriculate shell, highly convex whorls separated by deep sutures, regular cancellate sculpture with squares or, in some cases, rectangles with their longest axis in the axial direction. Quite similar to the specimens described as “*Scalaria pellati*” by Boussac (1911: 83, p. 21, figs 14, 16, 17, coll. Pellat) from the Rupelian of the Chambre d’Amour (Biarritz, southwestern Aquitaine Basin), one of which is the holotype of this species. The studied specimen also exhibits a general shape similar to that of two specimens from Barton-on-sea (MNHN.F.J12482, Cossmann coll.) assigned to *Amaea (Acrilla) reticulata* (Solander in Brander, 1766) and to another two specimens of *A. (A.) reticulata* from Barton Beds-Barton-Highcliffe, figured by Morton (2018, <http://www.dmap.co.uk/fossils/>). However, in *A. (A.) reticulata* the ribs are far more protruding than the spiral cords, whereas in our specimen the axial and spiral sculptures show a similar development. Another morphologically close species is *A. (A.) dubuissoni* (Vasseur, 1882). A specimen from the Bartonian of Bois-Gouët (Loire-Atlantique; MNHN.F.J10308, Cossmann coll.) has, however, a more compressed reticulum in spiral direction, with a greater number of spiral cords than our specimen.

Amaea (Acrilla) sp.
(Fig. 9G)

MATERIAL. — Ardanatz Sandstone. 1 fragmentary specimen from AD sections (section and level unknown). AD2 section: 2 fragments from level AD2.1.

DIMENSIONS. — H > 24.0; W = 12.0.

DESCRIPTION AND REMARKS

The turriculate shell, convex whorls, finely cancellate sculpture, with axial ribs slightly more protruded than the spiral cords and the presence of basal cord, allow these specimens to be compared to those collected from the Bartonian marls of San Román de Basa (Huesca, Jaca Basin, South Pyrenean area) and assigned by Villalta Comella (1956) to *Amaea (Acrilla) reticulata* (Solander in Brander, 1766). Villalta Comella (1956) pointed out the similarity of his specimens to some figured by Cossmann from the Eocene of Barton-on-Sea (Hampshire, England). Two specimens from Barton-on-sea (MNHN.F.J12482, Cossmann coll.) assigned to *Amaea (Acrilla) reticulata* also show a general shape similar to our fossils. However, in these specimens the number of axial ribs is lower, and the ribs are arranged more regularly and are more protruding than in the Ardanatz fossils.

Superfamily EULIMOIDEA Philippi, 1853
Family EULIMIDAE Philippi, 1853

Genus *Niso* Risso, 1826

TYPE SPECIES. — *Niso eburnea* Risso, 1826 by monotypy.

Niso cf. terebellata (Lamarck, 1804)
(Fig. 9H)

Bulimus terebellatus Lamarck, 1804b: 291, 292.

MATERIAL. — Ilundain Marl Formation IV section: 1 incomplete specimen.

DIMENSIONS. — H > 11.5; W = 5.2.

DESCRIPTION AND REMARKS

This poorly preserved specimen is similar to that described and figured by Villalta Comella (1956: 128-129, pl. 1 figs 2a, 2b) from the Bartonian marls of Isún de Basa (Huesca, Jaca Basin, South Pyrenean area), which was assigned to the species *Niso terebellata* (Lamarck, 1804). Years later this species was also cited in the nearby locality of Yebra de Basa (Puigdefábregas 1975, determinations by Villalta Comella). The more angled base and slightly convex, instead of flat, whorls differentiate these two South-Pyrenean specimens from those figured by the Cossmann & Pissarro (1907: pl. 7, fig. 51-1) from the Lutetian of Chaumont-en-Vexin (Paris Basin) and

attributed to *Niso terebellata*. Interestingly, however, other *Niso terebellata* specimens figured in Caze *et al.* (2012: 41, pl. 15, figs A-C) from the Lutetian of Fer-court (Oise) also shows a remarkable variability of these morphological features.

Clade (Infraorder) NEOGASTROPODA Thiele, 1929

Superfamily TONNOIDEA Suter, 1913

Based on molecular phylogenetic analyses, the superfamily Tonnoidea is now placed in the clade Neogastropoda (Colgan *et al.* 2007; Cunha *et al.* 2009).

Family RANELLIDAE Gray, 1854

Genus *Sassia* Bellardi, 1873

TYPE SPECIES. — *Triton apennincum* Sassi, 1827 by subsequent designation (Cossmann 1903).

Sassia (*s.l.*) sp. 1
(Fig. 9I)

MATERIAL. — Ilundain Marl Formation: two specimens from IV section. Last whorl incomplete abapically.

DIMENSIONS. — $H > 10.8$; $W = 6.5$.

DESCRIPTION

Protoconch homostrophic, multispiral, with about 3.5 whorls, smooth, quite large; teleoconchal sculpture nodulose, with 4-5 primary cords (spiral ribs); profile of the whorls slightly keeled, angled, due to the greater development of the third nodulose cord (second primary cord?); 13 or more axial ribs per whorl; varices each around 120 degrees, the varix being especially strong on the last whorl.

REMARKS

Paleogene species of ranellids attributed to *Sassia* represent a polyphyletic assemblage including species of very different shapes. To clarify the systematic classification of this genus, a deep revision is necessary and for instance, we use *Sassia* (*s.l.*) for Paleogene species attributed to *Sassia* by the authors. The morphology of this specimen is close to that of fossils assigned to some *Sassia* (*s.l.*) species, such as *Sassia* (*s.l.*) *scabriuscula* (Deshayes, 1865) from the Bartonian of Paris basin, site of Le Guépelle, Saint-Witz (Val-d'Oise; MNHN.F.J13617, Cossmann coll.), and *Sassia* (*s.l.*) *nodularia* (Lamarck, 1803) from the Lutetian of Chaussy, Les Garennes (Val-d'Oise; MNHN.F.J13606, Cossmann coll.). Rouault (1850: pl. 18, figs 2, 3) described and figured two specimens as *Triton nodularium* Lamarck, 1803 from the Early Eocene of Bosdarros (southwestern Aquitaine Basin). Considering the figures given by Rouault these specimens from

the Aquitaine Basin seem morphologically close to our fossils, but they are juvenile. Cossmann (1923: pl. 6, figs 16-17) figured adult of this species from the Early Eocene of Gan under the name *Sassia* (*s.l.*) *delafossei* (Rouault, 1850), and they display a very different morphology. The morphology of our fossils is also similar to that of *Sassia* (*s.l.*) *biarritzense* (Oppenheim, 1906), from the Bartonian-Priabonian marls of the Côte des Basques (Biarritz, Côte des Basques Marls Formation, southwestern Aquitaine Basin), although the spiral sculpture is perhaps less nodulose in the latter species (?) (see Oppenheim 1906: pl. 9, fig. 2; Boussac 1911: pl. 12; fig. 8). The slightly keeled profile of the whorls of our specimens – in *S. (s.l.) scabriuscula* and *S. (s.l.) nodularia* whorls are more convex-sided – is closer to a specimen described by Villalta Comella (1956: 64, 7, fig. 2) from the Bartonian marls of San Román de Basa (Huesca, Jaca Basin, South Pyrenean area) and assigned to *Sassia* (*s.l.*) *arguta* (Solander *in* Brander, 1766).

Sassia *s.l.* sp. 2
(Fig. 9J, K)

MATERIAL. — Ardanatz Sandstone. 2 fragmentary specimens from AD sections (section and level unknown).

DIMENSIONS. — Largest specimen. $H > 29$; $W = 18$.

DESCRIPTION

Biconic shell of four elevated teleoconch whorls (protoconch not preserved), last whorl inflated. Suture relatively deep. Varices smooth, rounded and rather developed. Around 8 to 9 varices per whorl. Spiral sculpture with well developed primary cords. On first visible whorl: P1, P2 and P3 close to the suture; on second to fourth whorl: IP, P1 to P3. No threads. No shoulder. Intersection between axial and spiral sculpture without nodules. Aperture not preserved.

REMARKS

This species differs from the *Sassia* (*s.l.*) sp. 1 by the lower shape of its spire, by its deeper suture and by lacking nodules at the intersection between axial and spiral sculpture. This species belongs to a group of non nodulose *Sassia* (*s.l.*). In the Late Paleocene *S. (s.l.) antiqua* Deshayes, 1865 from the Thanetian of the Paris Basin displays a similar sculpture. In the Rupelian, two other species bear sculptural similarities with *Sassia* (*s.l.*) sp. 2: *Sassia* (*s.l.*) *flandrica* (de Koninck, 1838) and *Sassia* (*s.l.*) *subspinosa* (Gratoloup, 1833). In *S. (s.l.) flandrica* (de Koninck, 1838) from northern Europe, the spire is higher than in *Sassia* (*s.l.*) sp. 2, the suture shallower and the spiral cords are less marked. *Sassia* (*s.l.*) *subspinosa* looks like more *Sassia* (*s.l.*) sp. 2 in bearing a deep suture and marked primary cords. However, on the last whorls of *S. (s.l.) subspinosa*, the intersection points between the primary cords and the axial sculpture are moderately spiny, whereas they are not in *Sassia* (*s.l.*) sp. 2.

Superfamily BUCCINOIDEA Rafinesque, 1815
Family BUCCINIDAE Rafinesque, 1815
Genus *Metula* H. Adams & A. Adams, 1853

Subgenus *Celatoconus* Conrad, 1862

TYPE SPECIES. — *Buccinum protractum* Conrad, 1862 by monotypy.

Metula (Celatoconus) sp.
(Fig. 9L)

MATERIAL. — Ilundain Formation, IV section: 2 fragmentary specimens. Aperture not preserved.

DIMENSIONS. — H > 15.0; W = (9.0).

DESCRIPTION AND REMARKS

Shell with at least 7 teleoconch whorls; protoconch not well preserved, with at least 1.5 smooth convex whorls; teleoconch whorls convex, somewhat inflated in the abapical half; adult teleoconch cancellated, sculpture with 7 or more barely marked spiral cords, and 35 or more stronger orthocone or slightly opisthocone axial ribs, more prominent, with beaded or slightly nodous intersections with spiral cords; separation between the first and second spiral cord slightly larger and more pronounced than among other cords, producing a slight differentiation of an adapical beaded cord just below the sutures.

The studied fossils are similar to those of the species *Metula (Celatoconus) subdecussata* (d'Orbigny, 1850) from the Lutetian (Bartonian) of Mouchy-le-Châtel (Oise) (Cossmann & Pissarro 1911: 37; fig. 182-1) and *M. (C.) biarritzensis* Oppenheim, 1906 from the Bartonian of the Côte des Basques (Biarritz, Côte des Basques Marls Formation, southwestern Aquitaine Basin) (Oppenheim 1906: 86, 9, fig. 11a-c; Boussac 1911: 54). On the contrary, the studied specimens differ from *M. (C.) vasseuri* Cossmann, 1885, from the Lutetian of Grignon (Yvelines; MNHN.FJ02620), by their more elongated and slender spire, and by their axial sculpture, more developed than the spiral cords. Unfortunately, the available material does not allow further assessments.

Family FASCIOLARIIDAE Gray, 1853
Genus *Clavilithes* Swainson, 1840

Subgenus *Clavellofusius* Grabau, 1904

TYPE SPECIES. — *Clavellofusius spiratus* Grabau, 1904 by original designation.

Clavilithes (Clavellofusius) cf. *parisiensis*
(Mayer-Eymar, 1876)
(Fig. 9M-P)

Fusus parisiensis Mayer-Eymar, 1876 : 89.

MATERIAL. — Ardanatz Sandstone. 3 fragmentary specimens from AD sections (sections and levels unknown). AD1 section: 2 fragmentary specimens from level AD1.3. AD2 section: 2 fragmentary specimens from level AD2.1. Protoconch absent and last whorl and aperture incomplete in all specimens.

DIMENSIONS. — Largest specimen. H > 33.0; W = (23.0).

DESCRIPTION

Medium-sized shell, spire long and slender, whorls convex, well marked cancellate sculpture and protruding axial ribs (varices) swollen near the middle part, 6-7 (young spire)-9 (adult spire) axial ribs per whorl; last whorl barely ornamented (smooth surface) and very big respect to the spire, bell shaped (campaniform), with sharp shoulder, projected abaxially in one of the specimens.

REMARKS

Despite the poor preservation of the specimens, the large size of the last whorl with respect to the spire and the teleoconchal sculpture, with heavily ornamented spire and smooth last whorl, suggest the studied specimens are close to the genus *Clavilithes* and, more specifically, to the species *Clavilithes (Clavellofusius) parisiensis* (Mayer-Eymar, 1876). The presence of *Clavilithes* in fossil assemblages from the Eocene of the South Pyrenean area was previously noted by Villalta Comella (1956), who described and figured several fossils assigned to *Clavilithes maximus* (Deshayes, 1835) and *C. (Rhopalithes) sp.* (Villalta Comella 1956: 185-187, pls 7, 8, figs 4a-4b, 6a, 6b), from the Bartonian marls of San Román de Basa (Huesca, Jaca Basin). The specimens from Navarre are quite similar to the latter.

Superfamily MURICOIDEA Rafinesque, 1815
Family MURICIDAE Rafinesque, 1815
Genus *Paziella* Jousseume, 1880

Subgenus *Flexopteron* Shuto, 1969

TYPE SPECIES. — *Flexopteron philippinensis* Shuto, 1969 by original designation.

Paziella (Flexopteron) sp.
(Fig. 9Q, R)

MATERIAL. — Ardanatz Sandstone. AD2 section: one incomplete specimen from level AD2.1.

DIMENSIONS. — H = 28.0; W = (22.0), shell incomplete.

DESCRIPTION

Medium-sized and biconic shell. Three last whorls preserved. Shallow suture. Spiral sculpture with moderately marked spiral cords, except P1 (shoulder spine). P2 developed on the two last whorls. In some parts of the shell, surface covered by threads. P1 and P2 spiny on the last whorls. Axial sculpture of simple lamellar varices of one layer. Around 8-9 varices by whorl. No intervarical ribs. Fine micro-axial ribs (visible on the early whorls) covering the surface of the shell and crossing the spiral threads. Aperture not preserved.

REMARKS

By its sculpture of threads and fine micro-axial ribs, this specimen superficially resembles *Murex subfligra* Tournouër in Bouillé, 1876 (a junior subjective synonym of *Pterynotuis* (*Pteryarchia*) *defensus* (Fuchs, 1870), Priabonian from Italy) from the Priabonian marls of Côte des Basques (Biarritz, Côte des Basques Marls Formation, southwestern Aquitaine Basin; Bouillé 1876: pl. 3, fig. 7; Merle 1994: figs 7-8; Merle *et al.* 2011: pl. 89, figs 7-9). However, it strongly differs by lacking intervarical ribs. The shape and the sculpture fit more with *Paziella* (*Flexopteron*). Usually members of this subgenus don't exhibit threads and micro-axial ribs, and in the Paleogene from Europe few species display this type of sculpture (*Paziella* (*Flexopteron*) *elatior* (von Koenen, 1889) from the Middle-Late Eocene of France and Germany and *P. (F.) subplicatilis* (Wrigley, 1930) from the Middle Eocene from England; see Merle *et al.* 2011: pl. 138). A very similar micro-sculpture is shared with *P. (Flexopteron) vanuxemi* (Conrad, 1865) from the Middle Eocene of Alabama, Texas, Louisiana and Mississippi (see Merle *et al.* 2011: pl. 140).

Family VOLUTIDAE Rafinesque, 1815
Genus *Athleta* Conrad, 1853

Subgenus *Volutospina* Newton, 1906

TYPE SPECIES. — *Conus spinosus* Linnaeus, 1758 by original designation.

Athleta (*Volutospina*) *delvallei*
Astibia, Merle & Pacaud, n. sp.
(Fig. 10A-E)

[urn:lsid:zoobank.org:act:B67FFC21-062F-42A1-AF34-71DDFB2BBC60](https://doi.org/10.3897/zoobank.org/act:B67FFC21-062F-42A1-AF34-71DDFB2BBC60)

TYPE MATERIAL. — IV.5 (holotype) (Fig. 10A, B); IV.11, IV.12, AD2.1.14, AD.34 (paratypes). Aperture incomplete, siphonal canal broken.

DIAGNOSIS. — Shell biconic, short and conical spire; protoconch homeostrophic paucispiral; teleoconch multiwhorled; adult whorls shouldered with spiny tubercles and a nodule abapically from each spine; shoulder protrudes as a sharp border over the last whorl; aperture long (?), with about 5 or more columellar oblique folds; surface of the last whorl with smooth and straight axial costae.

OTHER MATERIAL EXAMINED. — Ardanatz Sandstone. Four specimens from AD sections (sections and levels unknown). AD2 section: six specimens from level AD2.1; AG1 section: three specimens from level AG1.3. Ilundain Marl Formation, three specimens from IV section. All incomplete specimens, protoconch and outer lip and siphonal region of the aperture generally not being preserved.

TYPE LOCALITY. — Itzagaondoa valley (Navarre, western Pyrenees), Bartonian-?early Priabonian (Middle-?Late Eocene) (Fig. 1).

DIMENSIONS. — Holotype. H > 25.0; W = (19.0) (incomplete specimen, about 35.0 high complete?).

ETYMOLOGY. — Species dedicated to Dr Joaquín del Valle de Lersundi Mendizabal (1923-2009), mining engineer and passionate researcher of the geology of Navarre and the Pyrenees.

DESCRIPTION

Shell medium-sized, biconic, with short and conical spire; protoconch homeostrophic paucispiral, with 2-2.5 (?) smooth whorls and transition to the teleoconch indistinct; about five teleoconch whorls; whorls shouldered, concave above the shoulder, convex below; teleoconchal sculpture with spiny tubercles (spinose cord) on shoulder of the last or body whorl and above sutures of spire whorls. Abapically, each spine there is a nodule, less protuberant and separated from the spine by a groove. The shoulder protrudes as a sharp border over the last whorl, forming a shirttail-like oblique surface except at the end (aperture zone) of the last whorl; the shirttail-like shoulder exhibits a thin axial striation; growth-lines ortoclines-prosoclines; aperture long (?), with about 5 or more inner lip (columellar) oblique folds. Smooth and straight axial costae marked on the surface of the last whorl.

REMARKS

Ruiz de Gaona & Colom (1950) mentioned the presence of fossils of *Voluta* sp. from the locality of Ardanatz-Eguesibar. D'Archiac (1850) cited an incomplete specimen of *Voluta* from the Eocene of Biarritz (southwestern Aquitaine Basin). Puigdefábregas (1975, determinations by Villalta Comella) pointed out the presence of *Voluta hericorum* Oppenheim and *Volutolithes* (*Volutocorbis*?) *pyrenaica* Villalta Comella, 1956 in the Bartonian localities of Isún de Basa and Yebra de Basa (Huesca, Jaca Basin, South Pyrenean area), respectively. Unfortunately, figures were not included in any of the cases. The teleoconchal shoulder with spine-tuber pairs of our specimens is a feature that appears in some species of *Athleta* (*Volutospina*), as for example in *A. (V.) spinosus* (Linnaeus, 1758) (see Courville *et al.* 2012), but tubers are not as developed as in *A. (V.) delvallei* Astibia, Merle & Pacaud, n. sp. An approximately similar sculpture can be observed in *Athleta* (*Volutopupa*) *intercrenatus* (Cossmann & Pissarro, 1909) from the lowermost Eocene Lakhra Formation (Pakistan) (Merle *et al.* 2014), but the general morphology of the shell is very different. *Athleta* (*V.*) *delvallei* Astibia, Merle & Pacaud, n. sp. has more angular shoulder, a spiny shell and axial ribs of the last whorl much less marked than in *A. intercrenatus*.

Superfamily CONOIDEA Fleming, 1822
Family CONIDAE Fleming, 1822

Conidae indet.
(Fig. 10F-H)

MATERIAL. — Ardanatz Sandstone. 2 incomplete specimens from AD section (levels unknown). Ilundain Marl Formation, IV section: 1 incomplete specimen.

DIMENSIONS. — Largest specimen. H > 27.0; W = (20.0).

DESCRIPTION AND REMARKS

Shell cone-shaped, with a low, conical spire; whorls shouldered, slightly concave above the shoulder. Sculpture reduced, tuberculate on shoulder (more marked in the young spire),

with 5–6 fine spiral cords and opisthocirrc growth lines. Aperture not preserved. Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949) and Ruiz de Gaona & Colom (1950) cited the presence of fossil Conidae (“*Conus rouaulti*” and *Conus* sp.) in the locality of Ardanatz-Eguesibar. *Conus rouaulti* d’Archiac, 1850 (synonym of *Conasprella rouaulti* (d’Archiac, 1850), see Pacaud 2016) was defined in the Eocene of Biarritz (d’Archiac 1850: 13, fig. 22a). The studied specimens share the tuberculate shoulder with *Conasprella rouaulti*, but they do not have the grainy spiral cord accompanying the suture, as described by d’Archiac for the fossils from Biarritz. In *C. rouaulti* the spire is higher and the borders are straighter than in our specimens. The low spire and concave borders of our specimens are closer to species such as *Eoconus diversiformis* (Deshayes, 1835) from the Eocene and Oligocene of France (Paris Basin, Contentin, etc.), England, Belgium (Bruxelles) and Italy (Roncà and San Gonini) (Cossmann & Pissarro 1910–1913: pl. 48, fig. 214–7; Brébion 1992; Courville *et al.* 2012: pl. 11, figs 1–4, 6, 11–12; MNHN.F.J15126, J15133, A30836). Unfortunately, the available material prevents further assessments.

Family TURRIDAE H. Adams & A. Adams, 1853
[Cochlespiridae Powell, 1942]

Genus *Nihonia* MacNeil, 1960

TYPE SPECIES. — *Nihonia shimajiriensis* MacNeil, 1960.

Nihonia aff. *transversaria* (Lamarck, 1804) n. comb.
(Figs 3D–E; 10I–L)

Pleurotoma transversaria Lamarck, 1804a: 166.

Surcula transversaria – Villalta Comella 1956: 209–211, pl. 10, figs 4a–4b.

MATERIAL. — Ardanatz Sandstone. 2 incomplete specimens from AD sections (levels unknown). AD2 section: 1 incomplete specimen from level AD2.2. Ilundain Marl Formation, IV section: 1 incomplete specimen (?). Aperture absent in all cases.

DIMENSIONS. — Largest specimen. H > 27.0; W = (14.5).

DESCRIPTION AND REMARKS

Fusiform in shape, with high slender spire; abapical part of the whorls convex-sided, slightly angled, with at least two weak spiral cords; adapical half of whorls less convex with a weak cord in the middle part. Spiral sculpture barely marked, cords and intermediate threads are more visible on the last whorl of one specimen. Axial sculpture cannot be observed.

The overall shape is close to that of the specimen of *Surcula transversaria nantheuilensis* de Boury, 1899 (synonym of *Nihonia transversaria nantheuilensis* (de Boury, 1899)), figured by Cossmann & Pissarro (1910–1913: pl. 50, fig. 223

bis-1’) from the Bartonian of Jaignes (Paris Basin). However, the latter, perhaps due to its good preservation, presents the spiral ornamentation significantly more marked than that of our specimens. A specimen described and figured by Villalta Comella (1956: 209–211, pl. 10, figs 4a–4b) from the Bartonian of San Román de Basa (Huesca, Jaca Basin, South Pyrenean area), which exhibits lesser spiral sculpture than the specimen from Jaignes and was assigned to *Surcula transversaria*, is very similar to the fossils from Navarre.

Genus *Surculites* Conrad, 1865

TYPE SPECIES. — *Surcula annosa* Conrad, 1865 by monotypy.

Surculites sp. (Fig. 10M)

MATERIAL. — Ilundain Marl Formation, IV section: 2 fragmentary specimens. Protoconch and aperture not preserved.

DIMENSIONS. — The specimen is fragmentary and its original dimensions cannot be determined.

DESCRIPTION AND REMARKS

Conical spire; teleoconch prominently shouldered, strongly carinated in the central region of the whorls, sutural ramp concave; well marked, stepped, sutures; axial sculpture formed by numerous, rather irregular and narrow, opisthocline costae, reaching from suture to suture on spire; spiral sculpture very weak, with numerous closely spaced threads.

Despite the fragmentary state of the available material the morphology of the spire is coincident with that of the genus *Surculites* Conrad, 1865. *Surculites* is present in the Eocene (Ypresian-Bartonian) from the Paris and Hampshire basins, in the Atlantic area (*Surculites errans* (Solander in Brander, 1766), *Surculites bonneti* (Cossmann, 1889), and *Surculites vicenti* Glibert, 1938; colls. Cossmann and Van Hyfte, MNHN.F.J14181, J14183, J14184, A51217), and also in the Corbieres, Eastern Pyrenees (*Surculites bonneti* (Cossmann, 1889), coll. Cossmann MNHN.F.J14186). The morphology of the specimens studied is close to that of *S. errans* from the Bartonian of Barton-Highclife and New Forest (England, colls. Smith and Morton [http://www.dmap.co.uk/fossils/] and coll. Cossmann, MNHN.F.J14184), but the scarce material prevents further assessments.

Clade (Superorder) HETEROBRANCHIA
Unassigned HETEROBRANCHIA
Superfamily MATHILDOIDEA Dall, 1889
Family MATHILDIDAE Dall, 1889

Genus *Mathilda* Semper, 1865

TYPE SPECIES. — *Turbo quadricarinatus* Brocchi, 1814 by subsequent designation (de Boury 1883).

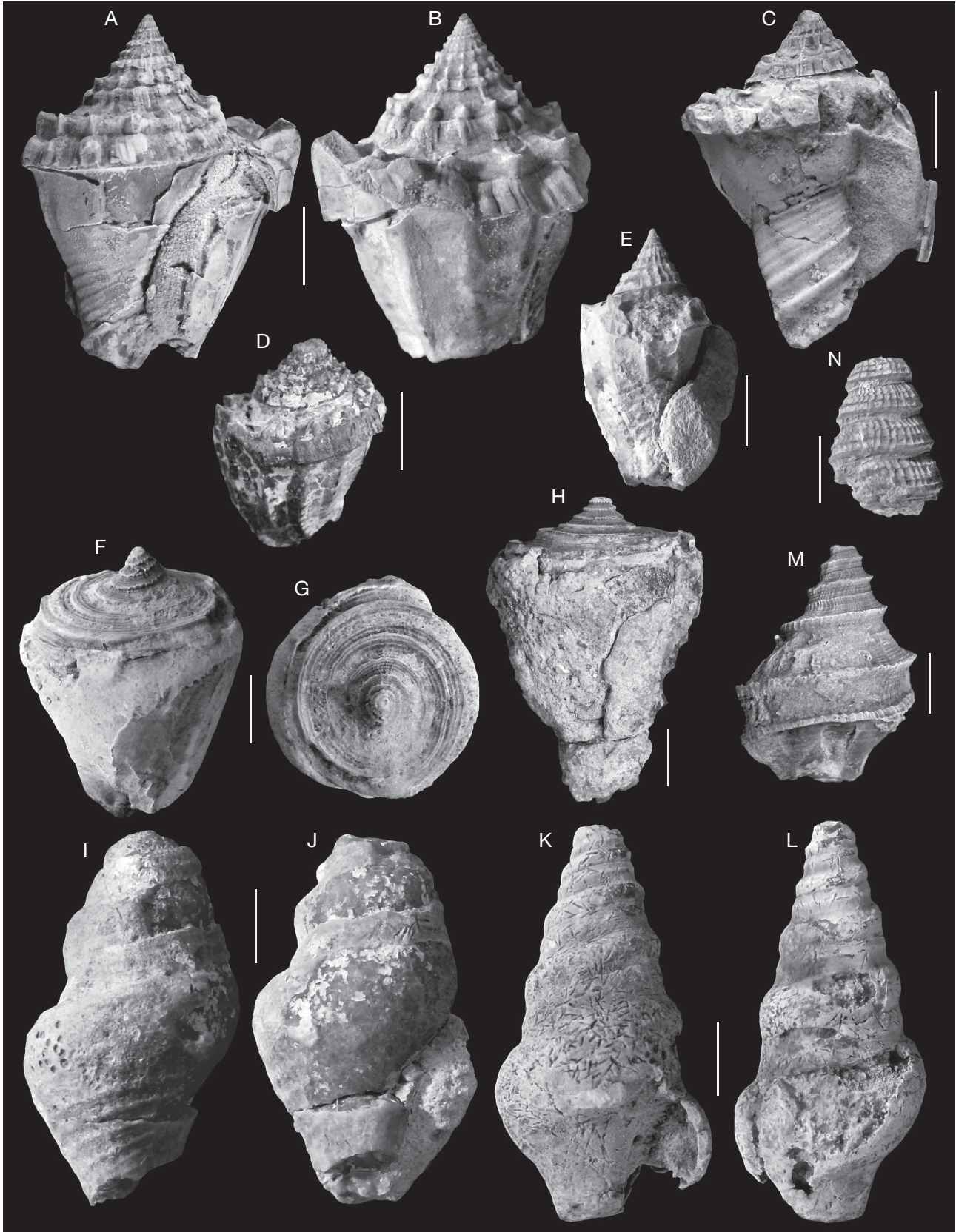


FIG. 10. — Fossils of gastropods from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A-E**, *Athleta (Volutospina) delvallei* Astibia, Merle & Pacaud, n. sp.: **A, B**, IV.5, holotype, apertural and dorsal views; **C**, AD2.1.14, apertural view; **D**, IV.34, oblique dorsal view; **E**, AD.34, apertural view; **F-H**, Conidae indet.: **F, G**, AD.35, oblique dorsal and apical views; **H**, IV.35; **I-L**, *Nihoaia* aff. *transversaria* (Lamarck, 1804) n. comb.: **I, J**, AD.17; **K, L**, AD2.2.1; **M**, *Surculites* sp., IV.36; **N**, *Mathilda* sp., IV.37. Scale bars: 5 mm.

Mathilda sp. (Fig. 10N)

MATERIAL. — Ilundain Marl Formation, IV section: one fragmentary specimen. Protoconch and aperture missing.

DIMENSIONS. — H > 11.5; W = (8.0).

DESCRIPTION

Teleoconch whorls frustoconical, moderately convex; deep sutures; cancellate shell sculpture; main spiral ornament consists of 3(-4) strong cords, the strongest being the third from the adapical suture, with wider interspaces; axial sculpture consists of numerous orthocone-opisthocircic ribs weaker than the spirals.

REMARKS

The genus *Mathilda* is common in the Eocene of Northern France and Southern England in the Atlantic area (Paris Basin, Loire-Atlantique, Hampshire Basin), being also present in the Eocene (Ypresian-early Lutetian) of Lillebelt Clay (Denmark) (Schnetler & Heilmann-Clausen 2011). The described specimen bears some resemblance to those of *Mathilda bourdoti* (de Boury, 1883) from the Lutetian of Parnes (Oise, MNHN.F.J02403) and the Bartonian of Lower Barton Bed A3 (Barton-Highcliffe) (coll. Morton, <http://www.dmap.co.uk/fossils/>).

However, the shape of our specimens' whorls is frustoconical and more angular (whorl profile frustate) than in *M. bourdoti*, which exhibits convex-shaped whorls. *Mathilda bourdoti* has a lower number of main spiral cords than *M. baylei* (de Boury, 1883) from the Lutetian of Hérouval (Oise, MNHN.F.J02402) and Upper Bracklesman Beds (New Forest) (coll. Morton, <http://www.dmap.co.uk/fossils/>), and even less than *M. cossmanni* (de Boury, 1883), from the Lutetian of Parnes (Oise, Picardie, holotype MNHN.F.J02404). The axial ribs of our specimen and *M. bourdoti* are weaker than those of *M. baylei* and *M. cossmanni*. The teleoconchal sculpture of our studied specimen differs from that of other Eocene *Mathilda* species, such as *M. crossei* (de Boury, 1883), *M. serrata* Semper, 1865 and *M. abbreviata* Gougerot & Le Renard, 1981 (colls. Morton and Tracey, <http://www.dmap.co.uk/fossils/>), all of which have strong and continuous spiral cords and very weak axial ribs. The genus *Mathilda* has also been reported from the Paleogene series of the North Pyrenean area, in the outcrop of Villa Lady Bruce, near the town of Biarritz (Bartonian-Priabonian, Côte des Basques Marls Formation, southwestern Aquitaine Basin) (Bouillé 1876: 60, pl. 3, fig. 4). The species *M. biarritzensis* was erected for the latter (Tournouër *in* Bouillé 1876), but both the fossil described by Tournouër and the material from Navarre are fragmentary, preventing classification beyond genus level.

Class BIVALVIA Linnaeus, 1758
Subclass AUTOBRANCHIA Grobben, 1894
Infraclass PTERIOMORPHIA Beurlen, 1944
Order ARCIDA J. Gray, 1854

Superfamily ARCOIDEA Lamarck, 1809
Family GLYCYMERIDIDAE Dall, 1908 (Leach *in* J. Gray 1847)

Genus *Glycymeris* Da Costa, 1778

TYPE SPECIES. — *Arca glycymeris* Linnaeus, 1758 by tautonymy.

Glycymeris jacquoti (Tournouër *in* Bouillé, 1873)
(Fig. 11A-D)

Pectunculus jacquoti Tournouër *in* Bouillé, 1873: 41, pl. 8, fig. 1.

Complete synonymies in Abad (2001: 374).

MATERIAL. — Ilundain Marl Formation, IV section: four specimens.

DIMENSIONS. — H = 14.0-22.9; L = 14.2-19.8; W = 7.1-14.5.

DESCRIPTION

Small to medium sized; glycymeriform shell (*sensu* Carter *et al.* 2012), bi-convex, equivalve, somewhat inequilateral, slightly longer than wider, bulged in the central part; short and straight cardinal margin; reduced ligamental area, rounded and crenulated ventral margin; umbones hardly prominent, slightly oblique. Outer surface of the shell ornamented with more than twenty (23-24) finely granulated main radial ribs and wide intercostal spaces; numerous growth lines parallel to the outer contour of the shell. The characteristics of the interior of the shell cannot be observed, as all the specimens contain the two valves.

REMARKS

This species was defined by Tournouër (*in* Bouillé 1873: 8, fig. 1) in the Eocene of Biarritz (southwestern Aquitaine Basin), being later described and figured by Boussac (1911: 10, fig. 3) and Cossmann, (1921: 8, figs 31-34) in the same area (outcrops of Côte des Basques and Lady Bruce, Bartonian-“Auversian”, Côte des Basques Marl Formation). *G. jacquoti* is a common species in the Mediterranean region (Combes [Dauphiné], Puget-Théniers [Provence-Alpes-Maritimes], Sant Llorens dels Piteus [Catalan Pyrenees], Borgo Valsugana [East Trentino Province, Italy, Early Oligocene]) (Boussac 1911; Cossmann 1921; Boschele *et al.* 2011). Almela & Ríos (1951) cited the presence of this species in the Bartonian of Yebra de Basa (Huesca, Jaca Basin, South Pyrenean area). Abad (2001) recognized this species in several localities from the Eocene (Bartonian-Priabonian) of Igualada and Vic regions (Catalonia), in the eastern part of the Ebro Basin.

Order OSTREIDA Férussac, 1822
Suborder OSTREIDINA Férussac, 1822
Superfamily OSTREOIDEA Rafinesque, 1815
Family GRYPHAEIDAE Vialov, 1936
Subfamily PICNODONTEINAE Stenzel, 1959

Genus *Pycnodonte* Fischer de Waldheim, 1835

TYPE SPECIES. — *Pycnodonte radiata* Fischer de Waldheim, 1835 by original designation.

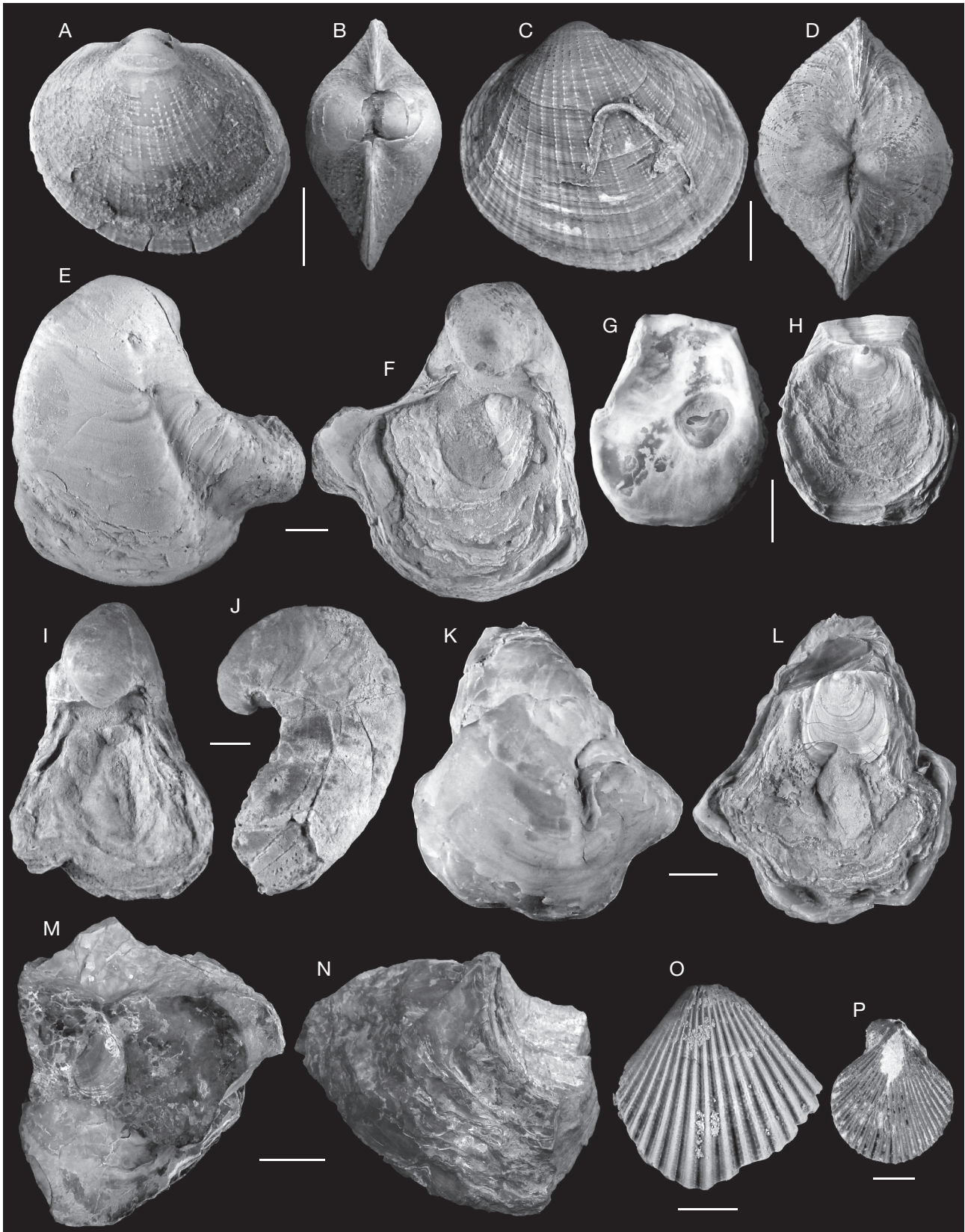


FIG. 11. — Fossils of bivalves from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A-D**, *Glycymeris jacquoti* (Tournouër in Bouillé, 1873): **A, B**, IV.39, left valve, external and umbonal views; **C, D**, IV.38, left valve, external and umbonal views; **E-L**, *Pycnodonte brongniarti* (Bronn, 1831): **E, F**, IV.9, left and right valves, external views; **G, H**, IV.40, right valve, internal and external views; **I**, IV.42, right and left valves, external views; **J**, IV.42, left valve, anterior view; **K, L**, IV.41, left and right valves, external views; **M, N**, *Hyotissa martinsii* (d'Archiac, 1850), AD.38, left valve, internal and external views; **O**, *Chlamys* cf. *biarritzensis* (d'Archiac, 1846), AD.39, right valve?; **P**, *Chlamys infumata* (Lamarck, 1806), AD6.1.1. Scale bars: A-H, O, P, 5 mm; M, N, 50 mm.

Pycnodonte brongniarti (Bronn, 1831)
(Fig. 11E-L)

Gryphaea brongniarti Bronn, 1831: 630.

Complete synonymies in Abad (2001: 548).

MATERIAL. — Ilundain Marl Formation, IV section: 37 specimens; 16 of them incomplete; 5 left valves, three of them incomplete; 7 right valves.

DIMENSIONS. — See Table 1.

DESCRIPTION

Medium sized; gryphaeiform shell (*sensu* Carter *et al.* 2012) strongly inequivalved, inequilateral and irregularly shaped, longer (higher) than wider. Left valve strongly convex, arched; umbo prominent and recurved, prosogyrate, with straight and diverging side edges; radial posterior sulcus originating below umbonal area, leading to the development of an ala or lobe, convex, which can be projected backwards prominently in the largest specimens; external ornament smooth, with low, irregular growth line welts; interior of left valve smooth; ligamental pit small, subtriangular, with rectilinear growth-lines parallel to the base; shallow resiliifer; little vermiculate chomata, more-or-less perpendicular to the edge of the shell, more evident in the posterior margin; commissure line well marked; adductor muscle scar small, sub-circular, situated just posterior to the centre of valve.

Right valve much smaller, concave to flat, as an operculum; ventral (pallial) area semicircular; dorsal (umbonal) area narrower, with rectilinear umbo; external ornamentation smooth, with low, irregular growth-line welts; ligamental pit morphology similar to that of the left valve but turned back with an angle with the inner surface greater than 90°; vermiculate chomata not very extensive, more developed in the posterior margin of the valve; adductor muscle scar semicircular to ovoid shaped located just posterior to the centre of valve.

REMARKS

The samples exhibit a remarkable morphological variability, especially in the development, width and curvature of the umbo, as well as in those of the groove (sulcus) and posterior lobe of the shell.

Pycnodonte brongniarti is quite similar to the species *Pycnodonte pharaonum* (Oppenheim, 1903) but, according to Abad (2001), it differs by having a more rounded anteroposterior profile of the left valve than that of *P. pharaonum*, which can be very sharp with a keeled profile, and by the absence of one or two hyote spines, which are instead often present in the latter species. *Pycnodonte brongniarti* differs from the Cretaceous species *P. vesicularis* (Lamarck, 1806) because its wing shaped posterior lobe is absent in the latter and by their different ligamental pit morphologies (Abad 2001).

Pycnodonte brongniarti has a wide biostratigraphic and paleobiogeographic distribution, Paleocene-Miocene,

throughout northern Africa and southern Eurasia. *Pycnodonte brongniarti* is abundant in numerous localities of the Eocene (Bartonian-Priabonian) of Igualada and Vic regions (Catalonia), in the eastern part of the Ebro Basin. The dimensions of our material match the higher end of the biometric range of *P. brongniarti* provided by Abad (2001: fig. 170) from the site of El Saió, in the upper part of the Igualada Formation (Priabonian, Cascella & Dinarès-Turell 2009; Costa *et al.* 2013). However, the development of the sulcus and the posterior lobe of the left valve are bigger in some of our specimens than in those figured by Abad (2001) from the Eocene of the Camí a Serramitja site (Vespella marls, Gurb, Vic region).

Pycnodonte brongniarti is also present in the upper part (lower Oligocene, Rupelian?) of the Paleogene series of the Basque Coast (southwestern Aquitaine Basin), more specifically on the site Chambre d'Amour (Anglet/Angelu), being first referred to as "*Ostrea vesicularis*" by d'Archiac (1846) and figured later by the same author (d'Archiac 1850: pl. 13, fig. 24). Tournouër (*in* Bouillé 1873: pl. 7, figs 1-3) described fossils of *P. brongniarti* – classified as "*Ostrea brongniarti*" and *Ostrea vesiculosa* Sowerby var. *nummulitica* (*Ostrea* (*Gryphaea*) *vesiculosa nummulitica* Tournouër, 1873; MNHN.F.B20990) – from outcrops of the Phare de Biarritz and Chambre d'Amour. However, following the description by Abad (2001) both "*Ostrea vesicularis*" and *O. vesiculosa* var. *nummulitica* fit within the range of variability of *P. brongniarti*. Tournouër (*in* Bouillé 1876) also cited the presence of "*Ostrea brongniarti*" in La Gourèpe (?), Chambre d'Amour, Roche d'Haïtzar and Lou Cout. Boussac (1908, 1911) confirmed the occurrence of "*Ostrea brongniarti*" in the Oligocene of Anglet and Biarritz, in the sections Chambre d'Amour and Le Phare. Cossmann (1921: 12, figs 28-30) also described fossils of "*Liostrea* (*Pycnodonta*) *brongniarti*" from the same (Rupelian?) outcrops of the Aquitaine Basin.

Genus *Hyotissa* Stenzel, 1971

TYPE SPECIES. — *Mytilus hyotis* Linnaeus, 1758 by original designation.

Hyotissa martinsii (d'Archiac, 1850)
(Fig. 11M, N)

Ostrea martinsii d'Archiac, 1850: 438.

Complete synonymies in Abad (2001: 582).

MATERIAL. — Ardanatz Sandstone, 1 incomplete left valve (section and level unknown).

DIMENSIONS. — H > 170.0; L = >200.0; W = (80.0).

DESCRIPTION

Incomplete left valve of a very large specimen. Irregular shape; growth striae well marked; three (antimarginal?) folds or ribs not very strong, with triangular profile and

TABLE 1. — Dimensions (in mm) of *Pycnodonte brongniarti* (Bronn, 1831) from the Eocene (Bartonian-?Priabonian) of the IV (Itzagaondoa Valley) section, uppermost part of the Ilundain Marl Formation (Navarre, western Pyrenees). Abbreviations: see Material and Methods.

| | H | | | | L | | | | W | | | |
|-------------|------|-----------|-------|----|-------|-----------|-------|----|------|-----------|-------|----|
| | min | \bar{x} | max | n | min | \bar{x} | max | n | min | \bar{x} | max | n |
| Left valve | 14.9 | 29.96 | 36.77 | 14 | 13.32 | 26.78 | 34.63 | 14 | 8.56 | 17.85 | 22.23 | 10 |
| Right valve | 9.81 | 14.97 | 20.51 | 13 | 7.88 | 14.01 | 22.65 | 13 | 1.57 | 3.28 | 5.77 | 13 |

more or less perpendicular to the growth lines. Internal surface smooth; adductor muscle scar net, with irregular ovoid contour and fine striae parallel to its lower margin. The specimen has a strongly concave attachment area, large, forming a natural cast that reflects a root or woody stem (substratum bioimmuration, xenomorphic sculpture; see: Autoecological remarks).

REMARKS

Hyotissa martinsii was described by d'Archiac (1850) as “*Ostrea martinsii*” using one single fossil from the Eocene “Nummulitique” of Biarritz (southwestern Aquitaine Basin) (d'Archiac 1850: 438, pl. 13, fig. 25). This specimen is much smaller and exhibits a greater number of ribs or folds than the fossil from Ardanatz Sandstone. According to Abad (2001), however, larger specimens of *H. martinsii* have more attenuated ribs. This can explain the morphological differences between our fossil and the specimen described by d'Archiac.

Morphologically and biometrically the studied specimen matches the larger specimens of *H. martinsii* from the Eocene regions of Igualada and Manresa (Catalonia), studied by Abad (2001). *Pycnodonte gigantea* (Solander in Brander, 1766) is another Pycnodontinae, which can also reach a large size. The distinction between large-sized specimens of both species is not straightforward but, according to Abad (2001), *H. martinsii* has ribs, whereas they are absent in *P. gigantea*.

Order PECTINIDA J. Gray, 1854
Suborder PECTINIDINA J. Gray, 1854
Superfamily PECTINOIDEA Rafinesque, 1815
Family PECTINIDAE Rafinesque, 1815

Genus *Chlamys* Röding, 1798

TYPE SPECIES. — *Pecten islandicus* Müller, 1776 by subsequent designation (Herrmannsen 1846).

Chlamys cf. *biarritzensis* (d'Archiac, 1846)
(Figs 3A; 11O)

Pecten biarritzensis d'Archiac, 1846: 210, 211, pl. 8, fig. 9a, b.

Complete synonymies in Abad (2001: 419, 420).

MATERIAL. — Ardanatz Sandstone, numerous fragmentary specimens and fragments from AD2 and AD3 sections.

DIMENSIONS. — Largest specimen. H = (28.0); L = (26.2).

DESCRIPTION

Shells with oval ventral outline, lateral margins slightly curved; sculpture composed of distinct radial ribs (costae) both externally and internally. Outer surface radial ribs three-lobed (ribbed) longitudinally, with trapezoidal-triangular sections, the central lobe being the most developed; intercostal spaces slightly narrower than the ribs. Scaled costal and intercostal external surfaces, with wavy and imbricated transverse striations (lamellae), especially marked on both sides of the ribs, with lobes on the crest of ribs pointing towards the ventral edge of the shell.

REMARKS

Ruiz de Gaona & Colom (1950) indicate the abundance of “*Pecten subtripartitus*” in the sandstone levels of Ardanatz-Eguesibar, forming true lumaquellas in some cases, such as in section AD3 (Fig. 3A).

The morphology of the studied specimens is similar to that of *Chlamys biarritzensis* (d'Archiac, 1846) and *Chlamys subtripartita* (d'Archiac, 1850), described for the first time in the Eocene “Nummulitique” of Biarritz (southwestern Aquitaine Basin), especially to a fossil of “*Pecten subtripartitus*” figured by d'Archiac (1850: pl. 12, fig. 16). The species *C. biarritzensis* and *C. subtripartita* from Biarritz were described and figured again by Boussac (1911: pl. 3, figs 4, 5, 7, 9, pl. 7, fig. 6, pl. 17, fig. 9) and Cossmann (1921: pl. 10, figs. 39-41, pl. 11, fig. 8). D'Archiac (1950) created several other species now assignable to the genus *Chlamys*. Tournouër in Bouillé (1876) stressed the difficulty to differentiate the species “*Pecten subtripartitus*”, “*P. gravesi*” and “*P. subopercularis*” created by d'Archiac, and suggested that all of them could be considered synonymous with “*P. biarritzensis*”. Boussac (1911) noted that the ornamentation is more marked and more squamous (scaly) in *C. biarritzensis* than in *C. subtripartita*, and that both species appear to be separated stratigraphically (Handia levels for the former and Phare and Chambre d'Amour for the latter, among other outcrops). However, other authors, such as Oppenheim (1901), Fabiani (1915) and Piccoli & Mocellin (1962), considered both species synonymous. Wozny (1977) regraded *C. subtripartita* as a subspecies of *C. biarritzensis*. Abad (2001) studied numerous fossils from the Eocene of the Igualada, Manresa, Vic and Girona in Catalonia assigned to *C. biarritzensis*. This author indicated that specimens which approximate both *C. biarritzensis* as *C. subtripartita* occur in the same sites, ruling out the temporality of these species and consequently considering them synonymous. *Chlamys biarritzensis* is present in many other Eocene (Lutetian-Priabonian) and Oligocene sites from Europe and North Africa (see Abad 2001).

Chlamys infumata (Lamarck, 1806)
(Fig. 11P)

Pecten infumata Lamarck, 1806: 354.

MATERIAL. — Ardanatz Sandstone, AD6 section: one incomplete specimen from level AD6.1.

DIMENSIONS. — H = 17.8; L = 15.0; W = 3.6.

DESCRIPTION AND REMARKS

Shell elongate-ovate in outline, thin, equivalve; posterior ear partially preserved, with distinct radial ridges; outer radial sculpture with about 24 radial ribs (costae), tightly arranged. The central part of the ribs is quite smooth, except in those closer to the margins, which show visible concentric lamellae.

The tighter arrangement and less marked ornamentation of the radial costae differentiate this specimen from the species *Chlamys biarritzensis* (d'Archiac, 1846) and makes it more closer to *Chlamys infumata* (Lamarck, 1806). The latter species was also reported ("*Pecten infumatus*") by d'Archiac (1850) from the Eocene of Biarritz. *Chlamys infumata* has a wide biogeographic (Atlantic Area, Alps, Balkans, etc.) and stratigraphic (Ypresian-Bartonian) distribution (Abad 2001; Cossmann & Pissarro 1906: pl. 41, figs 131-15, 131-16, syn-types MNHN.EA58595, J06988, J07731, J04928, J04070, R53984, colls. Lamarck, Cossmann, Vasseur and Viaud).

Family SPONDYLIDAE J. Gray, 1826

Genus *Spondylus* Linnaeus, 1758

TYPE SPECIES. — *Spondylus gaederopus* Linnaeus, 1758 by subsequent designation (Schmidt 1818).

Spondylus cf. *caldesensis* Carez, 1881
(Figs 3G; 12A, B)

Spondylus caldesensis Carez, 1881: 311, pl. 4, fig. 22. pl. 7, fig. 1.

Complete synonymies in Abad (2001: 489).

MATERIAL. — Ardanatz Sandstone, AD5 section: 4 incomplete specimens and 1 incomplete right valve from level AD5.1 (c. level AD1.1-2).

DIMENSIONS. — Largest specimen: H, right valve > 97.2, L > 60.0; H, left valve > 100.0, L > 80.0.

DESCRIPTION

Large-sized shells, inequivalved, inequilateral, biconvex; right valve more convex and higher than the left valve, without any lamellose surface to attach to a hard substrate; umbo more developed and prominent than in the left valve; side margins fairly straight, forming an angle of about 90 degrees; posterior margin more developed than the anterior margin. Ornamentation of the two valves similar; about 9-10 radial costae (primary radial ribs) on right valve and 6-7 on left valve, with rounded sections and imbricated squamous (crenulated) surface with

prominent growth-lines; thick spines irregularly distributed on costae, with a longitudinal groove on the bottom that results in a circumflex accent section. The spines are somewhat less marked on the left valve. Wide intercostal spaces, with 3-6 (7) spinose, squamous, finer costellae, more or less developed (secondary and tertiary radial ribs). Small spines also of open inverted V cross section, crossed by commarginal growth striae welts. The hinge and cardinal areas, the ventral (pallial) margin and the internal surfaces of valves are not well preserved due to the fragmentary nature of the material.

REMARKS

The presence of *Spondylus* among the bivalves in the Eocene marly formations of Navarre was early mentioned by Ruiz de Gaona (1947), Mendizábal & Ruiz de Gaona (1949) and Ruiz de Gaona & Colom (1950), who cited the species *Spondylus eocenus* Leymerie, 1881 in the Bartonian of Ardanatz-Eguesibar. However, according to Carrasco (1994), *S. eocenus* has a subequivalve and subequilateral (orbicular outline) shell, both features being different to those in the studied specimens.

The above described features are more in line with the original description of *S. caldesensis* Carez, 1881, and match the characteristics which Carrasco (1994) and Abad (2001) attributed to *S. caldesensis* from several Catalan sites in the upper Bartonian (and most likely Priabonian) Igualada Formation, such as the Igualada, Manresa and Vic regions (Taberner *et al.* 1999; Cascella & Dinarès-Turell 2009; Costa *et al.* 2013). However, our most complete specimen (AD5.1.2) is higher than the specimens measured by Abad (2001) from the sites of El Saió and C. Vilaseca (Sta. Margarida de Motbui) and Collsuspina (Vic), although our fragmentary sample does not allow precise assessments.

Other species of the genus *Spondylus* present in the Middle-Upper Eocene of Catalonia are *S. buchi* Philippi, 1846, *S. cisalpinus* Brongniart, 1823 and *S. radula* Lamarck, 1806 (Abad 2001). According to Carrasco (1994) and Abad (2001), the shell of *S. buchi* is, unlike that of *S. caldesensis*, almost equivalve and sub-equilateral, pectiniforme, with short and angular intercostal spaces. The primary ribs of the former are more numerous than in *S. caldesensis* and have, unlike the species erected by Carez, angled sections. The central part of the ribs of *S. buchi* is smooth, with a few alternately arranged spines (one rib with spines and several without). The left valve only exceptionally has spines and, when present, they are very small.

The irregular distribution of the strong spines and the scaly surface of the costae, due to the strong and prominent growth striae and the wider intercostal spaces (?), differentiate our specimens from *S. cisalpinus*. The latter are significantly larger than the largest specimens of *S. radula* measured by Abad (2001) and two specimens of the Cossmann collection (MNHN.F.J07457) from the Lutetian of Parnes (Oise, Paris Basin). Further taxonomic assessments are not possible with the available material.

The genus *Spondylus* has also long been known from the "Nummulitic" from Biarritz, in the Basque Coast (south-western Aquitaine Basin). The classic studies by d'Archiac (1846, 1850), Rouault (1850), Bouillé (1876), Boussac

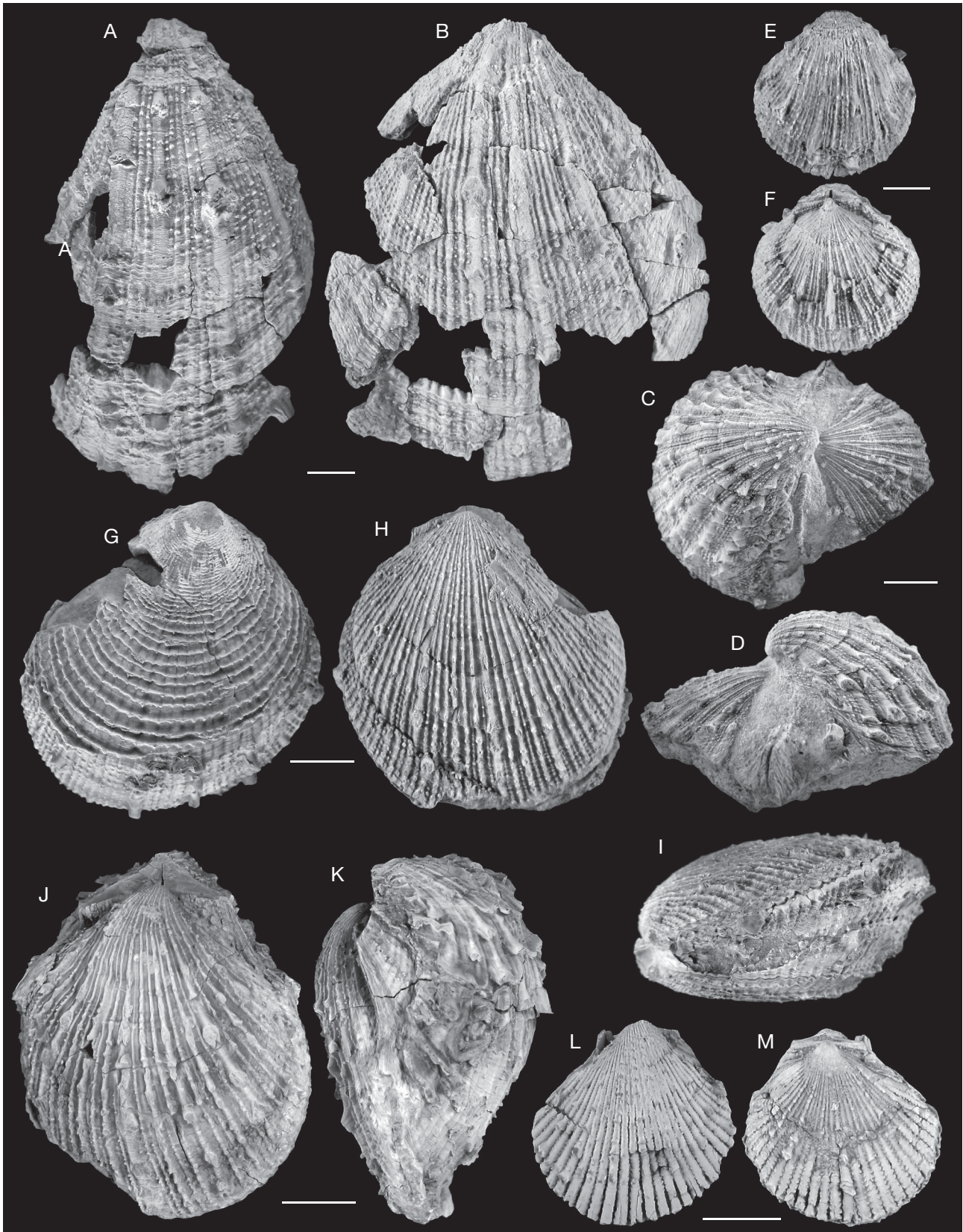


FIG. 12. — Fossils of bivalves from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A, B**, *Spondylus cf. caldesensis* Carez, 1881, AD5.1.2, right and left valves, external views; **C, D**, *Spondylus cisalpinus* Brongniart, 1823 (ecomorph *bifrons*), AG1.4.4, double-valved fragmentary specimen, posterior and umbonal – dorsal – views; **E, F**, *Spondylus* sp., AD2.1.20, right and left valves, external view; **G-K**, *Spondylus cisalpinus* Brongniart, 1823: **G, H**, IV.6, right and left valves, external views; **I**, IV.6 right and left valves, anterior views; **J**, IV.43, left valve, external view; **K**, IV.43, right and left valves, posterior views; **L, M**, *Spondylus planicostatus* d'Archiac, 1847, IV.44, right and left valves, external views. Scale bars: A-D, G-K, 10 mm; E, F, L, M, 5 mm.

(1908, 1911) and Cossmann (1921) reported, with descriptions and figures, the presence of up to 12 species of this genus. The most frequently mentioned species are *Spondylus subspinosus* d'Archiac, 1847, *S. buchi* Philippi, 1846, *S. planicostatus* d'Archiac, 1847, and *S. nysti* d'Archiac, 1846 in the Bartonian and Priabonian strata of the Biarritz-Anglet area. However, Boussac (1911) did not report *S. caldesensis* from the Paleogene of the Basque coast. This author and Abad (2001), in line with Oppenheim (1901), confirmed the synonymy between *S. subspinosus* and *S. buchi*. In fact, the morphology of the right valve of *S. subspinosus* figured by d'Archiac (1850: pl. 3, fig. 1) is very similar to that of *S. buchi* figured by Abad (2001: pl. 12, fig. 3) from the Eocene of Catalonia.

Spondylus cisalpinus Brongniart, 1823 (ecomorph *bifrons*)
(Fig. 12C, D)

Spondylus bifrons Münster in Goldfuss, 1836: 99, 100, pl. 106, fig. 10.

MATERIAL. — Ardanatz Sandstone. AG1 section: 1 incomplete specimen with the umbonal region of the two valves from level AG1.4; 1 fragmentary specimen from level AG1.3. Ilundain Marl Formation, ARR1 section: 1 fragment of left valve from level ARR1.1.

DESCRIPTION

Asymmetric valves, strongly convex; right valve with prominent and recurved umbo, with a tiny attachment area; angle between anterior and posterior margins of about 90 degrees; about 12 radial costae, with numerous spines arranged quite regularly at short intervals; costae surface quite smooth, barely marked growth lines, narrow intercostal spaces with 2-4 costulae. AG1.4.4 retains a small posterior ear with sinuous striation (growth-lines) parallel to the lateral margin. Left valve with fewer and smaller spines.

REMARKS

The following characteristics differentiate these specimens from others described above and tentatively assigned to *S. caldesensis*: 1) The less marked spines of the left valve; 2) the more numerous spines, which are regularly arranged at short intervals on the ribs; 3) the smoother rib surface; and 4) the narrower intercostal spaces. These features are closer to the species *S. cisalpinus* Brongniart, 1823 and *S. bifrons* Münster in Goldfuss, 1840, both of which are known from several Eocene sites in Catalonia (Carrasco 1994: pl. 1, figs 1, 2; Abad 2001: pl. 13, figs 3-5, pl. 14, figs 1, 2). Zavarei (1973) included both species and *S. nysti* d'Archiac, 1846, in the same group ("Groupe de *S. cisalpinus*"). According to Carrasco (1994), the left valve of *S. cisalpinus* is flat, while that of *S. bifrons* is convex. According to Abad (pers. comm., via Calzada) *S. cisalpinus* and *S. bifrons* are synonymous. *Spondylus cisalpinus* is known to have developed stronger spines (*bifrons* ecomorph) on muddy bottoms, such as is our case. Therefore, the studied specimens should be classified as either *S. bifrons* (*sensu* Carrasco 1994) or *S. cisalpinus* (ecomorph *bifrons*) (*sensu* Abad pers. comm.).

Spondylus sp.
(Fig. 12E, F)

MATERIAL. — Ardanatz Sandstone. 4 specimens from AD sections (levels unknown); AD2 section: 3 specimens, from level AD2.1; AG1 section: 1 specimen from AG1.4.

DIMENSIONS. — Right valve. H = 6.0-14.9; L = 5.0-13.4; W = 3.6-7.8.

DESCRIPTION

Small specimens, almost equilateral, rounded pallial margin; right valve more convex and spiny than the left valve; right umbo with a small attachment area more or less perpendicular to the umbo-pallial plane; costae with longitudinally grooved spines of circumflex in cross sections, costae surface between spines quite smooth. The right valve of specimen AD2.1.20 (Fig. 12E, F) has 6(7) radial costae (primary radial ribs). About 3 secondary ribs are intercalated between primary ribs, with smaller spines. There are 2-4 tertiary spinulose ribs on each side between the primary and secondary ribs. However, on the right valve of another specimen there are about 11 radial costae, some less developed (secondary radial ribs), as well as another 2-4 costellae (tertiary ribs). Trigonal cardinal area, broad, elongated in the antero-posterior sense, concave, bounded by more or less equal ears with sinuous striation parallel to their lateral margins. On the inner surface of a left valve fragment are two hinge dental sockets, deep, elongate and sub-parallel to the margins of the shell; the anterior socket arranged sub-vertically and the posterior one obliquely. Except for the hinge, the rest of the inner surface of the shell cannot be seen.

REMARKS

These fossils with spinose surfaces and circular contours are very similar to the umbonal region of the shells described as *S. cisalpinus* Brongniart, 1823 (ecomorph *bifrons*). They could therefore belong to juvenile individuals of that species. The levels from which all the specimens were collected (AD2.1, AG1.3, AG1.4) are stratigraphically higher than the level (AD1.1) from which the specimens assigned to cf. *S. caldesensis* came (Fig. 2 and further below: Fossil associations and palaeoenvironments).

Spondylus cisalpinus Brongniart, 1823
(Fig. 12G-K)

Spondylus cisalpinus Brongniart, 1823: 76, pl. 5, fig. 1a-c.

MATERIAL. — Ilundain Marl Formation, IV section: 3 almost complete specimens; numerous shell fragments corresponding to at least 7 specimens (including 7 fragments of the umbonal area of right valves).

DIMENSIONS. — Right valve. H = (47.6)-77.0; L = (38.5)-62.5; W = 26.0-51.0.

DESCRIPTION

One of the most complete specimens (IV.6, Fig. 12G-I) has a markedly inequivalve and inequilateral shell; right valve with

anteroposteriorly trapezoidal section due to the development of a broad flat (slightly domed) area that occupies most of the external surface. Flat area with lamellar-cancellate sculpture, resulting from the intersection of numerous commarginal lamellae and tight radial ribs; ventral region of right valve highly convex, with about 10 radial costae (primary and secondary radial ribs) displaying some longitudinally grooved and laterally compressed spines; wide intercostal surfaces with 4-5 costellae (tertiary radial ribs) with spines at their intersections with growth lines; broad and quite flat trigonal cardinal area, elongated anteroposteriorly, which extends into a small anterior ear or auricle (the posterior ear of specimen IV.6 is broken) with sinuous and spiny striation more or less parallel to the lateral margin. The development of the lamellar surface of the right valve of the specimens from Itzagaondoa Valley is variable. Some fragments show a large attachment area identical to that of IV.6. In contrast, the specimen IV.13 (Fig. 12J, K) and other fragments exhibit a much smaller lamellar surface. Left valve pectiniform, slightly convex with less and smaller spines; umbo small and sharp; striated and spiny ears or auricles, the posterior ear being larger than the anterior; left valve surface with 6-7 radial costae, poorly developed; 3-6 secondary ribs between costae, with tertiary radial ribs, bristling with tiny spines, in the pallial region.

REMARKS

According to Zavarei (1973), the following characteristics prevent our specimens from being classified as *Spondylus bifrons* Münster in Goldfuss, 1840 and make them closer to the species *S. cisalpinus* Brongniart, 1823: 1) the lower convexity; 2) finer spines of the left valve; as well as (3) the right valve sculpture, quite lamellar rather than spiny in some of our specimens.

Spondylus nysti was created by d'Archiac (1846) using material from the "Nummulitic" of Biarritz, in the Basque Coast (southwestern Aquitaine Basin). Specimen IV.6 is quite similar to those described and figured by d'Archiac (1846: pl. 2, figs 3a, 4) and to the material from the Eocene of the Igualada, Vic and Manresa regions in Catalonia assigned to this species by Carrasco (1994: pl. 1, fig. 3). In contrast, this comparison does not hold true for specimen IV.13, whose right valve, strongly spinose, is more similar to that of *S. cisalpinus*. Interestingly, however, Zavarei (1973) included all the species *S. cisalpinus*, *S. bifrons* and *S. nysti* in the same group. Abad (2001) strongly questioned the validity of *S. nysti*, as some *S. cisalpinus* present right valves with similar lamellar morphology. According to Abad (pers. comm., via Calzada), both *S. nysti* and *S. bifrons* are synonymous with *S. cisalpinus*.

Spondylus planicostatus d'Archiac, 1847 (Fig. 12L, M)

Spondylus planicostatus d'Archiac, 1847: 438.

MATERIAL. — Ilundain Marl Formation, IV section: 6 specimens.

DIMENSIONS. — H = 9.2-18.1; L = 9.2-20.0; W = 4.2-6.7.

DESCRIPTION

Semicircular ventral (pallial) outline, slightly inequilateral, biconvex shell, the right valve slightly more convex than the left valve; small umbonal attachment area, bigger in the right umbo; umbos slightly recurved; right umbo protrudes slightly over the left umbo; small ears, with marked growth-lines more or less parallel to lateral margins; cardinal area small, triangular flattened; margins of right valve forming an angle of about 90 degrees; 29-31 radial costae, of equal thickness, extend from the umbo to the pallial margin with no change in number, showing dorsally flattened section and lateral surfaces dentate-serrate (crenulate) by the intersection of commarginal growth-lines; about 9 of these costae – regularly arranged, at intervals of 3 to 5 – have short, broad, scaly spines, distributed at regular intervals along the dorsal surface of the costae; very narrow intercostal spaces. Ornamentation of the left valve more or less similar to that of the right valve, but the number of spiny ribs is lower in one specimen.

REMARKS

Spondylus planicostatus d'Archiac, 1847 was defined in the Paleogene of Biarritz (southwestern Aquitaine Basin; d'Archiac 1847, 1850: 438, pl. 13, fig. 2). Boussac (1911) also reported this species from the "couches lutétiennes" and the "Auversien" of Biarritz, in particular from the Bartonian marly limestones of La Gourèpe and Vallon de Beherecco, below the levels of the Côte des Basques (Côte des Basques Formation, Mathelin & Sztrákos 1993). *Spondylus planicostatus*, with specimens from the Côte des Basques, was also cited by Cossmann (1921: pl. 12, fig. 7-8). In addition, *S. planicostatus* was cited in the Eocene of Kressenberg (Bavaria) by Frauscher (1886). Zavarei (1973) included this species within the Group of *S. buchi* Philippi, 1846. However, *S. planicostatus* differs from *S. buchi* in its costae sections, which are rounded and flattened in the former but angled in the latter. In addition, intercostal spaces of *S. buchi* are also angled, width being similar to that of the ribs, while intercostal spaces are tighter in *S. planicostatus*. Another two species of the same group are *S. palensis* Rouault, 1848 – defined in the Early Eocene of Bosdarros (Béarn) (see Rouault 1850: 472, pl. 15, fig. 2) – and *S. eoecenus* Leymerye, 1881, defined from Lutetian deposits in the southeast of France and Catalonia. *Spondylus palensis* differs from *S. planicostatus* by having lesser bilateral symmetry and smaller number of spiny ribs; *S. palensis* differs from *S. eoecenus* because all of its ribs show similar development, while *S. eoecenus* has clearly defined costae and costellae (primary and secondary radial ribs).

Suborder ANOMIIDINA J. Gray, 1854
Superfamily DIMYOIDEA P. Fischer, 1886
Family DIMYIDAE P. Fischer, 1886

Genus *Dimya* Rouault, 1850

TYPE SPECIES. — *Dimya deshajesiana* Rouault, 1850 by monotypy.

Dimya pamplonensis (Carez, 1881) n. comb.
(Fig. 13A-C)

Plicatula pamplonensis Carez, 1881: 310, pl. 8, figs 2-5.

Dimya richei Doncieux, 1911: 34, pl. 6, figs 7a-b.

Anomyia [sic] *pamplonensis* – Ruiz de Gaona & Colom 1950: 332, pl. 54, figs 10-13.

MATERIAL. — Ardanatz Sandstone. 1 specimen from AD sections (section and level unknown). AG1 section: 2 specimens below level AG1.1. ZB1 section: 4 specimens, 1 incomplete right valve. TR1 section: 5 more or less complete specimens. Ilundain Marl Formation, ARR1 section: 5 specimens, 4 left valves, 3 incomplete right valves.

DIMENSIONS. — H = 7.7-11.2; L = 6.2-9.3; W = 2.0-3.8 (From Calzada & Astibia 1996; 102 specimens).

DESCRIPTION

Small-sized shell; inequivalve and inequilateral, oval and sometimes serrated or irregular outline; flat convex profile, with the maximum thickness towards the umbonal region; umbonal angle between 120° and 160°; left valve slightly convex, exterior surface foliaceous with 5 or 6 (7) commarginal lamellae, irregular in their spacing; antimarginal costae or ribs variable in development but, in general, almost imperceptible; right valve almost flat, sculpture also lamellose, ribs very blurred. Inner surface of the valves smooth and porcelainized. Three inner regions or areas can be distinguished: 1) umbonal, corresponding to the aragonitic inner shell in living species of *Dimya* (Waller 2012); 2) inner (internal) pallial; and 3) outer (external) pallial areas, the last two corresponding to the calcitic rim of extant *Dimya* species and being separated by a very visible denticulation line (chomata). Growth tracks (ontogenetic migration tracks) of the denticles (chomata) appear as fine lines and can be observed on the inner surface of the valves. Umbonal area deep, nearly circular outline, sharpened at the upper end, separated from the pallial region by a curved line (pallial line), with a different colour; adductor muscle scars generally difficult to observe, anterior adductor scar pyriform or triangular on the right valve, posterior adductor scar bilobed, components being oval or nearly circular, located on the inclined portion of the shell; inner pallial part as an area or circular segment; outer or more peripheral pallial region separated from the rest of the valve by chomata and contact the umbonal area, with two symmetrical concavities for the ligament, axially limited by small teeth or crura that are stronger in pallial sense.

ONTOGENY

Growth is very visible in the concentric lamellae; shell passes from a nearly circular contour (length than about 3 mm) to an elliptical or oblong outline. In the case of the gerontic specimens (length more than 12 mm) this outline is virguliforme (Calzada & Astibia 1996).

REMARKS

The species *Dimya pamplonensis* (Carez, 1881) n. comb. is based on specimens collected from marly levels to the south of the city of Pamplona (Navarre). Carez regarded the Pamplona marls as equivalent to the “marls with *Serpula spirulaea*” (“Marnes bleues

à *Serpula spirulaea*”) in Catalonia (Igualada, Vic) and Aragón (La Peña, Jaca, Fiscal). Ruiz de Gaona (1947) and Mendizábal & Ruiz de Gaona (1949) confirmed the presence of *Plicatula pamplonensis* in the towns of Oriz, Altos de Badoztain, Ardanatz-Éguesibar and Zabaltza. Later, Ruiz de Gaona & Colom (1950) assigned this species to the genus *Anomia* (“*Anomyia*”). Calzada & Astibia (1996) studied over 100 shells from some localities of the Basin of Pamplona and the valley of Itzagaondoa and included the abovementioned species in the genus *Dimya*, since the valves show two muscular impressions (two adductor muscle scars) and *Plicatula* is known to be monomyarian. *Dimya* differs from *Anomia* by having not perforated shell. Due to the unknown whereabouts of the Carez collection (probably lost) and the probable lost of the original outcrops under urban development, Calzada & Astibia (1996) suggested a new type locality in the Ardanatz Sandstone formation (transition to the overlying Ilundain Marl Formation) (Fig. 1) and erected a neotype for the species, which is stored in the Museu Geologic del Seminari de Barcelona (MGSB 60020.1). The age/stage type can now be constrained to the Bartonian, probably lower Bartonian, and not to the upper Bartonian or even lower Priabonian, as indicated by Calzada & Astibia (1996).

D’Archiac (1850: 441, pl. 13, figs 9-11) described and figured several specimens of a new species, called *Anomia intustiata*, among the fossils from the “Groupe Nummulitique” of the localities of Trabay and Hontet in Aquitaine. These specimens can now be assigned to the genus *Dimya* (*D. intustiata* (d’Archiac, 1850); Calzada & Astibia 1996), but they are different to *D. pamplonensis* n. comb. The size of *D. pamplonensis* n. comb. is smaller than the specimens figured by d’Archiac (1850) and at least one specimen has ribs (radials? antimarginals?), which are significantly more pronounced than those in *D. pamplonensis* n. comb.

D. pamplonensis n. comb. has been cited in the Eocene from Vic (Catalonia) (Farrés & Staid-Staad 1964) and Sobrarbe (Aragon) (<http://fosilesdesobrarbe.blogspot.com.es>). However, in the latter case, four of the specimens illustrated are slightly larger and have more pronounced ribs than in the Pamplona fossils. Consequently, they could probably be better assigned to *Dimya intustiata* (d’Archiac, 1850). Finally, the species *Dimya deshaysiana* Rouault, 1850 has no lamellose ornamentation (commarginal lamellae), being completely covered with antimarginal (radial?) ribs (Calzada & Astibia 1996). In a recent review of the Dimyidae, Waller (2012) included *D. pamplonensis* n. comb. within valid species of the family, *Dimya richei* Doncieux, 1911 being synonymous with *D. pamplonensis* n. comb.

Infraclass HETEROCONCHIA Hertwing, 1895
Order CARDITIDA Dall, 1889
Superfamily CRASSATELLOIDEA Férussac, 1822
Family CARDITIDAE Férussac, 1822
Subfamily VENERICARDIINAE Chavan, 1969

Genus *Venericardia* Lamarck, 1801

TYPE SPECIES. — *Venus imbricata* Lamarck, 1801 by subsequent designation (Schmidt 1818).



FIG. 13. — Fossils of bivalves from the Eocene (Bartonian-?Priabonian) marly formations of the Pamplona Basin and surrounding areas (Navarre, western Pyrenees): **A-C**, *Dimya pamplonensis* (Carez, 1881) n. comb.: **A**, TR1.1.2, left valve, external view; **B**, TR1.1.3, right valve, external view; **C**, TR1.1.4, left valve, external view; **D-G**, *Venericardia hortensis* (Vinassa de Regny, 1898): **D**, **E**, IV.7, left and right valves, external views; **F**, IV.7, umbonal view; **G**, IV.45, double-valved specimen, left valve, external view; **H-N**, *Chama pellati* Boussac, 1911: **H**, IV.46, left valve, external view; **I**, IV.8, right – and left – valve, external view; **J**, AD2.2.4, left valve, internal view; **K**, AD.41, right – and left – valve, external view; **L**, **M**, IV.47, left and right valves, external views; **N**, AD.40, right – and left – valve, external view; **O-Q**, *Chama granulosa* d'Archiac, 1850: **O**, **P**, AD4.1.5, left and right valves, external views; **Q**, AD.42, left valve, external view. Scale bars: 5 mm.

Venericardia hortensis (Vinassa de Regny, 1897)
(Fig. 13D-G)

Cardita hortensis Vinassa de Regny, 1897: 183-184, pl. 20, fig 4-6.

Venericardia junctinoda – Astibia et al. 2016: 15, fig. 6u.

Complete synonymies in Cossmann (1921: 124).

MATERIAL. — Ilundain Marl Formation, IV section: 33 specimens.

DIMENSIONS. — H = 6.8-16.9; L = 6.3-16.8; W = 4.2-9.4.

DESCRIPTION

Shell equivalve, dorsally inflated, trigonal ovate in outline, heart-shaped, inequilateral; umbones prosogyrate and prominent; lunule short and deep; (22) 23 strong radial ribs (costae), bristling with thick transverse lamellae, of scaly appearance. Deep intercostal spaces, wider than the ribs in the anterior third.

REMARKS

The morphology is similar to that of *Venericardia hortensis* (Vinassa de Regny, 1897), defined in the Eocene from Possagno (Southern Alps, northern Italy) (Vinassa de Regny 1897: 183-184, pl. 20, figs 4-6; Oppenheim 1901: 154, 155, pl. 4, figs 5-7). *Venericardia hortensis* is also present in the Eocene (Bartonian and mainly Priabonian, Mathelin & Sztrákos 1993) from the Côte des Basques (Biarritz, Côte des Basques Formation, southwestern Aquitaine Basin), as described and figured by Boussac (1911: 44, 45, pl. 10, fig. 16) and Cossmann (1921: 124, pl. 7, figs 37-40; MNHN.F.J07469, Cossmann coll.). *Venericardia hortensis* can be distinguished from *Venericardia junctinoda* Cossmann, 1898, from the “Nummulítico medio” (Ypresian) of Ager (Ager basin, South Pyrenean Foreland Basin) (Cossmann 1898a; De Renzi 1971) by its smaller size and its lower number of costae (23 vs 25). However, differences could fall within intraspecific variation and the two species be synonymous. Another similar species is *Venericardia basiteroti* (Deshayes, 1851) from the Oligocene (Rupelian) of Larrat (Landes, Aquitaine Basin; MNHN.F.A2505, Lozouet coll.), but it has fewer costae than *V. hortensis* (17 according Cossmann 1921).

These species clearly differ from *Venericardia acuticostata* Lamarck, 1806 from the Eocene of Ferme de l’Aulnaie (Oise; MNHN.F.A25073, Faullummel coll.), which has sharper lamellae, developed only on the central portion of the ribs.

Order CARDIIDA Férussac, 1822
Suborder CARDIIDINA Férussac, 1822
Superfamily CHAMOIDEA Lamarck, 1809
Family CHAMIDAE Lamarck, 1809

Genus *Chama* Linnaeus, 1758

TYPE SPECIES. — *Chama lazarus* Linnaeus, 1758 by subsequent designation (Children 1823).

Chama pellati Boussac, 1911
(Fig. 13H-N)

Chama pellati Boussac, 1911: 46, pl. 10, figs 18, 21-23.

MATERIAL. — Ardanatz Sandstone. AD1 and AD2 sections: 2 specimens from level AD1.2; 2 specimens from level AD1.3; 13 specimens more or less complete, from level AD2.1; 9 specimens from level AD2.2; 10 specimens more or less complete (sections and levels unknown). AG1 section: 4 fragmentary specimens from AG1.4. Ilundain Marl Formation, IV section: 38 specimens (14 incomplete).

DIMENSIONS. — H = 7.3-21.8; L = 6.5-21.0; W = 4.4-12.0.

DESCRIPTION

Shell small; subcircular to dorsoventrally elongate outline, inequivalve, asymmetrical; left valve larger and strongly concave, with small or absent umbonal attachment area; right valve less concave; prosogyrate and strongly enrolled umbones; valves ornamented with commarginal (concentric) foliaceous lamellae (more irregularly marked and spaced on the left valve than on the right valve) and marked radial ribs or folds. In some cases some quite small spines occur at the intersection of the radial folds and the lamellae. All but one specimen have both valves, meaning that the internal morphology of the shell cannot generally be observed. However, the hinge can be observed in a left valve fragment (AD2.2.4) (Fig. 13J), the anterior cardinal tooth being large and solid, elongated anteroposteriorly along the margin of the hinge plate, curved upper surface and with 5-7 ridges more or less perpendicular to its outer margin; deep socket (depression) between this tooth and the next one. Second cardinal tooth narrow and long, sub-parallel to the posterior margin of the shell; third cardinal tooth (?) less developed, parallel to the second one. Hinge broken at the level of a possible posterior lateral tooth.

REMARKS

The ornamentation of our specimens is similar to that of both *Chama subcalcarata* d’Archiac, 1846 and *C. granulosa* d’Archiac, 1850. D’Archiac (1846) separated *C. subcalcarata* from *C. calcarata* Lamarck, 1809, on the basis of the former being covered with thin radial ribs (“stries fines”) between the lamellae, which are not present in the latter. The morphology of the hinge of AD2.2.4 – specially the anterior cardinal tooth – is different to that of *C. calcarata* (see Kennedy et al. 1970: 385, pl. 72). *Chama calcarata* was considered synonymous with *C. punctata* Bruguiere, 1792 (Le Renard & Pacaud 1995). According to d’Archiac (1850), *C. granulosa* differs from other species of the genus “par la régularité de ses lignes granuleuses” and the small number of lamellae. The specimens from Navarre have more and tighter lamellae, meaning that they could be better assigned to *C. subcalcarata*. Unfortunately, however, *C. subcalcarata* was created using one single and incomplete fossil and further comparison is therefore hampered.

The studied specimens also resemble a fossil from the Eocene of Bosdarros (southwestern Aquitaine Basin) that Rouault (1850) assigned to the species *C. rusticula* Deshayes,

1830, as this also has numerous commarginal folds or lamellae and radial ribs, similar to *C. subcalcarata*. However, Rouault (1850) acknowledged that *C. rusticola* was synonymous with *C. squamosa* Solander in Brander, 1766, which implies that our specimens should be compared to *C. squamosa*. This species is present in the Eocene from the Paris Basin and in Barton-Highcliffe (Upper Barton Bed H, England) (coll. Morton, <http://www.dmap.co.uk/fossils/>).

Our fossils bear a closer resemblance to *C. pellati* Boussac, 1911. This species was created using several specimens collected from the Eocene (Bartonian and mainly Priabonian) of Côte des Basques (Biarritz, Côte des Basques Formation, southwestern Aquitaine Basin; Boussac 1911: pl. 10, figs 22, 23). Oddly, *C. pellati* hardly appears in other scientific works carried out elsewhere (e.g. Cossmann 1921; Cuvillier 1933; Farrés & Staid-Stadt 1964). Pending a thorough review of the Eocene species of the genus *Chama*, synonymy between *C. pellati*, *C. subcalcarata*, *C. rusticola* and *C. squamosa* is highly possible.

Chama granulosa d'Archiac, 1850
(Fig. 13O-Q)

Chama granulosa d'Archiac, 1850: 433, pl. 12, figs 9, 10.

MATERIAL. — Ardanatz Sandstone. 1 incomplete left valve from AD sections (section and level unknown). AD2 section: 1 specimen from level AD2.2. AD4 section: 2 specimens from level AD4.1.

DIMENSIONS. — H = 14.5-(31.0); L = 12-(26); W = 9.1->13.0.

DESCRIPTION AND REMARKS

A low number of commarginal lamellae, a finely porous surface and very thin radial ribs differentiate these fossils from those assigned to *Chama pellati*. The low number of lamellae and the very fine radial ribs approach these specimens to the species *C. granulosa* D'Archiac, 1850, especially to the specimens from the Eocene of Côte des Basques figured by Boussac (1911: pl. 10, figs 20-25, 29), and to the specimens from the Priabonian of Les Bains (Biarritz, southwestern Aquitaine Basin) described by Cossmann (1921: 85-87, pl. 5, figs 21-24; MNHN.F.J04250, coll. Cossmann).

FOSSIL ASSOCIATIONS, PALAEOECOLOGICAL AND PALAEOBIOGEOGRAPHIC REMARKS

AUTOECOLOGICAL REMARKS

Gastropods

Extant Pleurotomariidae are mainly represented by rare deep-water species, although some inhabit shallow-waters. The diet of extant pleurotomariids consists primarily of sponges, but includes also crinoids, octocorals and, in aquarium conditions, fish and clam tissue (Harasewych 2002). *Ptychocerithium*, *Diastoma* and Ampullinidae are phytophagous gastropods that thrive in euphotic shallow waters. Extant Cerithiidae are mainly confined to tropical and subtropi-

cal regions (Poutiers 1998). Except for one species adapted to estuaries and coastal areas, all extant Pachychiliidae are freshwater molluscs from tropical and equatorial regions (Gómez-Berning *et al.* 2012; Pacaud & Harzhauser 2012). Living Turritellidae are filter-feeders, mostly dwelling on subtidal soft substrates (Poutiers 1998). Ranellidae, Volutidae, Conidae and Turridae are active predators, mainly found in tropical seas. Epitoniidae are associated with coelenterates, either as ectoparasites or as foraging predators (Kilburn 1985). Eulimidae are parasitic marine micromolluscs, which in some cases live on echinoderms.

Bivalves

Glycymeris is a mobile shallow-burrowing bivalve that usually dwells in sandy or muddy sediments at shallow to intermediate depths. Accordingly, *G. jacquoti* from the region of Igualada (Vic-Igualada Formation, Catalonia) was interpreted as a semi-infaunal or partially infaunal species that lived buried in the mud, in the subtidal area (Abad 2001). Piccoli & Savazzi (1983) considered this species a non-siphonate infaunal suspension feeder.

Pycnodonte is a steno-haline genus, an indicator of stable marine paleo-salinity (Bottjer 1982; Abad 2001). In the Eocene of Igualada and Vic regions *Pycnodonte* occurs in shaley and marly lithologies, forming groups of many separated individuals that do not touch each other. They probably inhabited infra-littoral muddy substrates, lying on their left valves on (reclined shape). Something similar is observed in the specimens from the marly levels of the Itzagaondo Valley, although the number of preserved individuals is much lower than in the outcrops from Catalonia. The absence of both bio-erosion structures and encrusting organisms on the shells (only one specimen has a small polychaete tube) strongly suggests a lifestyle partially buried in the substrate.

In the Eocene of Catalonia the left valve of *Hyotissa martinsii* is attached to corals in some cases, or shows evidence of attachment to other objects. It is an epifaunal species, which inhabited littoral and upper infralittoral areas (Abad 2001). *Hyotissa hyotis* (Linnaeus, 1758) (giant honey comb oyster or black oyster) is an extant species that dwells in tropical (or warm enough) shallow subtidal waters, often cemented on coral reefs. Our specimen AD.38 (Fig. 11M, N) is an example of encrusting xylobiont (*sensu* Taylor & Wilson 2003). Oysters like *Crassostrea rhizophorae* (Guilding, 1828) along with other molluscs, commonly grow attached to submerged roots of red mangroves (Márquez & Jiménez 2002). Plaziat (1970) described mould bioimmurations of wood (mangroves) on the attachment area of oysters from the Ypresian of Corbières.

Zavarei (1973) indicated that today the genus *Spondylus* inhabits mainly warm seas in inter-tropical areas, generally between 1 and 50 meter water depths. *Spondylus caldesensis* probably lived slightly buried (infaunal) in infra-littoral muddy sediments, lying on its left valve (reclined shape). This explains why the fossil shells of *Spondylus cf. caldesensis* from Ardanatz do not have fossil epibionts. Conversely, the

specimens of *S. cisalpinus* from Ardanatz, Aranguren and Itzagaondoia Valley do have epibionts, being encrusted by bryozoans, small bivalves and polychaetes, which indicates cemented fixation.

Dimyids cement their right valve on hard substrates, skeletons and rocks. Most recent dimyids thrive in tropical and subtropical, relatively deep marine waters in the middle and outer continental shelf, and seem to prefer habitats with very low sedimentation rates (Waller 2012). The latter may explain the fact that *Dimya pamplonensis* n. comb. is mainly found in the marly levels of the Ardanatz Sandstone (AG1.1, ZB1, TR1) and in the lower part of the Ilundain Marl Formation (Arraitza outcrops) (Figs 1, 2), as these levels probably corresponded to relatively deep environments.

Carditidae are suspension-feeding animals. Some case they are attached to the substrate by their byssus (e.g. *Venericardia borealis* (Conrad, 1867)) or they are superficial burrower (e.g. *Cardites floridanus* (Conrad, 1838)) (Stanley 1970). They are common in shallow seas (Poutiers 1998).

Chamidae are filter-feeding bivalves, characteristic of tropical and sub-tropical seas, although they also inhabit temperate seas, similar to *Spondylus*. Most species of the genus *Chama* inhabit sublittoral environments, but some are intertidal. *Chama* commonly colonises rocky shores and is a typical member of the coral reef community (Kennedy *et al.* 1970). This does not seem to be the case for *Chama pellati* from the Eocene of Navarre, as most individuals are associated with silty and sandy marls (Ardanatz-Aranguren) or purely marly levels (Itzagaondoia Valley). Bernard (1976) indicated that species with small and highly ornamented shells and with a reduced cemented area live in depths greater than 20 m, attached to corals and in rock crevices and cracks. Attached bivalves such as *Chama*, *Arca*, *Spondylus* and *Plicatula* are indicative of shallow, clear waters (Schnetler & Heilmann-Clausen 2011).

FOSSIL ASSOCIATIONS AND PALAEOENVIRONMENTS

This study includes different localities and fossiliferous levels. At least five different fossil assemblages can be distinguished in the study area, three successive assemblages in the deposits from Ardanatz-Aranguren (Ardanatz Sandstone), another assemblage to the west, near the locality of Arraitza (lower part of Ilundain Marl Formation) and a fifth assemblage from the Itzagaondoia Valley to the east, at the top of the Ilundain Marl Formation. These essemblages probably do not correspond to individual shell beds but to narrow fossiliferous intervals, that we call levels. The poorly lateral continuity of the sandstone layers in the studied zone, the general marly nature of the series (difficulty in differentiating bedding surfaces), the apparently dispersed character of the fossils in the marls, and the fact that the collected fossils appear loose, concentrated on the thin regolith on the surface, precludes further precision.

Ardanatz-Eguesibar and Aranguren outcrops

The stratigraphic sections sampled in the localities of Ardanatz and Aranguren are up to 80 m thick (Fig. 2). A tentative

correlation between sections and the main fossil-bearing levels was provided by Astibia *et al.* (2014). Three intervals with different fossil assemblages can be distinguished from base to top:

1) The lower interval (levels AD1.1, AD3.1, AD4.1 [c. AD3.1], AG1.1) is the poorest in fossil molluscs. *Leptomaria peresii* or *Chama granulosa* are only present in the lower interval (AD4.1). *Ptychocerithium baylei* n. comb. and *Haustator altavillensis* are present, but they are less common than in the overlying levels. Other molluscs found in higher intervals, such as *Sigmesalia* sp., Ampullinidae indet., *Globularia* sp., *Athleta (Volutospina) vallei*, *Nihonia* aff. *transversaria* n. comb., *Spondylus cisalpinus* and *Chama pellati*, are absent in the lower interval. Some outcrops also contain abundant fossils of stellate and cyathiform hexactinellid and “lithistid” sponges (Astibia *et al.* 2014) along with erect bryozoan colonies, often in growth position (especially in AD3.1, AD4.1 and AG1.1). *Terebratulina*-like brachiopods are also common in the lower interval (Bitner *et al.* 2016). Such fossils are absent or less abundant in the rest of the intervals.

2) The middle interval (levels AD1.2, AD2.1, AG1.2, AG1.3) is richer in specimens and more diverse in taxa, especially some sites of level AD2.1, *Ptychocerithium baylei* n. comb. being especially abundant. Corals are also more frequent (Astibia *et al.* 2014). However, fossil preservation is generally poor.

and 3) The upper interval (levels AD1.3, AD2.2, AG1.4) is also rich in mollusc fossils, yielding assemblages rather similar to those in the middle interval, with the absence of the species *Amaea (Acrilla)* sp., *Athleta (Volutospina) vallei*, and *Dimya pamplonensis* n. comb. in our samples. However, the upper interval can be differentiated macro-paleontologically from the rest of the succession by the abundance of fossils of the tube-dwelling polychaete *Rotularia spirulaea*, which is also present, but much more sporadically, in the underlying levels.

Micropaleontological data of the AD3.1 and AD2.1 levels suggest a shelfal depth of deposition (Astibia *et al.* 2014). Most hexactinellids live in rather deep waters on soft substrates (Vacelet 1988; Tabachnik 1991; Charbonnier *et al.* 2007; Pisera *et al.* 2006). The local abundance of conic siliceous sponges and erected bryozoans in the lower interval (mainly in AD3.1, AD4.1 and AG1.1) suggests slightly quieter and deeper environments. The presence of Pleurotomaridae (*Leptomaria peresii*) in the lower interval also supports this hypothesis, as this family of gastropods is represented today by rare deep-water species. Extant shallow-water species have perforations or patelliform shells, but this is not the case in our fossils.

Arraitza outcrop

In addition to the vertical changes in the fossil associations of the Ardanatz-Aranguren outcrops, changes also occur both eastwards and westwards of this area. Westwards, near the locality of Arraitza (ARR1 section, Ilundain Marl Formation) (Fig. 1), macrofossil assemblages are less diverse, including hexactinellid and “lithistid” sponges,

bryozoans, brachiopods, mollusc bivalves (mainly ostreoids, spondylids and *Dimya pamplonensis* n. comb.), arthropods (maxillopods), echinoderms (echinoid spines and test fragments, asteroid ossicles), shark teeth and teleostean teeth and otoliths (Astibia *et al.* 2014). Sponges are locally very abundant. The paleontological and stratigraphical data indicate that Arraitza corresponded to somewhat deeper environments than the Ardanatz-Aranguren area. Micropaleontological data (scarcity of planktic foraminifera but comparatively more abundant than in Ardanatz, along with the diversity and composition of benthic foraminifera assemblages) are indicative of outer-platform to upper-slope environments at approximately 200 m water depth (Astibia *et al.* 2014).

Itzagaondoa Valley outcrops

Eastwards from the Ardanatz y Aranguren area, at the top of Ilundain Marl Formation (Fig. 1), neither fossil sponges nor macrovertebrates occur. The micropaleontological content is rich and dominated by solitary corals, bryozoans, tube-dwelling polychaetes (*Rotularia spirulaea* and others) and mollusc bivalves, gastropods and scaphopods. Noteworthy is the local abundance of the bivalve *Pycnodonte brongniarti*, which is absent in the outcrops of Ardanatz-Aranguren and Arraitza. Other taxa found in Itzagaondoa, such as *Benoistia* sp., *Jponisia* sp., *Sassia* sp. 1, *Niso* sp., *Mathilda* sp., *Metula* sp., *Spondylus planicostatus* and *Venericardia hortensis*, are also absent in the fossil levels located both stratigraphically lower and geographically further west. By contrast, other taxa common in the Ardanatz-Aranguren outcrops, such as Ampullinidae, Epitoniidae, *Dimya pamplonensis* n. comb., *Chama granulosa*, were not found in Itzagaondoa localities. The abundance of *Diastoma costellatum* and the scarcity of *Ptychocerithium baylei* n. comb. are also noteworthy in Itzagaondoa, in contrast to what happens in the Ardanatz-Aranguren area. *Haustator* cf. *imbricatarius* is also more common in the Itzagaondoa outcrops. Interestingly, the micropaleontological content is indicative of inner shelf environments in Itzagaondoa (Astibia *et al.* 2016), therefore corresponding to the shallowest deposits in this study.

COMPARISONS WITH OTHER AREAS AND PALAEOBIOGEOGRAPHICAL IMPLICATIONS

On a regional scale, the Eocene (Bartonian-?Priabonian) mollusc assemblages of the Ardanatz Sandstone and Ilundain Marl formations are comparable to those found at the Basque Coast, in the surroundings of the town of Biarritz, (southwestern Aquitaine Basin, Nord Pyrenean area), studied since the nineteenth century (d'Archiac 1846, 1850; Bouillé 1876; Boussac 1911), and to those from the west-central and eastern part of the South Pyrenean area, in Aragon (Villalta Comella 1956; Puigdefábregas 1975) and Catalonia (Igalada and Vic regions) (Abad 2001; Busquets *et al.* 1994; Carrasco 1994; Piserà & Busquets 2002).

However, the associations of the Pamplona Basin are less diverse (species richness) than those from the above-

mentioned areas. The lower palaeontological diversity may be apparent due to the preliminary nature of the studies carried out to date, which involves sampling biases (only fossils from rock – regolith – surfaces were collected) and/or due to taphonomic biases, or, on the contrary, it may be real due to palaeoecological differences (more restricted environments). Additionally, Sanders *et al.* (2015) highlighted the great impact that diagenesis has on the evaluation of paleobiodiversity in fossil sites, a factor that may also be influential in our case study.

Most of the gastropods found in the studied outcrops, such as *Ptychocerithium baylei* n. comb., *Diastoma costellatum*, *Haustator imbricatarius*, and the bivalves *Glycymeris jacquoti*, *Spondylus cisalpinus* (*S. bifrons* and *S. nysti*), *Spondylus planicostatus* and *Chama pellati*, among other molluscs, are also present in the Paleogene series of the Basque Coast, specifically in the outcrops of Villa Marbella and in the upper part of the Côte des Basques (Bartonian and mainly Priabonian, Côte des Basques Marls Formation, Boussac 1908, 1911; Mathelin & Sztrákos 1993; Sztrákos *et al.* 1998). 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. *Glycymeris jacquoti*, *Spondylus nysti* d'Archiac, 1846, *Spondylus planicostatus* d'Archiac, 1850, *Chama granulosa* d'Archiac, 1850 and *Chama pellati* Boussac, 1911 were all defined in the Paleogene of Biarritz. *Hytissa martinsii* was also erected by d'Archiac (1850) as “*Ostrea martinsii*” in the “Nummulitique” of Biarritz. *Pycnodonte brongniarti* is also 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). Interestingly, however, *P. brongniarti* is absent from other stratigraphically lower and palaeoenvironmentally deeper levels of the Côte des Basques, consistently with its occurrence in the Itzagaondoa outcrops, but its absence from the Ardanatz-Aranguren area in Navarre.

Other mollusc assemblages, partially comparable to those from Navarre, are the assemblages from the Eocene (Bartonian) marls of the Basa Valley (Sobás, Yebra de Basa, San Román de Basa and Isún sites, Pamplona Marls *sensu lato*, Jaca Basin, west-central South Pyrenean area, Puigdefábregas 1975; Oms *et al.* 2003), in the neighbouring territory of Huesca (Aragon), about 120 km to southeast from our study area. The fossil gastropods from these localities, which were studied by Villalta Comella (1956), share with our assemblages the genera *Niso*, *Globularia*, *Clavilithes*, *Sassia*, *Jponisia* (?) (as *Faunus* in Villalta Comella (1956), some Epitoniidae and, at least, the species *Haustator altavillensis* and *Diastoma costellatum*. The Basa Valley levels are probably slightly older than those of the Ardanatz Sandstone and Ilundain Marl Formation and their mollusc fauna seem to be more diverse than those from Navarre. Villalta Comella

(1956) describes 81 species of gastropods in the Basa Valley, while the number of species described in this work is 25.

Regarding the Eocene molluscs from Catalonia (Carrasco 1994; Abad 2001), *Spondylus caldesensis* and *Spondylus cisalpinus* (*S. bifrons* and *S. nysti*) are present in several sites from the Igualada, Manresa and Vic regions, in the Igualada Formation (late Bartonian to, most likely, Priabonian in age, Taberner *et al.* 1999; Cascella & Dinarès-Turell 2009; Costa *et al.* 2013). *Pycnodonte brongniarti*, which has a wide biostratigraphic and palaeobiogeographic distribution (Paleocene-Miocene, throughout northern Africa and southern Eurasia), is also abundant in numerous Eocene localities of the Igualada and Vic regions (Abad 2001).

Finally, with regard to the biogeographic relationships with 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* (*Clavellofusis*) *parisiensis* and *Diastoma costellatum* (Quaggiotto & Mellini 2008). These two faunal elements correspond to cosmopolitan species and have also been found in the Middle Eocene of the Paris Basin (Courville *et al.* 2012). *Leptomaria peresii* has also been found in the Tethys area, more specifically in the Priabonian of the Alps (France) (Pacaud 2007). Other species found in Navarre have also been reported from the North-West Atlantic area, such as *Haustator imbricatarius*, *Nihonia* aff. *transversaria* n. comb. from the Paris Basin and *Haustator altavillensis*, originally described from the Middle Eocene of Normandy (Cossmann & Pissarro 1900).

Taking everything into account, most of the mollusc fossils found in Navarre seems to be specific to the Pyrenean area. Consequently, endemic faunal associations seem to have dominated in the area. Additionally, or alternatively, an early beginning of the faunal differentiation between the Northern (Paris Basin, Normandy) and the southern areas (Pyrenean and Aquitaine basins), which has previously been documented to occur since at least the Rupelian (Lozouet & Maestrati 1986; Lozouet 2014 for the mollusk assemblage and Merle *et al.* 2002 for the fish assemblage), is also very likely.

CONCLUSIONS

Gastropods and bivalve associations from the middle and ?upper Eocene (Bartonian and ?Priabonian) sedimentary succession of the Pamplona Basin and surrounding areas are described. Fossils are generally fragmentary and many correspond to remains that underwent taphonomic reworking. Bioerosion traces and fossil encrusters are common. Significant effects of diagenesis have also been detected, with evidence of compression or deformation, dissolution, aragonite-calcite neomorphism and cementation by celestite.

Fossils of 37 taxa (25 gastropods and 12 bivalves) have been identified, but the number of species is probably considerably higher. Amongst them, a new species, *Athleta* (*Volutospina*)

delvallei Astibia, Merle & Pacaud, n. sp. (Gastropoda, Volutidae), has been described.

The comparison of mollusc associations of the locality of Ardanatz and the Itzagaondo valley outcrops shows notable differences. This can be explained because the Itzagaondo outcrops are higher in the stratigraphic series and represent a shallower sedimentary environment. Westwards, near the locality of Arraitza, macrofossil assemblages are less diverse. The paleontological and stratigraphical data indicate that Arraitza corresponded to somewhat deeper environments than other areas.

Gastropod and bivalve assemblages of the Ardanatz Sandstone and Ilundain Marl formations show similarities, but also differences, with coeval associations of the Basque Coast (southwestern Aquitaine Basin, North Pyrenean area), specifically in the outcrops of the Côte des Basques Marls Formation, and with those from the west-central and eastern part of the South Pyrenean area, in Aragon (Pamplona Marls *sensu lato*, Jaca Basin) and Catalonia (Vic Marls and Igualada formations). The studied associations seem to be less diverse than those from the above-mentioned areas. The lower palaeontological diversity (specie richness) of the Pamplona Basin may be due to the sampling and taphonomic biases or differences in the life assemblages. Whatever the case, faunal differences provide the Pamplona Basin a distinctive character and increase its interest for palaeobiodiversity studies. Consequently, future studies will focus on specific fossil groups.

Most of the mollusc taxa seem to be endemic to the Pyrenean area, but several Tethyan and Northern elements have also been recorded. These results enlarge the database for a better understanding of the evolution of global marine biodiversity throughout the Eocene.

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