

Eocene to Miocene holoplanktonic Mollusca (Gastropoda) of the Aquitaine Basin, southwest France

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Holoplanktonic Mollusca collected from c. 60 localities in Cenozoic (Eocene-Ypresian to Miocene-Serravallian) rocks of the Aquitaine Basin (southwest France) are represented by 75 taxa: five supposed Heteropoda (Pterotracheoidea) and 70 Pteropoda (69 Thecosomata, one Gymnosomata). All Heteropoda and 19 species of the Pteropoda had to be included in open nomenclature or with a query. Twelve species of pteropods are described as new to science: *Heliconoides daguini* sp. nov., *H. merlei* sp. nov., *H. pyrenaica* sp. nov. and *Limacina? vegrandis* sp. nov. from the Ypresian; *Creseis antoni* sp. nov. and *Vaginella gaasensis* sp. nov. from the Rupelian; *Clio lozoueti* sp. nov. and *Clio vasconiensis* sp. nov. from the Chattian; *Diacrolinia cluzaudi* sp. nov., from the Aquitanian; *Creseis roesti* sp. nov. from the Aquitanian/Burdigalian; and *Heliconoides mermuysi* sp. nov. and *Creseis tugurii* sp. nov. from the Early Burdigalian. Neotypes are designated for *Diacrolinia aquensis*, *D. orbignyi* and *Vaginella depressa*. The Aquitaine Basin assemblages are correlated with the existing holoplanktonic mollusc zonation for the North Sea Basin. Zones 9 (Ypresian), 10 (Lutetian) and 11/12 (Priabonian) could be recognised in the Aquitaine Basin Eocene, zones 15a (Rupelian) and 16b (Chattian) in the Oligocene, and zones 17 (Aquitanian-Burdigalian), 18 (Late Burdigalian), 18a (Langhian) and 19 (Serravallian) in the Miocene. Zone 17 could be subdivided on the basis of occurrences observed in the Aquitaine Basin, into three subzones, 17a (Aquitanian), 17b (earliest Burdigalian) and 17c (middle Burdigalian).

Mots-clés – Heteropoda, Pteropoda, taxonomie, biostratigraphie, espèces nouvelles, Bassin d'Aquitaine, Eocène-Miocène.

Des mollusques holoplanctoniques collectés dans environ 60 localités du Cénozoïque (Eocène-Yprésien à Miocène-Serravallien) du Bassin d'Aquitaine (sud-ouest de La France) sont représentés par 75 taxons: cinq Heteropoda (Pterotracheoidea) supposés et 70 Pteropoda (69 Thecosomata, une Gymnosomata). Tous les Heteropoda et 19 espèces de Pteropoda ont dû être laissés en nomenclature ouverte ou comportent un doute. Douze espèces de ptéropodes sont décrites comme nouvelles pour la science: *Heliconoides daguini* sp. nov., *H. merlei* sp. nov., *H. pyrenaica* sp. nov. et *Limacina? vegrandis* sp. nov., de l'Yprésien; *Creseis antoni* sp. nov. et *Vaginella gaasensis* sp. nov., du Rupélien; *Clio lozoueti* sp. nov. et *Clio vasconiensis* sp. nov. du Chattien; *Diacrolinia cluzaudi* sp. nov., de l'Aquitaniens; *Creseis roesti* sp. nov. de l'Aquitaniens/Burdigalien; et *Heliconoides mermuysi* sp. nov. et *Creseis tugurii* sp. nov., du Burdigalien inférieur. Des néotypes sont désignés pour *Diacrolinia aquensis*, *D. orbignyi* et *Vaginella depressa*. Les assemblages du Bassin d'Aquitaine sont corrélés avec la zonation de mollusques holoplanctoniques existant pour le Bassin de la Mer du Nord. Les zones 9 (Yprésien), 10 (Lutétien) et 11/12 (Priabonien) ont pu être reconnues dans l'Éocène du Bassin d'Aquitaine, les zones 15a (Rupélien) et 16b (Chattien) dans l'Oligocène, et les zones 17 (Aquitanien-Burdigalien), 18 (Burdigalien supérieur), 18a (Langhien) et 19 (Serravallien) dans le Miocène. La zone 17 a pu être subdivisée sur la base des occurrences observées en Aquitaine en trois sous-zones, 17a (Aquitanien), 17b (Burdigalien basal) et 17c (Burdigalien moyen).

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Introduction

The rich and world-famous mollusc faunas from the Miocene of the Aquitaine Basin were monographed by 19th and early 20th century researchers such as B. de Basterot (1825), de Grateloup (1827, 1828, 1836, 1840-1847), and E.-A. Benoist (1873-1874a, 1874b, 1889), but the most famous publication series from this realm, beyond doubt, is the 'Conchologie néogénique de l'Aquitaine', started in 1909, by M. Cossmann and A. Peyrot and, after Cossmann's death in 1924, continued by Peyrot until 1935. This monograph appeared more or less simultaneously in the 'Actes de la Société Linnéenne de Bordeaux', as well as in a six volume separate edition (with a different pagination), constituting a voluminous book honoured as 'Ouvrages couronnés par l'Académie des Sciences, Arts et Belles-Lettres de Bordeaux'. It is certainly because of the rich mollusc faunas that the names of two international Miocene stages, Aquitanian and Burdigalian (named after the city of Bordeaux), found their origin in this part of France.

The Aquitanian GSSP (Global Boundary Stratotype Section and Point), however, was not defined in France, but in northern Italy, 35 m from the top of the Lemme-Carrosio section, Carrosio village, north of Genoa (ratified by the International Union of Geological Sciences, 1996, as published by Steininger *et al.*, 1997), defining also the beginning of both the Neogene system and the Miocene series. A GSSP for the start of the Burdigalian has not yet been ratified.

Although pteropods from the fossiliferous deposits in Aquitaine have not attracted much attention, it still was from the Bordeaux area that the first fossil pteropod ever was described. In a very short paper (just 11 lines), F.M. Daudin (1800) introduced what he considered to be a 'ver à tube calcaire, voisin des serpules et des dentales' as *Vaginella depressa*. A few further species were described in later years, all from Miocene rocks (names are given as published originally): *Hyalaea Orbignii* Rang, 1827, *H. aquensis* Grateloup, 1827, *Cleodora Moulinsii* Benoist, 1874a, and *Cleodora eburnea* Benoist, 1874b (the latter taxon described almost at the same time as his *C. Moulinsii*, but indicated by Benoist himself as synonymous). In Benoist (1889), two further species were introduced, *Cleodora Ortheziana* Benoist, 1889, and *Creseis Aquensis* Benoist, 1889. Together with some species recognised in Aquitaine, but described from elsewhere, *viz.* '*Vaginella Calandrellii* (Michtt.)' and '*Vaginella Austriaca* E. Rittl' ('Rittl' is a *lapsus* for Kittl), Benoist arrived at a total of seven pteropod species for the Aquitaine Basin, considering *H. Orbignii* and *H. aquensis* to be synonymous.

In 1932 Peyrot, describing the pteropods, was not able to add further species and basically referred to the same taxa as Benoist, although he, correctly, arrived at the conclusion that *Hyalaea orbigny* and *H. aquensis* are not synonyms. At that time, pteropod species from the various Eocene and Oligocene deposits were still unknown.

The rich pteropod assemblage from the Ypresian of Gan, referred to by Curry (1965, p. 357) and monographed by Curry (1982), yielded no less than 12 species, seven of them being introduced as new to science. Curry (1982) included furthermore some occurrences of pteropods in the Late Eocene clays of Biarritz, arriving at a total of 14 species. The first three species from Rupelian deposits in southwest France were recorded by Lozouet & Maestrati (1982). A single Lutetian species was documented in Lozouet & Le Renard (2007), and three Chattian species were added by Zorn & Janssen (1993) and Janssen (2008a, b), bringing the total number of species for the Cenozoic of Aquitaine to 29.

In the present paper, the result of a long period of collecting started back in the 1980s and covering material housed in numerous collections, no less than 75 holoplanktonic mollusc species (five supposed Heteropoda, 70 Pteropoda) are recorded from c. 60 localities. All heteropods and 19 pteropods had to be included in open nomenclature or with a query, and 12 pteropod species are described as new to science.

Geological setting (BC)

The Aquitaine Basin, bordered in the south by the mountain chain of the Pyrenees, opens widely towards the Atlantic Ocean and the Bay of Biscay in the west. During the early Tertiary, it was structurally composed of a north Aquitaine platform and a deep southern, pre-Pyrenean trough, these two separated by an intermediate zone.

The north Aquitaine platform shows restricted subsidence. During the Tertiary, neritic sediments built up to a maximum thickness of 600 m. In the south this platform is bordered by a flexure zone called 'celtaquitaine flexure', running from Arcachon to Toulouse.

The southern Aquitaine represents the headland of the northern Pyrenees, a chain of mountains resulting from Paleogene orogeny. This area shows numerous anticlines and diapirs, as well as the frontal northern Pyrenean overlap. At the start of the Tertiary, the north Pyrenean trough was a remnant of a deep Late Cretaceous gulf with deposition of numerous flysch units. In the southern Aquitaine Basin and western (Basque) Pyrenees, the continuous presence of turbidites during Danian times provides evidence for the instability of the southern slope of this trough. During the Paleocene-Eocene, significant marine sedimentation in this trough resulted in a progressive filling up from east to west (Fig. 1). Then, the centre of subsidence, located in this north Pyrenean trough since the early Cenozoic, migrated to the northwest into the Adour basin from the Late Ypresian onwards. Deep (bathyal type) and thick (up to 500 m in boreholes) marly sediments were deposited during the Middle Eocene in this Adour basin, a west-east subsiding trough; the latter was bordered by various platform environments with fossiliferous limestone sequences, often imbricated in very rapidly changing lateral facies.

All over the southern Aquitaine, during the Eocene, facies and palaeobathymetries were variable geographically, according also to the situation with respect to anticlines and synclines which were very active during this epoch.

The south Aquitaine lithostratigraphic framework was revised and detailed by Sztrákóš *et al.* (1998) and others. Eocene rocks in outcrop give evidence of this large diversity of deposits. Localities which yielded pteropods include circalittoral to epibathyal (at Peyrehorade-Trompe, Biarritz-Les Bains) and open neritic palaeoenvironments (at Gan-Tuilerie, Peyrehorade-Arribaouts). The progressive marine filling up of this area and the supply of abundant detrital sediment, originating from erosion of the Pyrenees after each tectonic phase, resulted in a westward progradation of the shoreline and the continental slope-platform boundary during the Tertiary (Nolf *et al.*, 2002; Cahuzac, 1980; Fig. 1).

After a period of relative tectonic inactivity and of important subsidence in the north Pyrenean trough during the Paleocene-Ypresian, the major folding phases of the Pyrenean orogenesis took place in pre-Lutetian and Bartonian times, followed in the Late Rupelian by a new compressive phase, mobilizing allochthonous terrains which overlap northward up to 30 km in the southwestern Aquitaine basin (Fig. 1). These

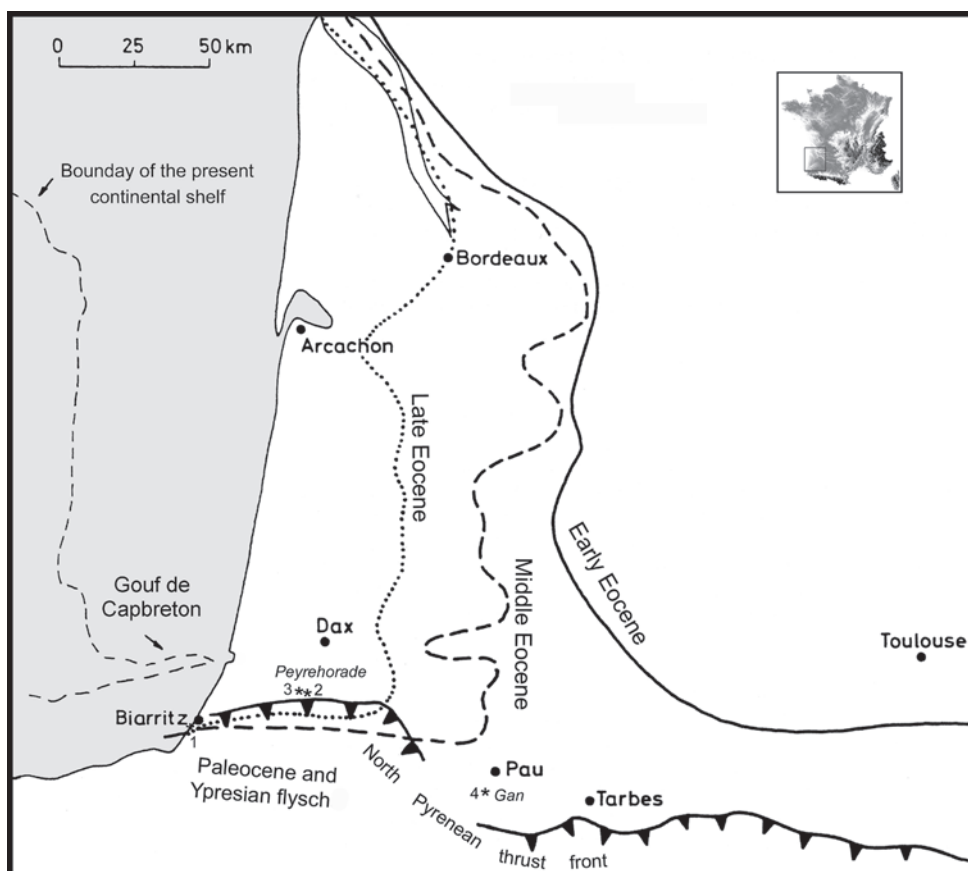


Fig. 1. Schematic palaeogeography of the Aquitaine Basin (shorelines) during the Eocene (modified from Nolf *et al.*, 2002, fig. 2) and location of studied localities (black stars). **Priabonian**: 1. Biarritz ('Marnes des Bains'); 2. Peyrehorade, Arribaouts. **Lutetian**: 3. Peyrehorade, Trompe. **Ypresian**: 4. Gan, Bosdarros and Tuilerie.

Pyrenean tectonics are linked to the Tertiary northward movements of the Iberian plate in relation to the Eurasian plate.

The Rupelian is distinctly transgressive at the scale of the whole basin, the bathyal facies being henceforth restricted to the westernmost margin of the Aquitaine Basin. A tropical climate favoured the growth of coral reefs and the complete northern part of Aquitaine, up to beyond the present Dordogne river eastward (see Fig. 2), is widely overlain by a strongly bioclastic, infralittoral succession, known as the 'Calcaire à Astéries' facies. In the south, shoreline patterns fit closely to the limits of emerged anticlines (for example, in the small gulf of Gaas), sheltered to the west by an alignment of anticlines running from Dax to Peyrehorade (see palaeogeographic map *in* Nolf *et al.*, 2002). Locally, marly sediments very rich in molluscs were laid down in quiet environments.

At about the Rupelian-Chatian transition, an epoch of a strong worldwide eustatic fall, a palaeocanyon was eroded in the Saubrigues-Bélus area (southwest Aquitaine; Fig. 2), with a filling of mainly marly sediments, extending from east to west during the Chatian up to the Langhian (Cahuzac *et al.*, 1995; Nolf *et al.*, 2002; Cahuzac & Poignant, 2004). This structure is the precursor of the present 'Gouf de Capbreton' (= 'Capbreton Deep'), the major submarine canyon in the Bay of Biscay (Fig. 1).

During the Chatian, a transgression developed, well-documented especially in the southern Aquitaine, during which the climate again became tropical. The deposits of this age were recently restudied, and yielded very rich assemblages of foraminifera, ostracods, molluscs, scleractinian corals and bryozoans (see references *in* Cahuzac, 1980; Cahuzac & Poignant, 1988, 2002; Cahuzac & Chaix, 1996; Lozouet, 1997). In the eastern part of the canyon referred to above (east of the Adour river; Fig. 2), which has the shape of a narrow gully, the facies of the marly sediments deepens from east (Bélus, Peyrehorade, with locally reefal environments) to west (Saint-Etienne-d'Orthe, with circalittoral facies). Locally, this deep marly series contains calcareous, sandy, lenticular intercalations rich in organisms from littoral environments (such as larger benthic foraminifera), transported downslope from internal neritic zones along the steep canyon walls. More to the north, in the Saint-Paul-lès-Dax area, the Chatian sea was bordered in the west and the south by two diapirs emerging since the Eocene. The facies represented there are predominantly 'faluns' (= shelly sands) and littoral calcareous sands of peri-reefal environments, with abundant hermatypic corals and molluscs, and with proliferation of larger foraminifera (nummulitids, miogypsinids, lepidocyclinids); small patch-reefs developed in this area. Toward the east (Pontonx area), a rather sheltered gulf with temporarily reduced or changing salinity is characterised by marly deposits rich in fauna. Scleractinian assemblages appear remarkably diversified in the south Aquitaine Chatian, with up to 150 taxa (Cahuzac & Chaix, 1996), and likewise for molluscs and other organisms. This area seems very favourable for the diversification of the neritic faunas.

During the Early Miocene, two important transgressions expanded rather far in an eastern direction, but with environments generally remaining of infralittoral character throughout the area (Fig. 2). The shoreline patterns and the distribution of facies were once more clearly influenced by the previously settled structural frame.

During the Aquitanian, the sedimentation is often enriched by fine-grained clastic elements (clays, marls) and brackish or lagoonal conditions existed in numerous areas. This is the case in the 'classical' series of the Aquitanian stage, described from

Saucats and La Brède. Recently, four main depositional sequences were recognized in this area (Parize *et al.*, 2008), as well as evidence of periods of emersion anticipating the transgressive phases, suggesting possible fluvial erosion. Moreover, several localities yield faluns rich in molluscs and calcareous bioclastic sands of very shallow environments. Coral facies are known from Lariéy (Saucats) and Mainot (Saint-Paul-lès-Dax), outcrops that also yielded pteropods. The Aquitanian stage ended by an obvious regressive phase at the scale of the basin, which is marked by a lacustrine episode well-represented regionally ('Calcaire gris de l'Agenais' Formation). All over the eastern part of the Aquitanian gulf (Agen/Nérac area; Fig. 2), this lacustrine limestone overlies a lagoonal sequence of marls with *Crassostrea aginensis* (Tournouer, 1880).

The Early Burdigalian sea extended further to the east, and the environments are more distinctly marine in character and more open water in setting than during the Aquitanian. The temperatures were subtropical at least, favouring flourishing hermatypic coral communities. Numerous outcrops rich in molluscan assemblages are well-known from the entire Aquitaine Basin. The name of the Burdigalian stage originates from the latin *Burdigala* (= Bordeaux) and the stage was originally described on the basis of the 'faluns de Léognan et de Saucats' (Depéret, 1892; Poignant & Pujol, 1978; Cahuzac *et al.*, 1997, 2003). Many localities of this age yielded pteropods (Table 1a, b, see p. 120-125). Locally, reefal facies originated in turbulent littoral environments, such as at Saucats (Péloua) or Saint-Paul-lès-Dax (Cabanes); 40 coral species could be recognised in each of these sites (Cahuzac & Chaix, 1996). The assemblages are predominantly composed of massive colonies (compared to branched forms), confirming an environment influenced by rather high energy hydrodynamics. Most other pteropod localities represent shelly carbonate sands with a strongly reduced clastic component, related to inner platform environments with abundant endofaunas and epifaunas among molluscs. The tests of these fossils are excellently preserved; no overlying rocks have been present to cause compaction and diagenesis was restricted. Large carnivorous marine Cetacea (*Squalodon*, Odontoceti; Cahuzac *et al.*, 2005) also occurred in this Burdigalian gulf. Toward the east, a new lagoonal deposit sequence occurred in the Agen gulf, again with marls containing *Crassostrea aginensis*.

Late Burdigalian marine deposits are only known from the western Atlantic frontage (evidenced in borehole sections) and from the southwesternmost part of the Aquitaine basin, in the area of the Saubrigues palaeocanyon (Cahuzac & Poignant, 2004). There, a marly sequence filled the trough up to 450 m in thickness ('Marnes de Saubrigues' Formation; examples of localities yielding pteropods are the Saint-Jean-de-Marsacq outcrops). The facies are open neritic, generally indicating quiet environments, with abundant microfaunas and commonly scattered molluscs. From east to west, the bathymetry increased in this area; otherwise, indications derived from the microfauna (such as the presence of siliceous organisms) can be linked to upwelling currents. In general, as far as Aquitaine is concerned, this interval seems to have been plainly regressive compared to the Early Burdigalian time interval.

A new transgression developed during the Langhian, with an extended marine gulf, eastward reaching to Condom (Fig. 2; Cahuzac *et al.*, 1995; Cahuzac & Poignant, 2000, 2002, 2004). Facies are infralittoral everywhere in this central Aquitaine gulf, rich in malacofaunas in calcareous sandy rocks and coastal faluns; some subreefal

facies developed as well, such as in the area of Manciet, south of the Barbotan-les-Thermes anticline (d in Fig. 2). In the eastern part of this gulf, periods of reduced salinity occurred and marly deposits with lagoonal oysters existed locally. In the northwestern part of the Saubrigues palaeocanyon, the environments remained open

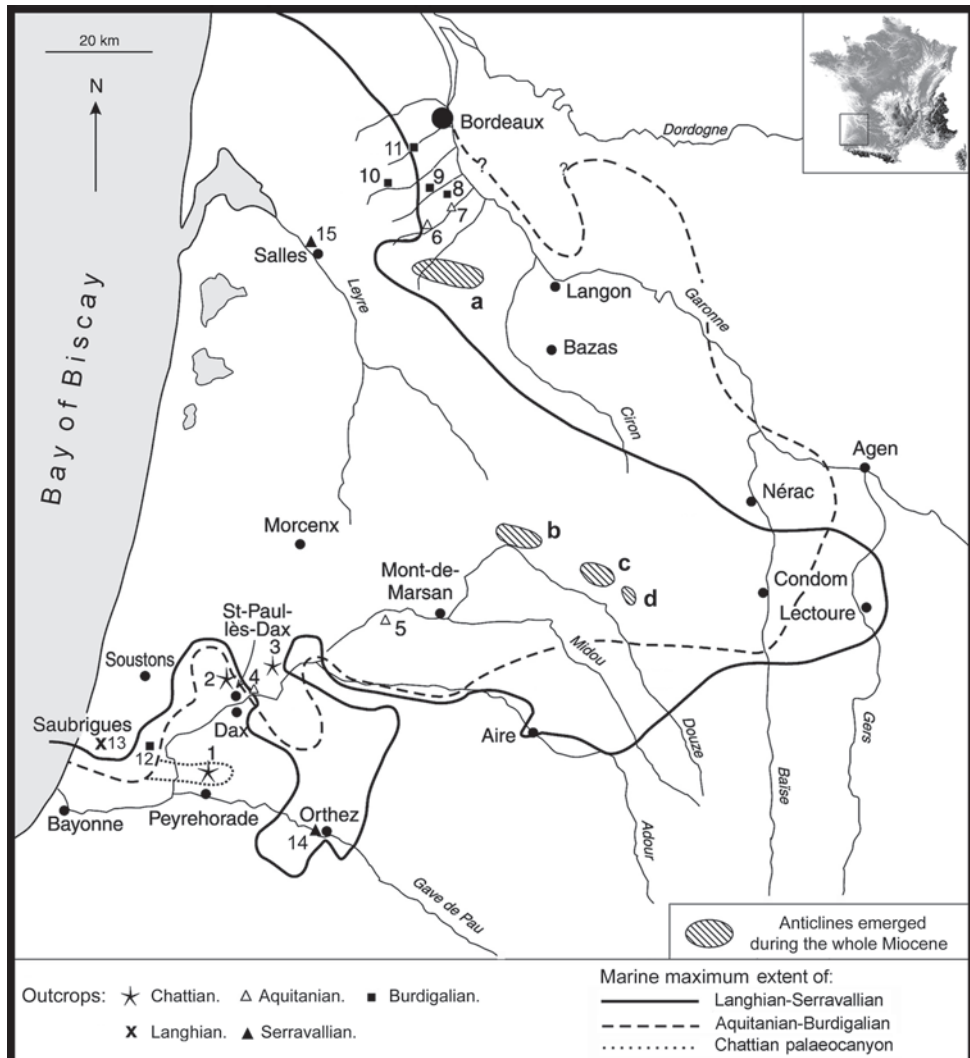


Fig. 2. Schematic palaeogeography of the Aquitaine Basin during the Miocene and Chattian (modified from Cahuzac *et al.*, 1995, figs. 4, 5; Cahuzac & Poignant, 2004, fig. 1) and location of some important localities. Outcrops: **Chattian**: 1. Peyrehorade, Peyrère; 2. Saint-Paul-lès-Dax, Abesse; 3. Pontonx, Mineur-A. **Aquitanian**: 4. Saint-Paul-lès-Dax, Le Mainot; 5. Meilhan, Carrière Vives; 6. Saucats, Lariey; 7. La Brède. **Burdigalian**: 8. Martillac, Barreau-1; 9. Léognan, Le Coquillat; 10. Cestas, Pré-Cazeaux; 11. Pessac, Lorient; 12. Saint-Jean-de-Marsacq, Lahitet and Pinot. **Langhian**: 13. Saubrigues, Les Tauziets. **Serravallian**: 14. Orthez, Le Paren; 15. Salles, Moulin Ruiné ('Debat Moulin'). Mesozoic emerged anticlines: a. Villagrains-Landiras; b. Roquefort-des-Landes; c. Créon-d'Armagnac; d. Barbotan-les-Thermes.

marine, demonstrating infra- to circalittoral facies of marls with rich microbenthos and few molluscs (Ducasse & Cahuzac, 1996), as at Saubrigues-Tauziets and Saubrigues-Jean Tic. The filling up of the canyon came to an end with the Langhian deposits.

During the Serravallian, a vast transgression spread far eastward, unto the eastern Aquitaine basin, where the so-called 'Golfe de l'Armagnac' developed (Condom and Lectoure area; Cahuzac *et al.*, 1995; Cahuzac & Poignant, 1996; Ducasse & Cahuzac, 1997; Fig. 2 herein). In the south of the basin, another marine gulf extended southward into the Orthez and Salies-de-Béarn area, the sea being transgressive in a synclinal zone situated between several anticlinal/diapiric structures, previously eroded. There, the marine domain is clearly more extensive than in both the Burdigalian and Langhian; faluns and shelly marls were deposited in infralittoral euhaline facies (as at Orthez, Le Paren, locality with pteropods), and algal rhodolith-rich levels occur locally. In northern Aquitaine, marine Serravallian rocks are well known in the Salles area, located on the western periclinal of the Villagrains-Landiras anticline (Fig. 2), where alternating faluns and calcareous sands are rich in molluscs, predominantly bivalves. The malacofauna of this area is comprised of more than 370 taxa. For instance, in the Salles-Moulin Debat section (with pteropods), the three most common palaeobiofacies are medium- to coarse-grained calcareous sands with large *Gigantopecten gallicus* (Mayer, 1864) and *Glycymeris bimaculata* (Poli, 1795); medium-grained sands with *Flabellipecten vasatensis* (Benoist in Cossmann & Peyrot, 1914), *Glycymeris* spp., *Astarte* and *Clausinella*; and a *Spisula-Megacardita-Nassarius* facies of an infralittoral sandy euhaline environment with many endofaunal bivalves and carnivorous gastropods (Folliot *et al.*, 1993). Globally, the Aquitaine Serravallian climate was still warm, but clearly less so than previously and hermatypic corals disappeared regionally; the whole Serravallian fauna gives evidence of a warm temperate to subtropical climate. In the eastern 'Golfe de l'Armagnac', the Formation of 'Sables fauves marins' developed widely, consisting of fawn-coloured ferruginous detrital sands, often coarse-grained, in a very shallow environment, with clypeasteroids such as *Amphiope bioculata* (Des Moulins, 1837) and *Parascutella faujasii* (Defrance, 1827), and balanids. Locally, brackish or lagoonal facies occurred, marked by levels with *Crassostrea gryphoides* (Schlotheim, 1813). After this ultimate marine episode, all the central and eastern Aquitaine basin finally emerged.

Localities

Holoplanktonic mollusc material was studied from a large number of localities, enumerated below. For each locality, as far as known, the topographical position (coordinates), the chrono- and lithostratigraphy, biostratigraphy with important literature references and possible further details are given. In the systematic part, these localities are mentioned with the short-cut given here in **bold**.

In the marine Aquitaine Cenozoic deposits, sedimentary rocks are commonly unconsolidated. They are soft and crumbly outcropping sediments, never deeply buried nor submitted to strong diagenesis, which pass easily through a sieve during processing. We indicate them as sand or marl, instead of sandstone or marlstone.

Biozones referred to are P (Paleogene) and N (Neogene) = planktonic foraminifera; NP and NN = nannoplankton; and SBZ = Shallow Benthic Foraminifera Zones (Cahuzac & Pognant, 1997; Serra-Kiel *et al.*, 1998). Lamb. = Lambert zone III (geographic coordinates). Coordinates in ED50 system, related to Greenwich meridian, are added between brackets. Sr estimated ages indicated below have been adjusted to the 'GTS 2004' = 'Global Time Scale 2004' (Gradstein *et al.*, 2004).

Bélus (Marcon) - Bélus (Landes department; Fig. 4), Marcon, sometimes also indicated as 'Marcon (Sas)' in collections. Lamb. III: x = 320.125, y = 3148.450 (1° 7' 43.5" W, 43° 35' 2.4" N), Chattian, grey to yellowish marl. Circalittoral facies.

Biarritz - Biarritz (Pyrénées-Atlantiques department; Fig. 4), locality referred to in Curry (1982). Late Eocene, marls near 'Établissement des Bains', Marnes des Bains Member, Marnes de la Côte des Basques Formation, greyish-blue marls with microbenthos, bryozoans, echinoids and crinoids. According to their label, some specimens were collected from foreshore gravels. The Marnes des Bains Member is Priabonian (NP19-20 zones *in* Mathelin & Sztrákos, 1993), depositional sequence E18 (Sztrákos *et al.*, 1998). The rich association of foraminifera (*c.* 400 taxa) indicates epibathyal-circalittoral depths, decreasing slightly towards the top of the series (Mathelin & Sztrákos, 1993).

Bordeaux - Bordeaux (Gironde department), probably Early Miocene, without any possible precision (older collections).

Canéjan (Bouscaut) - Canéjan (Gironde department; Fig. 3), Haut Bouscaut (also named 'Haut-Bouscat' on topographic maps), Lamb. III: x = 364.110, y = 3277.850 (0° 38' 32.8" W, 44° 45' 47.7" N). Early Burdigalian, fine yellow calcareous sands with some molluscs. Infralittoral facies.

Cestas (Fourcq) - Cestas (Gironde department; Fig. 3), Fourcq inférieur, Lamb. III: *c.* x = 360.960, y = 3277.040 (0° 40' 54.6" W, 44° 45' 17.7" N). Early Burdigalian, yellow calcareous sands with molluscs. Infralittoral facies.

Cestas (Cazeaux) - Cestas (Gironde department; Fig. 3), Pré-Cazeaux, Lamb. III: x = 360.430, y = 3275.575 (0° 41' 16.3" W, 44° 44' 29.7" N). Early Burdigalian, yellow calcareous sands with molluscs. N5 and NN2 zones (Müller & Pujol, 1979; Pognant & Pujol, 1978) and lower SBZ25 zone, Sr age 18.4 Ma according to 'GTS 2004' (18.9 Ma *in* Cahuzac & Turpin, 1999). Infralittoral facies.

Corbleu (Carro) - Corbleu (Landes department; Fig. 4), Moulin de Carro (also named 'Carreau'), Lamb. III: x = 380.835, y = 3193.250 (0° 23' 45.1" W, 44° 0' 27.1" N). Earliest Burdigalian, Faluns de Saint-Avit Formation, faluns and beige orange calcareous sands, uncommonly with coarse-grained detritus, rich in corals and molluscs. High energy, littoral facies.

Gaas (Espibos) - Gaas (Landes department; Fig. 4), Espibos, Lamb. III: x = 326.275, y = 3151.850 (1° 3' 15.8" W, 43° 37' 0.8" N). Rupelian, shelly grey marls and calcareous

sands; section described in Janssen (1985a), some samples refer to bed numbers in that paper. SBZ21 zone (larger foraminifera; Cahuzac & Poignant, 1997) and Sr estimated age 31.6 Ma. Infralittoral facies.

Gaas (Lagouarde) - Gaas (Landes department; Fig. 4), Lagouarde, Lamb. III: $x = 326.300$, $y = 3151.400$ ($1^{\circ} 3' 13.9''$ W, $43^{\circ} 36' 46.2''$ N). Rupelian, shelly marls. SBZ21 zone. Infralittoral facies.

Gan (Bosdarros) - Gan (Pyrénées-Atlantiques department; Fig. 4), 1.25 km north of Bosdarros, along road D24, ditch on north-side of the road, just east of entry to Esquilot, Lamb. III: $x = 380.725$, $y = 3106.125$ ($0^{\circ} 21' 41.8''$ W, $43^{\circ} 13' 25.4''$ N). Late Ypresian, Marnes de Gan Formation. Zone NP13 (*in* Nolf *et al.*, 2002), here rich in nummulites, small molluscs and fish otoliths. The mollusc fauna (more than 100 taxa) from this locality was described by Rouault (1850). Coastal facies.

Gan (Tuilerie) - Gan (Pyrénées-Atlantiques department; Fig. 4), former clay pit of tileworks Lartigue & Dumas ('Tuilerie de Gan'), Lamb. III: outcrops around the point $x = 378.100$, $y = 3107.200$ ($0^{\circ} 23' 39.6''$ W, $43^{\circ} 13' 57.4''$ N). Middle-Late Ypresian, Marnes de Gan Formation, greyish-blue marls and clays, locally a little sandy. Top NP 12 and NP 13 (Nolf *et al.*, 2002, pp. 185-186), SBZ10 (Serra-Kiel *et al.*, 1998), depositional sequence E8 (Sztrákos *et al.*, 1998). A rich mollusc fauna was described by Cossmann (1923) and pteropods by Curry (1982). In a detailed study, Merle (1986) concluded that the lower part of the section demonstrates a circalittoral, quiet environment, whereas the upper part represents inner neritic environments. In the lower part, rich in molluscs, no fewer than 440 species of macrofauna are listed by Merle; the fish otolith (Nolf *et al.*, 2002) and ostracod (Yassini, 1969) assemblages included both deep neritic taxa and infralittoral taxa.

La Brède - La Brède (Gironde department; Fig. 3), sampled by J. Gunst, July 1982, probably at 'route de Saint-Morillon', in ditch along the D220 road, 750 m southwest of La Brède, probably at Lamb. III: $c. x = 372.770$ to 372.780 , $y = 3267.680$ to 3267.780 ($0^{\circ} 31' 43.2''$ to $0^{\circ} 31' 42.9''$ W, $44^{\circ} 40' 28.4''$ to $44^{\circ} 40' 31.6''$ N). Aquitanian, yellow shelly sands. N4 and SBZ24 zones. Littoral facies.

La Brède (Moras) - La Brède (Gironde department; Fig. 3), Moras (also named 'Brousteyrot-supérieur', sometimes 'Courtan'), in streambed of 'Le Brousteyrot' brook, Lamb. III: $x = 369.700$, $y = 3269.085$ ($0^{\circ} 34' 4.7''$ W, $44^{\circ} 41' 10.4''$ N). Early Burdigalian, Faluns de Léognan Formation, upper part of exposed section, just above a pale grey lacustrine limestone of top Aquitanian; orange-yellow faluns with turritellids and *Glycymeris*, few hermatypic scleractinian corals. N5 and NN2 zones, Sr age 19.6 Ma according to 'GTS 2004' (20.3 Ma *in* Cahuzac & Turpin, 1999).

Léognan - Léognan (Gironde department), without possible precision of outcrop, probably Early Burdigalian (older collections).

Léognan (Bougès) - Léognan (Gironde department; Fig. 3), Les Bougès, Lamb. III: $x = 365.850$, $y = 3272.360$ ($0^{\circ} 37' 4.8''$ W, $44^{\circ} 42' 51.9''$ N). Early Burdigalian, Faluns de

Léognan Formation, shelly grey-blue calcareous fine-grained sands. N5 zone (Poignant & Pujol, 1978) and lower SBZ25 zone. Infralittoral facies.

Léognan (Château de France) - Léognan (Gironde department; Fig. 3), Château de France, Lamb. III: $x = 366.660$, $y = 3272.885$ ($0^{\circ} 36' 28.9''$ W, $44^{\circ} 43' 9.9''$ N), Early Burdigalian, Faluns de Léognan Formation, orange falun with turritellids. Lower SBZ25 zone.

Léognan (Coquillat) - Léognan (Gironde department; Fig. 3), Le Coquillat (or 'Bois de Coquillat'), several outcrops in the area of Lamb. III: $x = 366.600$, $y = 3272.700$ to 3273.050 ($0^{\circ} 36' 31.3''$ W, $44^{\circ} 43' 3.8''$ to $44^{\circ} 43' 15.2''$ N). Early Burdigalian, Faluns de Léognan Formation, yellowish sandy falun. N5 zone (Poignant & Pujol, 1978) and lower SBZ25 zone. Infralittoral facies. The 'classic' Coquillat section quoted in older literature was located c. 250 m to the northeast, near Coquillat mill, in an area not accessible now.

Léognan (Thibaudeau) - Léognan (Gironde department; Fig. 3), Thibaudeau, Lamb. III: $x = 367.225$, $y = 3273.650$ (from Steurbaut, 1984) ($0^{\circ} 36' 4.5''$ W, $44^{\circ} 43' 35.3''$ N). Earliest Burdigalian, fine yellowish calcareous shelly sands.

Marcon (Sas), Chattian, same as Bélus (Marcon), see above.

Martillac (Barreau) - Martillac (Gironde department; Fig. 3), Barreau-1, outcrop in streambed of 'Le Martillac' brook, also commonly named 'Pas-de-Barrau' or 'Pas-de-Barreau', Lamb. III: $x = 369.250$, $y = 3271.250$ ($0^{\circ} 34' 28.6''$ W, $44^{\circ} 42' 19.9''$ N). Early Burdigalian, grey calcareous sands, very shelly ('falun') with turritellids. N5 and lower SBZ25 zones (cf. Cahuzac *et al.*, 2005). Infralittoral, euhaline, subtropical environment.

Martillac (vigne) - Martillac (Gironde department; Fig. 3), 'classic' outcrop in the vineyard, also indicated as 'La Gravette', Lamb. III: $x = 369.630$, $y = 3271.580$ ($0^{\circ} 34' 11.9''$ W, $44^{\circ} 42' 31.1''$ N). Early Burdigalian, yellow to orange calcareous sands, 'falun' with *Glycymeris*, *Cardium*, turritellids, very shelly. N5 and lower SBZ25 zones. Infralittoral, subtropical environment.

Meilhan (Vives) - Meilhan (Landes department; Fig. 4), Carrière Vives, sometimes indicated as Saint-Martin-d'Oney, coordinates Lamb. III: $x = 359.100$, $y = 3182.800$ ($0^{\circ} 39' 43.1''$ W, $43^{\circ} 54' 24.2''$ N). Late Aquitanian, marly sands with scleractinian corals and coarse-grained detritus (level 5 in Lozouet *et al.*, 2001). N4 and SBZ24 zones (Cahuzac & Gautret, 1993; Cahuzac & Poignant, 1997), Sr age 21.1 Ma (Cahuzac & Turpin, 1999). Reefal facies. Sediment from the interior of several hundreds of large specimens of *Globularia compressa* (de Basterot, 1825) (collected 2006/2007, made available by Stef Mermuijs and Henk Mulder) was extracted for a specific search for holoplanktonic molluscs. The result, however, was poor: just a few specimens and fragments of *Vaginella depressa* were found in fractions > 1 mm. Specific weight separation of finer fractions in carbon tetrachloride yielded many juvenile *Vaginella depressa* and *Heliconoides inflata?*, and also a number of *Creseis roesti* sp. nov.

Mérignac - Mérignac (Gironde department), Miocene, probably Early Burdigalian (older collections).

Mérignac (couche 6) - Mérignac (Gironde department), 'couche nr. 6 Tournouer', 'mollasse marine' overlying lacustrine levels (Tournouer, 1862). Probably Early Burdigalian (older collections).

Mérignac (Pontic) - Mérignac (Gironde department; Fig. 3), Pontic, in streambed of 'Les Ontines' brook, Lamb. III: $c. x = 363.980, y = 3284.490$ ($0^{\circ} 38' 49.7''$ W, $44^{\circ} 49' 22.5''$ N). Early Burdigalian, levels locally named 'faluns mixtes', probably upper part of the outcropping section, yellowish-beige shelly calcareous sands (Drooger *et al.*, 1955) (older collections).

Orthevielle (Tauzia) - Orthevielle (Landes department; Fig. 4), northeast of Tauzia, Lamb. III: $x = 320.300, y = 3147.500$ ($1^{\circ} 7' 33.9''$ W, $43^{\circ} 34' 31.9''$ N). Chattian, grey marls (upper part).

Orthez (Le Paren) - Orthez (Pyrénées-Atlantiques department; Fig. 4), Le Paren, Lamb. III: $x = 352.400, y = 3137.650$ ($0^{\circ} 43' 27.9''$ W, $43^{\circ} 29' 54.2''$ N). Serravallian, grey shelly sands. NN6-7 zones (Steurbaut, 1984; Cahuzac *et al.*, 1995; Cahuzac & Poignant, 1996; Ducasse & Cahuzac, 1997), Sr age from outcrops in this area: $c. 12-12.8$ Ma. Open marine, infralittoral environment.

Pessac (Lorient) - Pessac (Gironde department; Fig. 3), Lorient, near the 'Le Peugue' stream (locality also named 'Pont de Lorient'), Lamb. III: $c. x = 363.720, y = 3283.630$ ($0^{\circ} 39' 0.1''$ W, $44^{\circ} 48' 54.3''$ N). Early Burdigalian, yellow shelly sands, probably upper part of the section (levels locally named 'faluns mixtes'; Drooger *et al.*, 1955) (older collections).

Peyrehorade (Arribaouts) - Peyrehorade (Landes department; Fig. 4), Ruisseau d'Arribaouts, Lamb. III: $x = 322.000$ to $322.250, y = 3145.600$ (*in* Nolf, 1988) ($1^{\circ} 6' 14.7''$ to $1^{\circ} 6' 3.6''$ W, $43^{\circ} 33' 32.7''$ N). Late Eocene, Priabonian, grey marls. Deep neritic facies.

Peyrehorade (Peyrère) - Peyrehorade (Landes department; Fig. 4), abandoned marl pit at Peyrère, Lamb. III: $x = 322.400, y = 3147.050$ ($1^{\circ} 5' 59.6''$ W, $43^{\circ} 34' 20.2''$ N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls with *Eulepidina*, and some molluscs and corals. Samples collected *ex situ* from sediment dump.

Peyrehorade (Tauziède) - Peyrehorade (Landes department; Fig. 4), Tauziède-A (sometimes indicated as Cagnotte, Tauziède), Lamb. III: $x = 323.000, y = 3148.150$ ($1^{\circ} 5' 34.9''$ W, $43^{\circ} 34' 56.6''$ N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, greyish-blue marls. NP25 and P22 zones (Müller & Pujol, 1979; Cahuzac, 1980). Circalittoral facies.

Peyrehorade (Trompe) - Peyrehorade (Landes department; Fig. 4), Trompe, Lamb. III: $x = 321.500, y = 3145.840$ ($1^{\circ} 6' 37.4''$ W, $43^{\circ} 33' 39.8''$ N). Middle Eocene, Lutetian, grey

marls. NP15 zone (Sturbaut *in* Lozouet & Le Renard, 2007). Epibathyal to circalittoral facies.

Pontoux (Mineur) - Pontoux (Landes department; Fig. 4), Mineur-A, Lamb. III: x = 334.150 y = 3167.975 (0° 57' 53.7'' W, 43° 45' 53.2'' N). Chattian, pale grey shelly sands with *Strombus*. P22 and SBZ23 zones (Cahuzac, 1980). Shallow littoral facies, with some brackish influences (euryhaline organisms present).

Saint-Etienne-d'Orthe (Casenave) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Casenave, outcrop in Ruisseau de l'Église, Lamb. III: x = 316.750, y = 3149.350 (1° 10' 15.5'' W, 43° 35' 26.9'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls. Circalittoral facies.

Saint-Etienne-d'Orthe (Église A) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Ruisseau de l'Église A, northeast of the bridge, Lamb. III: x = 316.060, y = 3149.380 (*in* Lozouet, 1997) (1° 10' 46.3'' W, 43° 35' 26.9'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls. NP25 and P22 zones (Müller & Pujol, 1979; Cahuzac, 1980; Cahuzac *et al.*, 1995), SBZ23 zone (Cahuzac & Poignant, 2002). Circalittoral facies.

Saint-Etienne-d'Orthe (Église B) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Ruisseau de l'Église B, southeast of the bridge, Lamb. III: x = 316.380, y = 3149.150 (*in* Lozouet, 1997) (1° 10' 31.6'' W, 43° 35' 19.9'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls. NP25 and P22 zones (Müller & Pujol, 1979; Cahuzac, 1980; Cahuzac *et al.*, 1995), SBZ23 zone (Cahuzac & Poignant, 2002), Sr estimated age *c.* 25.3 Ma. Circalittoral facies.

Saint-Etienne-d'Orthe (Église C) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Ruisseau de l'Église C, Lamb. III: x = 316.400, y = 3149.200 (*in* Lozouet, 1997) (1° 10' 30.8'' W, 43° 35' 21.6'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls. NP25 and P22 zones (Müller & Pujol, 1979; Cahuzac, 1980; Cahuzac *et al.*, 1995), SBZ23 zone (Cahuzac & Poignant, 2002). Circalittoral facies.

Saint-Etienne-d'Orthe (Hondelatte) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Hondelatte, outcrop in brook near a small former barrage, Lamb. III: x = 317.500, y = 3148.850 (1° 9' 41.2'' W, 43° 35' 11.7'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marl. NP25 and P22 zones (Cahuzac, 1980; Cahuzac *et al.*, 1995), SBZ23 zone. Circalittoral facies.

Saint-Etienne-d'Orthe (Lartigaou) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), outcrop in Ruisseau de l'Église, east of Lartigaou, Lamb. III: x = 316.400, y = 149.800 (1° 10' 31.9'' W, 43° 35' 40.9'' N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marls. Circalittoral facies.

Saint-Etienne-d'Orthe (Lestelle) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Lestelle-A, marl pit alongside the road, also referred to as 'Lesteules', Lamb. III: x = 316.000, y = 3148.750 (1° 10' 47.8'' W, 43° 35' 6.4'' N). Chattian, Marnes de Saint-Etienne-

d'Orthe Formation, grey marls. NP25 zone (Cahuzac *et al.*, 1995), SBZ23 zone. Circalittoral facies.

Saint-Etienne-d'Orthe (Verdun) - Saint-Etienne-d'Orthe (Landes department; Fig. 4), Ruisseau de Verdun, Lamb. III: $x = 316.200$, $y = 3148.600$ ($1^{\circ} 10' 38.6''$ W, $43^{\circ} 35' 1.9''$ N). Chattian, Marnes de Saint-Etienne-d'Orthe Formation, grey marl and sandy detritic bed. P22 zone. Circalittoral facies.

Saint-Jean-de-Marsacq (Lahitet-1) - Saint-Jean-de-Marsacq (Landes department; Fig. 4), Lahitet-1 (also named 'Le Bragas'), Lamb. III: $x = 310.250$, $y = 3150.750$ (*in* Lozouet, 1997) ($1^{\circ} 15' 7.7''$ W, $43^{\circ} 36' 3.1''$ N). Late Burdigalian, greyish-orange thin sandy level. NN4 and N6 *pars*-N7 zones (Cahuzac *et al.*, 1995; Cahuzac & Poignant, 2004). Littoral facies.

Saint-Jean-de-Marsacq (Lahitet-2) - Saint-Jean-de-Marsacq (Landes department; Fig. 4), Lahitet-2 (also named 'Le Bragas'), Lamb. III: $x = 310.250$, $y = 3150.750$ (*in* Lozouet, 1997) ($1^{\circ} 15' 7.7''$ W, $43^{\circ} 36' 3.1''$ N). Late Burdigalian, Marnes de Saubrigues Formation, lower level, grey marl with microbenthos. NN4 and N6 *pars*-N7 zones (Cahuzac *et al.*, 1995; Cahuzac & Poignant, 2004), Sr age 17.4 Ma data adjusted to 'GTS 2004' - (17.7 Ma *in* Cahuzac *et al.*, 1997). Open infralittoral to circalittoral facies.

Saint-Jean-de-Marsacq (Pinot) - Saint-Jean-de-Marsacq (Landes department; Fig. 4), Pinot, 'grande marnière abandonnée' (= large abandoned marl pit), Lamb. III: $x = 309.500$, $y = 3151.0875$ ($1^{\circ} 15' 41.8''$ W, $43^{\circ} 36' 13''$ N). Late Burdigalian, Marnes de Saubrigues Formation, grey marls with microbenthos (base of section). NN3-4 and N6 *pars*-N7 zones (Cahuzac *et al.*, 1995; Cahuzac & Poignant, 2004), Sr age 17.3 Ma - data adjusted to 'GTS 2004' - (17.7 Ma *in* Cahuzac & Turpin, 1999). Open marine facies of base of infralittoral zone (Nolf *et al.*, 2002).

Saint-Martin-de-Hinx (Secat) - Saint-Martin-de-Hinx (Landes department; Fig. 4), Secat near Lanot, also named Lanot, abandoned marl pit of Mr D. Jaureguy, see Janssen (1985a), Lamb. III: $x = 309.350$, $y = 3149.750$ ($1^{\circ} 15' 45.9''$ W, $43^{\circ} 35' 29.5''$ N). Possibly Langhian (mainly from the pteropod assemblage therein), Marnes de Saubrigues Formation, sandy grey marls with rich assemblage of predominantly small molluscs, *Mitrella nassoides* (Grateloup, 1827) and rare *Genota ramosa* (de Basterot, 1825), of infralittoral to circalittoral environment (Steurbaut, 1984; Cahuzac & Poignant, 2004). This outcrop was assigned to the Late Burdigalian by Cahuzac & Poignant (2004) (locality named 'Sécat Jaureguy') and by Lozouet (1997). NN4 zone (*in* Cahuzac *et al.*, 1995). Probably the age is close to the Burdigalian-Langhian transition, probably in earliest Langhian as far as pteropods are concerned. Some specimens in MNHN from the P. Lozouet collection have slightly different coordinates ($309.250/3149.800$, or $1^{\circ} 15' 50.4''$ W, $43^{\circ} 35' 30.9''$ N), which most probably refer to the same outcrop or, at least, to the same abandoned marl pit.

Saint-Médard (Gajac) - Saint-Médard-en-Jalles (Gironde department), Gajac, Early Burdigalian (older collections).

Saint-Paul-lès-Dax (Abesse) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Abesse (Château), on right bank of Poustagnac (= Abesse) river (also named 'Ruisseau d'Abesse'), Lamb. III: $x = 323.760$, $y = 3166.800$ ($1^{\circ} 5' 35.7''$ W, $43^{\circ} 45' 1.4''$ N). Chattian, faluns and grey shelly sands. P22, NP25 and SBZ23 zones (Cahuzac *et al.*, 1995; Cahuzac & Poignant, 1988, 1997), Sr age 23.4 Ma with 'GTS 2004' (24.6 Ma *in* Cahuzac *et al.*, 1997). Reefal littoral facies.

Saint-Paul-lès-Dax (Abesse-B) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Abesse-B, Lamb. III: $x = 324.125$, $y = 3166.750$ ($1^{\circ} 5' 19.3''$ W, $43^{\circ} 45' 0.3''$ N). Chattian, grey beige sands. SBZ23 zone.

Saint-Paul-lès-Dax (Bezoye) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Bezoye, Lamb. III: $x = 323.100$, $y = 3166.850$ ($1^{\circ} 6' 5.3''$ W, $43^{\circ} 45' 2.1''$ N). Chattian, faluns with corals and grey-blue shelly coars-grained sands, locally indurated as sandstones. SBZ23 zone. Reefal coastal facies.

Saint-Paul-lès-Dax (Cabanes) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Cabanes (also named 'Moulin de Cabanes' or 'Cabannes'), Lamb. III: $x = 328.335$, $y = 3164.600$ ($1^{\circ} 2' 7.3''$ W, $43^{\circ} 43' 56.3''$ N). Basal Burdigalian, reefal and shelly coarse-grained sands. N5 and lower SBZ25 zones. Coastal facies.

Saint-Paul-lès-Dax (Estoti) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Estoti, Lamb. III: $x = 324.260$, $y = 3166.450$ to 3166.475 ($1^{\circ} 5' 12.7''$ W, $43^{\circ} 44' 50.8''$ to $43^{\circ} 44' 51.6''$ N). Chattian, yellow-orange, shelly, calcareous sands or faluns, with hermatypic corals. P22 and SBZ23 zones (Cahuzac, 1980; Cahuzac & Poignant, 1988, 1997).

Saint-Paul-lès-Dax (Lestrilles) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Lestrilles, Lamb. III: $x = 324.050$, $y = 3163.600$ ($1^{\circ} 5' 16.8''$ W, $43^{\circ} 45' 18.2''$ N). Chattian, yellow, shelly calcareous sands, with larger foraminifera. SBZ23 zone.

Saint-Paul-lès-Dax (Mainot) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Le Mainot (also named 'Maïnot' or 'Maynot'), Lamb. III: $x = 328.400$, $y = 3164.050$ ($1^{\circ} 2' 3.4''$ W, $43^{\circ} 43' 38.6''$ N). Aquitanian, yellow-orange coral faluns and shelly sands. N4 and SBZ24 zones. Infralittoral facies.

Saint-Paul-lès-Dax (Mandillot) - Saint-Paul-lès-Dax (Landes department; Fig. 4), Mandillot, Lamb. III: $x = 327.950$, $y = 3165.250$ ($1^{\circ} 2' 25.7''$ W, $43^{\circ} 44' 16.8''$ N). Burdigalian, yellow-orange, coarse-grained shelly sands. N5-6 and SBZ25 zones (Cahuzac, 1980). Coastal facies.

Salles - Salles (Gironde department), without any precision. Serravallian (older collections).

Salles (Moulin Ruiné) - Salles (Gironde department; Fig. 3), Moulin Ruiné ('Debat Moulin'), Lamb. III: $x = 344.900$ to 345.350 , $y = 3257.310$ to 3257.400 ($0^{\circ} 52' 29.2''$ to $0^{\circ} 52' 9''$ W, $44^{\circ} 34' 19.3''$ to $43^{\circ} 34' 22.8''$ N). Serravallian, former local stage 'Sallomacien'

(from *Sallomacus* = latin name of Salles), along the small valley and in streambed of Dubern brook, upper level with *Flabellipecten vasatensis* (Benoist in Cossmann & Peyrot, 1914), reddish shelly sands. NN6-7 and c. N11-13 zones (Müller & Pujol, 1979; Folliot *et al.*, 1993; Cahuzac *et al.*, 1995), Sr ages from the Salles area c. 11-12.4 Ma (cf. Cahuzac & Turpin, 1999). Infralittoral environment.

Salles (Larieux) - Salles (Gironde department; Fig. 3), Moulin Ruiné ('Debat Moulin'), western part (Larieux, also named 'Larrieu' on topographic maps), Lamb. III: x = 344.720, y = 3257.290 (0° 52' 37.4" W, 44° 34' 18.4" N). Serravallian, collected by F.A.D. van Nieulande, downstream from the 'Debat Moulin' outcrop cited above (Salles 'Moulin Ruiné'), in streambed of Dubern brook, shelly sands.

Saubrigues (Jean Tic) - Saubrigues (Landes department; Fig. 4), Jean Tic, Lamb. III: x = 305.700, y = 3152.125 (1° 18' 33.1" W, 43° 36' 41.2" N). Langhian, Marnes de Saubrigues Formation, grey marls with microbenthos and few molluscs. N8-N9 *pars* and NN5 zones (Cahuzac *et al.*, 1995; Ducasse & Cahuzac, 1996; Cahuzac & Poignant, 2000). A nearby synchronous outcrop (at Lafaurie) yielded a Sr age of 15.6 Ma with 'GTS 2004'. Open infralittoral to circalittoral facies.

Saubrigues (Tauziets) - Saubrigues (Landes department; Fig. 4), Les Tauziets, Lamb. III: x = 306.550, y = 3151.050 (1° 17' 53.2" W, 43° 36' 7.6" N). Langhian, Marnes de Saubrigues Formation, dark grey, slightly sandy marl with microbenthos. N8-N9 *pars* and NN5 zones (Szöts, 1968; Cahuzac *et al.*, 1995; Ducasse & Cahuzac, 1996; Cahuzac & Poignant, 2000). Lower infralittoral to circalittoral facies.

Saucats (Coquillière) - Saucats (Gironde department; Fig. 3), La Coquillière (also named 'Coquilleyre'), Lamb. III: x = 367.500, y = 3264.750 to 3265.300 (0° 35' 37.6" W, 44° 38' 47.5" to 44° 39' 5.3" N). Early Burdigalian, yellow shelly sands. N5, NN2 and lower SBZ25 zones. Some of the samples are from levels B 1-2 and A 1-4, as given in Janssen (1985a, p. 89). Infralittoral facies.

Saucats (Église) - Saucats (Gironde department; Fig. 3), Moulin de l'Église (same area as 'Giraudot' or 'Girardeau' in literature; see Drooger *et al.*, 1955; Poignant & Pujol, 1978), Lamb. III: c. x = 369.240, y = 3266.250 (0° 34' 21.1" W, 44° 39' 38.1" N). Early Burdigalian, shelly, orange calcareous sands, probably upper part of the section (above the uppermost Aquitanian lacustrine limestone). Infralittoral facies (older collections).

Saucats (Gieux) - Saucats (Gironde department; Fig. 3), Gieux (also named 'Gieu' on topographic maps), outcrop along the 'Le Saucats' river, upstream (and westward) from 'Moulin de l'Église', locality nr. 30 in Drooger *et al.* (1955), Lamb. III: c. x = 368.515, y = 3265.470 (0° 34' 52.7" W, 44° 39' 11.9" N) (older collections). Early Burdigalian, grey-blue shelly sands. N5 and lower SBZ25 zones. Infralittoral facies.

Saucats (La Cassagne) - Saucats (Gironde department; Fig. 3), La Cassagne (name of a house situated a little upstream from the 'Moulin de l'Église' locality, between the latter and Gieux), in left bank and above the small valley of 'Le Saucats' river. Early Burdigalian (older collections).

Saucats (Lagus) - Saucats (Gironde department; Fig. 3), Lagus (or 'Moulin de Lagus'), in streambed of 'Le Saucats' river, a little upstream (and westward) from 'Gieux', Lamb. III: $x = 368.138$, $y = 3265.260$ ($0^{\circ} 35' 9.5''$ W, $44^{\circ} 39' 4.7''$ N). Early Burdigalian, dark greyish-blue sands and marls with numerous molluscs, e.g., *Turritella terebralis* Lamarck, 1799. N5 and lower SBZ25 zones. Infralittoral facies.

Saucats (Larief) - Saucats (Gironde department; Fig. 3), Larief (also named 'L'arief'), in right bank above 'Le Saucats' river, Lamb. III: $x = 369.570$, $y = 3266.350$ ($0^{\circ} 34' 6.3''$ W, $44^{\circ} 39' 41.7''$ N). Late Aquitanian, yellow shelly sands with molluscs, corals and microbenthos, level 'Larief 6', shelly deposit filling dissolution holes corresponding to a previous emersion/erosion period (see schematic section and photographs in Cahuzac *et al.*, 2003). N4 and SBZ24 zones, Sr age 20.9 Ma with 'GTS 2004' (21.3 Ma in Cahuzac *et al.*, 1997, level 'Larief 6'). Depositional sequence 'A_BA' in Parize *et al.* (2008). Another nearby Aquitanian outcrop, situated a little downstream from Larief, yielded NN1 zone (Müller & Pujol, 1979). Littoral facies.

Saucats (Péloua) - Saucats (Gironde department; Fig. 3), Le Péloua, sometimes also corresponding in literature to 'La Bourasse', a nearby locality, Lamb. III: outcrops in the area $x = 370.050$, $y = 3265.685$ to 3265.770 ($0^{\circ} 33' 43.4''$ W, $44^{\circ} 39' 20.7''$ to $44^{\circ} 39' 23.4''$ N). Early Burdigalian, coarse-grained reefal, orange falun, with reworked lacustrine calcareous pebbles (see section and photographs in Cahuzac *et al.*, 2003). N5, NN2 and lower SBZ25 zones, Sr age of coral crag level 19.5 Ma with 'GTS 2004' (20.2 Ma in Cahuzac *et al.*, 1997). Depositional sequence 'B_BP' in Parize *et al.* (2008). Infralittoral facies.

Saucats (Pont-Pourquey) - Saucats (Gironde department; Fig. 3), Pont-Pourquey, in right bank above 'Le Saucats' river, west of road D108, Lamb. III: $x = 366.400$, $y = 3265.320$ ($0^{\circ} 36' 28.4''$ W, $44^{\circ} 39' 4.7''$ N). Early Burdigalian, calcareous yellow, fine-grained sands, more or less shelly, with levels of faluns very rich in *Glycymeris cor* (Lamarck, 1805) (see section and photographs in Cahuzac *et al.*, 2003). N5, NN2 (Müller & Pujol, 1979; Poignant & Pujol, 1978) and lower SBZ25 zones, Sr age 19.2 Ma with 'GTS 2004' (19.8 Ma in Cahuzac *et al.*, 1997), depositional sequence 'B_BP' in Parize *et al.* (2008). Infralittoral facies. We notice that the present section of Pont-Pourquey (above documented) is now in a Geologic Natural Reserve, but we emphasize that the 'classic Pont-Pourquey' section quoted in literature (which yielded the material in older collections) was located further downstream along the 'Le Saucats' river (and east of road D108) in a now urbanized area (coordinates: $x = 366.600$, $y = 3265.250$ or $0^{\circ} 36' 19.2''$ W, $44^{\circ} 39' 2.6''$ N), this section being now inaccessible.

Uzeste (Gamachot) - Uzeste (Gironde department; Fig. 3), Moulin de Gamachot, outcrop in bank of Ruisseau du Font de la Lève. Also found as 'Villandraut' (Moulin de Gamachot). Lamb. III: $x = 386.500$; $y = 3242.850$ ($0^{\circ} 20' 43.4''$ W, $44^{\circ} 27' 19.4''$ N). Earliest Burdigalian, Falun de Bazas Formation, pale grey to yellowish faluns and marly sands with many molluscs and corals, level numbers after Janssen (1985a). Infralittoral facies.

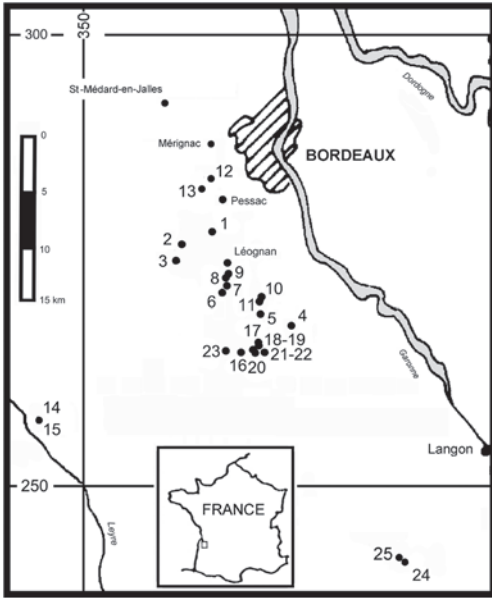
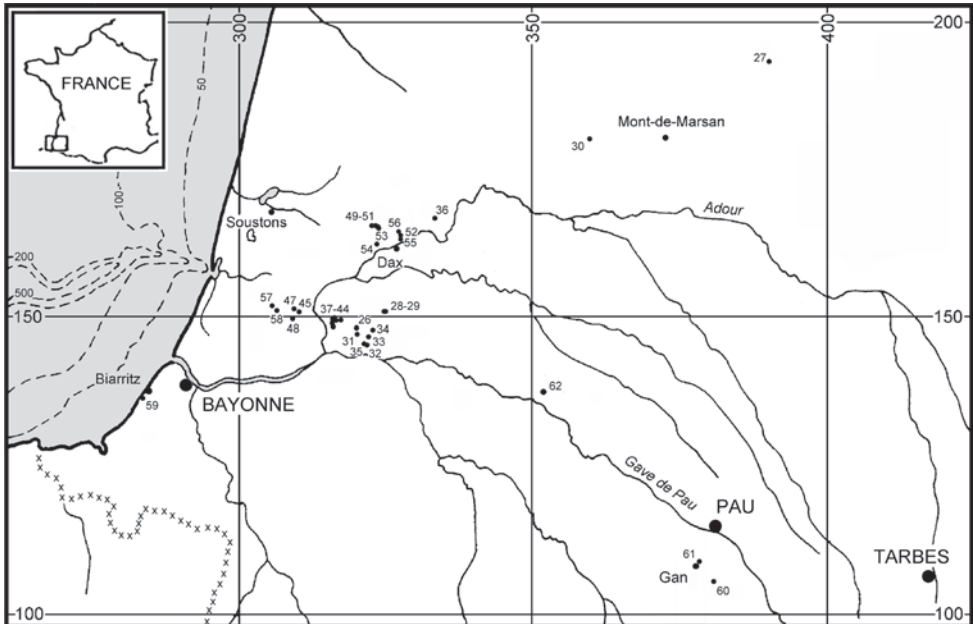


Fig. 3. Localities in the northern part of the Aquitaine Basin (**Gironde** department, France). 1. Canéjan, Haut Bouscaut; 2. Cestas, Fourcq inférieur; 3. Cestas, Pré-Cazeaux; 4. La Brède; 5. La Brède, Moras; 6. Léognan, Les Bougès; 7. Léognan, Château de France; 8. Léognan, Le Coquillat; 9. Léognan, Thibaudeau; 10. Martillac, Barreau-1; 11. Martillac, classic outcrop along the vineyard; 12. Mérignac, Pontic; 13. Pessac, Lorient; 14. Salles, Moulin Ruiné ('Debat Moulin'); 15. Salles, Moulin Ruiné, Larieux; 16. Saucats, La Coquillière; 17. Saucats, Moulin de l'Église; 18. Saucats; Gioux; 19. Saucats, La Cassagne; 20. Saucats, Lagus; 21. Saucats, Lariey; 22. Saucats, Le Péloua; 23. Saucats, Pont-Pourquey; 24. Uzeste, Moulin de Gamachot; 25. Villandraut, Les Berdigots-1.

Villandraut, Berdigots - Villandraut (Gironde departement; Fig. 3), Les Berdigots-1, "Grès de Bazas", Lamb. III: $x = 385.750$, $y = 3243.850$ (*in Moyes, 1966*, with a schematic section) ($0^{\circ} 21' 18.8''$ W, $44^{\circ} 27' 50.9''$ N). Early Burdigalian (see discussion in Cahuzac & Turpin, 1999), yellow-reddish calcareous sands, locally indurated, with few molluscs. Infralittoral facies.



Material and methods (AWJ)

Material for the present paper is the rich collections of three French institutions, *viz.* the Muséum de Bordeaux, of Bordeaux; the Faculté des Sciences, Université de Bordeaux-1, of Talence; and the Muséum national d'Histoire naturelle, Paris, supplemented by specimens from other museums, the most important of which are The Natural History Museum in London (UK), the Senckenberg Museum, in Frankfurt am Main (Germany) and the NCB Naturalis in Leiden (The Netherlands). Apart from this, a number of private collections were consulted, among which especially also those of several members of the Dutch society 'Working Group for Tertiary and Quaternary Geology', resulting from numerous collecting trips to the Aquitaine Basin from the early 1980s onwards.

Pteropods are holoplanktonic molluscs living in deeper water. In the northern part of Aquitaine, at localities around Léognan, Saucats and Salles, most fossiliferous deposits represent sandy rocks from rather shallow water environments, in which pteropods form only an insignificant constituent of the fauna. Such sites frequently yield very rich benthic mollusc assemblages (for which Aquitaine, in fact, is world famous) and collecting pteropods from sieving residues is very time consuming. It is clear that species from epipelagic environments and with a relatively solid shell are the most commonly occurring pteropods. The best example is the well-known species *Vaginella depressa*, of which very large samples are available. Such residues never yield specimens in perfect condition. Without exception the thousands of specimens collected from sieving residues that I have seen are without the fragile larval shell and practically always the apertural parts are damaged.

Pteropod specimens in better condition can only be obtained from such shallow water assemblages by carefully scrutinising the sediment from the interior of larger benthic gastropods, where fragile organisms are trapped in slack water conditions after they sank to the bottom as empty shells and where they were then protected against chemical and mechanical influences. Most of the pteropod specimens published by Curry (1982), from the Eocene clays outcropping at Gan, were obtained from the interior of a single large *Gisortia*-specimen (Curry, 1965, p. 357). From a study of late-Holocene pteropods in the Red Sea (Janssen, 2007a) it became clear that pteropod (and heteropod)

- ◀ Fig. 4. Localities in the southern part of the Aquitaine Basin (**Landes** department, France): 26. Béluas; 27. Corbleu, Moulin de Carro; 28. Gaas, Espibos; 29. Gaas, Lagouarde; 30. Meilhan, Carrière Vives; 31. Orthevielle, NE of Tauzia; 32. Peyrehorade, Ruisseau d'Arribauts; 33. Peyrehorade, abandoned marl pit at Peyrère; 34. Peyrehorade, Tauziède-A; 35. Peyrehorade, Trompe; 36. Pontonx, Mineur-A; 37. Saint-Etienne-d'Orthe, Casenave; 38. Saint-Etienne-d'Orthe, Ruisseau de l'Église A; 39. Saint-Etienne-d'Orthe, Ruisseau de l'Église B; 40. Saint-Etienne-d'Orthe, Ruisseau de l'Église C; 41. Saint-Etienne-d'Orthe, Hondelatte; 42. Saint-Etienne-d'Orthe, Lartigaou; 43. Saint-Etienne-d'Orthe, Lestelle-A; 44. Saint-Etienne-d'Orthe, Verdun; 45. Saint-Jean-de-Marsacq, Lahitet-1/2; 47. Saint-Jean-de-Marsacq, Pinot; 48. Saint-Martin-de-Hinx, Secat near Lanot; 49. Saint-Paul-lès-Dax, Abesse; 50. Saint-Paul-lès-Dax, Abesse-B; 51. Saint-Paul-lès-Dax, Bezoye; 52. Saint-Paul-lès-Dax, Cabanes; 53. Saint-Paul-lès-Dax, Estot; 54. Saint-Paul-lès-Dax, Lestrilles; 55. Saint-Paul-lès-Dax, Le Mainot; 56. Saint-Paul-lès-Dax, Mandillot; 57. Saubrigues, Jean Tic; 58. Saubrigues, Les Tauziets; (**Pyrénées-Atlantiques** department): 59. Biarritz; 60. Gan, Bosdarros, 61. Gan, Tuilerie; 62. Orthez, Le Paren.

shells reach the sea bottom after death completely intact. All damage to specimens (apart from being caused by predators), as seen in collections, has been caused subsequently by later mechanical or chemical influences on the sea bottom and/or in the sedimentary rock, or by collecting methods and processing.

Isolated protoconchs broken off from adult shells, but also larval specimens which died before metamorphosis from veliger to adult, can be collected from the finer sieving fractions and are easily separated by means of heavy liquids, such as bromoform (CHBr_3 , specific weight 2.89) or carbon tetrachloride (CCl_4 , specific weight 1.58). The application of these chemicals, however, is nowadays only allowed in protected environments, like fume-chambers, as they are highly aggressive to human health.

Especially in the southern Aquitaine, many outcrops exhibit more clayey or marly rocks from deeper water. This is true for the Miocene and Oligocene deposits of the Saubrigues palaeocanyon, and also for the Eocene strata of Gan and Biarritz. Pteropods from these rocks can be collected by careful processing of the sediment or, even better, by inspecting the surfaces of freshly broken matrix pieces under low magnification and saving specimens on small pieces of clay or marl. Such specimens on clay tablets or matrix pieces usually have to be protected with an artificial resin.

At Biarritz, where Late Eocene clays are exposed in coastal cliffs, inspecting foreshore residues is rewarding, as they contain pyritic specimens washed out of the clays. Pyritic specimens should be permanently kept in silicone oil, to (hopefully) prevent pyrite decay. Apart from these pyritic occurrences (usually in internal mould preservation), practically all pteropods known from Aquitaine are in shell-preservation, contrary to many occurrences in the central Mediterranean Miocene, where preservation as internal moulds, frequently as phosphoritic specimens, is common.

Abbreviations –

AJB	A.C. Janse collection, Brielle (The Netherlands).
ABH	A.W. Burger collection, Heerhugowaard (The Netherlands).
ACP	A. Cluzaud collection, Pessac (France).
AMS	The Australian Museum, Department of Malacology, Sydney, New South Wales (Australia).
BMNH	The Natural History Museum, Palaeontology Department, London (UK).
BRS	B.G. Roest collection, Silvolde (The Netherlands), later combined with the A.M. Mulder collection.
FSUB	Faculté des Sciences, Université de Bordeaux 1, Talence (France).
HMM	H.J. Mulder collection, Monster (The Netherlands).
JRP	J. Le Renard collection, Plaisir (France).
MBB	Muséum de Bordeaux, Bordeaux (France).
MGUH	Geological Museum, University of Copenhagen (Denmark).
MHB	Museum für Naturkunde der Humboldt Universität, Berlin (Germany).
MNHN	Muséum national d'Histoire naturelle, Paris (France). Informal PL numbers refer to the Pierre Lozouet <i>et al.</i> collection.
NMV	Naturhistorisches Museum, Vienna (Austria).
MVM	Museum of Victoria, Department of Invertebrate Palaeontology, Melbourne, Victoria (Australia).

RGM	Netherlands Centre for Biodiversity Naturalis, Department of Geology, Leiden (The Netherlands).
RGS	R��serve G��ologique, Saucats, France.
RMNH	Netherlands Centre for Biodiversity Naturalis, Department of Malacology, Leiden (The Netherlands).
SAM	South Australian Museum, Section Palaeontology, Adelaide, South Australia (Australia).
SMB	S. Mermuys collection, Bergschenhoek (The Netherlands).
SMF	Senckenberg Museum, Frankfurt am Main (Germany).
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USA).
D-V	dorso-ventral diameter
FOD	first occurrence datum
H	shell height
H/W-ratio	shell height x 100/shell width
LOD	last occurrence datum
W	shell width

Annotations preceding the synonyms are those of Richter (1948) and Matthews (1973):

- * - first valid introduction of a taxon;
- . - responsibility for the identification is accepted by the present author;
- (no symbol) responsibility for the identification is not accepted by the present author, but there is no reason for doubt;
- ? - in the opinion of the present author there is reason to doubt the identification;
- v - the original material of this reference was studied by the present author;
- () - (date between brackets) the year of publication is uncertain (or the reference has not been published officially, such as a thesis).

Systematic palaeontology (AWJ)

Herein, the indication 'clade' is applied as a taxonomic unit above superfamily, instead of the traditional order, suborder, *etc.*, indicating that 'recent cladistic analysis has resulted in recognizing a taxon as monophyletic' (Bouchet & Rocroi, 2005, p. 240).

Phylum Mollusca Linn  , 1758
Class Gastropoda Cuvier, 1797
Clade Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Pterotracheoidea Rafinesque, 1814
Family Atlantidae Rang, 1829

Remarks – Just a few very juvenile specimens supposed to belong to the Atlantidae were recovered from samples from Saint-Jean-de-Marsacq and Meilhan, the finest fractions of which were still available. None of the other localities yielded even fragments recognisable as belonging to this group of molluscs.

Genus *Atlanta* Lesueur, 1817

Type species – *Atlanta peronii* Lesueur, 1817 (Recent).

Atlanta sp. 1

Pl. 1, fig. 1.

Description – Only juvenile specimens of less than 4 whorls are available. They have a naticoid shape with straight tangents and are slightly higher than wide (H of illustrated specimen 0.49 mm), with an apical angle of slightly less than 90°. The initial whorl is covered with a granulated microornament (Pl. 1, fig. 1b), consisting of relatively coarse granules, in between which much smaller granules are seen. On the second whorl three spiral threads develop below the suture, whereas the base of the shell is covered with some 20 similar spirals, leaving a narrow smooth zone in between the two sets. Shoulder and keel spiral are not stronger developed and therefore difficult to distinguish. A very narrow umbilicus is just discernible.

Material examined – **St Jean-de-Marsacq (Pinot)**: RGM 541 379/4 juveniles; RGM 541 379a/1 juvenile (Pl. 1, fig. 1), leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Atlanta sp. 2

Pl. 1, fig. 2.

Description – A single, very juvenile specimen is available. It is globular, slightly wider than high (H = 0.47 mm), with a low conical spire. The initial whorl has a microornament (Pl. 1, fig. 2b) strongly resembling that of *Atlanta* sp. 1. The shell's surface is covered with relatively coarse, equidistant spirals, only two of which are visible on the narrow second whorl. On the last whorl, some 15 of these are present, covering also the base of the shell. In between the spirals the shell has a granulated microornament. A narrow umbilicus may be present, but is covered with matrix.

Material examined – **St Jean-de-Marsacq (Pinot)**: RGM 541 380/1 juvenile (Pl. 1, fig. 2), leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Atlanta sp. 3

Pl. 1, fig. 3.

Description – Juvenile, naticoid shells, slightly higher than wide (H = 0.47 mm) of 3½ whorls with concave tangents. The last whorl is distinctly shouldered. The initial whorl has a microornament of very small granules, only visible (Pl. 1, fig. 3b) close to the lower suture. On the second whorl three coarse spirals develop, decreasing in strength on the next whorl on which a further five, very weak spirals are present. The lowermost one of these is slightly stronger and seems to represent the keel spiral. The base of the shell is smooth. Strongly prosocyrte growth lines are visible on the last half whorl. A very narrow umbilicus is present.

Material examined – **Meilhan (Vives)**: RGM 569 426/3 juveniles, RGM 569 427/1 juvenile (Pl. 1, fig. 3), leg. S. Mermuys, 2006, don. 2007. Late Aquitanian.

Family Carinariidae de Blainville, 1818
Genus *Carinaria* Lamarck, 1801

Type species – *Carinaria cristata* (Linné, 1767) (Recent).

***Carinaria tournoueri* Peyrot, 1932**

- * 1932 *Carinaria Tournoueri* Benoist in Sched., Peyrot, p. 296, pl. 14, fig. 4.
- 1933 *Carinaria Tournoueri* Benoist in Sched.; Peyrot, p. 130, pl. 14, fig. 4.
- 1972 *Carinaria tournoueri* Benoist; Robba, p. 495.

Description – According to Peyrot (1932, 1933) this species differs from '*Carinaria hugardi*' (= *C. hugardi* Pictet, 1855) by more numerous, more close-set ribs that are less regularly distributed. The height of the shell is less than in *C. paretoi* Mayer, 1868, and its apex is less strongly curved. The shell is smaller than that of *C. mediterranea* Blainville, 1824.

Discussion – Unfortunately, it has not been possible to trace the only known specimen of this species in the Benoist collection, which is housed in MBB. The sample is either missing or mislaid. A search in the other Bordeaux collections in MBB and FSUB was unsuccessful. As the illustration in Peyrot (1932, 1933) is insufficient to recognise the specimen as one of the species described in literature, I can only refer to it with the data given above. The only known specimen is said to originate from Léognan.

Carinariidae? sp.

Pl. 1, fig. 4.

Description – A single, juvenile specimen is available, with a shell height of just 0.39 mm. It is wider than high with its maximum diameter above the horizontal midline. There are two rather convex whorls, rapidly increasing in diameter. The nucleus, separated from the next whorl by a double radial riblet, does not show a microornament, but may be worn. The second whorl is slightly flattened just below the suture, but gradually rounded towards a distinct umbilicus. Right after the boundary of the nucleus an ornament starts below the suture showing short radial crests that are slightly curved backwards and cover only the shoulder of the shell. The lower part of the last whorl is smooth.

Material examined – **St Jean-de-Marsacq (Pinot)**: RGM 541 381/1 juvenile (Pl. 1, fig. 4), leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Discussion – The present specimen agrees fairly well in shape with juvenile Carinariidae as described by Seapy & Thiriou-Quévieux (1994) and Janssen (2007b), but its ornament is utterly different. Crests as seen in the present specimen are absent in described

protoconchs of *Carinaria* or *Pterosoma*. In species of these genera, such crests are seen surrounding the umbilicus, whereas the upper side of the whorls may or may not show a spiral ornament. Therefore, an assignment to Carinariidae has to remain doubtful.

Clade Thecosomata de Blainville, 1824

Superfamily Limacinoidea Gray, 1847

Family Limacinidae Gray, 1847

Genus *Altaspiratella* Korobkov, 1966 (= *Plotophysops* Curry, 1982)

Type species – '*Limacina elongatoides*' (Aldrich) = *Physa elongatoidea* Aldrich, 1887 (Eocene, Ypresian). *Type species* of *Plotophysops* is *P. bearnensis* Curry, 1982.

***Altaspiratella bearnensis* (Curry, 1982)**

Pl. 2, figs. 1-4; Pl. 3, fig. 1.

- *v 1982 *Plotophysops bearnensis* Curry n. sp., p. 40, pl. 1, fig. 9a-c.
- v. (1986) *Spiratella tutelina* Curr.; Merle, p. 43 (*non* Curry).
- v. 1990b *Altaspiratella bearnensis* (Curry 1981); Janssen, p. 68.
- ? 1992 *Altaspiratella bearnensis* (Curry); Hodgkinson *et al.*, p. 13, pl. 1, figs. 1, 2.
- . (1996) *Altaspiratella bearnensis* (Curry, 1981); Kunz, p. 164, pl. 30, figs. 1-3.

Type locality – Gan (Tuilerie), Eocene, Middle-Late Ypresian, Marnes de Gan, NP12/13.

Type material – Holotype, BMNH GG. 21255/1, Curry, 1982, pl. 1, fig. 9a-b (= Pl. 2, fig. 2a-c herein); from **Gan (Tuilerie)**: paratypes, BMNH PITG25485/6 complete specimens mounted on card; paratypes BMNH PITG25486/c. 44 damaged or juvenile specimens/fragments; all D. Curry collection.

Description – Shell sinistral, conical, oblong, about twice as high as wide, with up to 6½ slightly convex, comparatively high whorls that gradually increase in diameter, separated by an oblique suture line. The whorls attach below the periphery of the preceding whorl, where the shell is slightly angular, especially so in immature individuals. The apical angle of the shell varies between 35 and 40°. The body whorl occupies more than half the shell height. The base of the shell is either separated by a slight angularity and then rather flat or there is no trace of a boundary between the supra-sutural and basal shell parts, in which case the gradual convexity of the body whorl is uninterrupted. An umbilicus is absent.

The aperture of adult specimens is oblong, angular in its upper part and rounded below. Its adaxial side is subdivided into a parietal and a columellar part. The columella itself is thickened and demonstrates a distinct torsion, in such a way that looking into the shell's interior is possible by a straight adapical view (Pl. 2, fig. 1c). The apertural margin is widened and internally reinforced with a rather solid ridge, connected with the thickened columella. The ridge accentuates the separation of the apertural margin, but seen from outside the widening of the aperture is gradual. In a lateral view the apertural margin is almost straight. Its lower part is somewhat projecting and shaped as an obtuse notch or tooth of variable strength. The surface of the shell is very smooth and

shiny when seen under the light microscope, with hardly visible opisthocyrt incremental lines. On the early whorls, an indication of short crests is seen just below the suture (Pl. 3, fig. 1b).

Material examined – **Gan (Bosdarros)**: RGM 396 612/35, leg. A.W. Janssen, 28 August 1990; **Gan (Tuilerie)**: BMNH PITG25495/12 juvenile specimens from unsorted sample, BMNH PITG25501/31 juvenile or damaged specimens, no paratypes, all D. Curry collection; RGM 229 304/c. 500, RGM 229 305/1 (Pl. 2, fig. 3a-b, RGM 229 306/1 (Pl. 2, fig. 1a-c), RGM 229 307/1 juvenile (Pl. 2, fig. 4a-b), RGM 569 449/1 (Pl. 3, fig. 1a-b), all leg. A.W. Janssen, 1981-1990; RGM 229 308/43, leg./don. C. Dolin, 1983; RGM 396 605/20, leg./don. D. Merle, 1987; SMF 332772/59, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – Janssen (1990b, p. 68) suggested that *Altaspiratella bearnensis* is closely related to and may be even identical with a New World species, namely *Physa elongatoidea* Aldrich, 1887, from Choctaw Corner, Alabama, U.S.A. (Early Eocene, Wilcox Group, Hatchetigbee Formation, Bashi Member; Early Ypresian, zone NP10; Collins, 1934, p. 178; Hodgkinson *et al.*, 1992, p. 14), the holotype and only known specimen of which is here illustrated (Pl. 2, fig. 5a-d). In the original publication (Aldrich, 1887, p. 83) the species was not illustrated. Aldrich (1895, p. 57, pl. 2, fig. 9) transferred *P. elongatoidea* to *Spirialis* among the pteropods and gave a drawing of the holotype. Harris (1899, p. 103, pl. 12, fig. 25) repeated Aldrich's information and gave a new illustration of the type. The same was done by Collins (1934, p. 177, pl. 7, fig. 1), who (p. 228) used a camera lucida for his drawing. His illustration agrees quite well with Aldrich's drawing, whereas Harris's illustration was less successful, representing the shell as too thick-set. Curry (1965, p. 366) compared *elongatoidea* with his *Spiratella tutelina*. Also Hodgkinson *et al.* (1992, pl. 1, fig. 3) illustrated the holotype of *Altaspiratella elongatoides*.

The type of *Altaspiratella elongatoidea* is still the only available specimen of this species (apart from a possible occurrence in New Zealand, see below). It was originally kept in the Aldrich collection, incorporated in the Johns Hopkins University collection (Baltimore), but is now housed in USNM (registration number USNM 638862). Thanks to the kind cooperation of Mr F.D. Collier I was able (June 1987) to execute a direct comparison between *A. bearnensis* and *A. elongatoidea*. I found the two forms very similar, although not identical. Compared to equal-sized specimens of *A. bearnensis* from Gan, the general shell-form, the proportions and the slight angularity of the whorls are identical. Although the apertural margin of *A. elongatoidea* is broken, the remaining part of the columella distinctly indicates that the margin is reinforced in full-grown *A. elongatoidea* shells. In both forms the columella is twisted in an identical way and the number of whorls is virtually identical.

There is, however, one distinct difference. In *A. elongatoidea* the first whorl is markedly more voluminous, relatively lower and wider than the corresponding whorl in *A. bearnensis*, resulting in a less regularly conical spire with slightly concave tangents. This difference is obvious in a frontal or lateral view (Pl. 2, fig. 5b or c), but an apical view (Pl. 2, fig. 5a) demonstrates this phenomenon particularly clearly. It cannot be decided, of course, whether or not full-grown *A. elongatoidea* has similar apertural reinforcements (such as the presence of a notch) as *A. bearnensis*. These considerations lead me,

in the absence of further material of *A. elongatoidea*, not to treat them as synonyms. If additional material becomes available, this concept should be reconsidered.

The minor differences established herein between *A. elongatoidea* and *A. bearnensis* did not convince me (Janssen, 1990b) that they belong to different genera, although each of them is the type species of a genus-group name (respectively *Altaspiratella* Korobkov, 1966, and *Plotophysops* Curry, 1982). Korobkov (1966, pp. 74, 75, 80) made “*elongatoides*” (all authors followed Collins’ misspelling of the species epitheton, except Curry, 1982, and Hodgkinson *et al.*, 1992) the type species of his subgenus *Altaspiratella*, in which he also included *choctavensis* Aldrich, *conica* von Koenen, *amudariensis* Korobkov and *stenogyra* Philippi. These latter four names admittedly represent rather high-spired forms, but, unlike the type species, they are all umbilicate.

Curry (1982, pp. 39, 40) based his genus *Plotophysops* on *P. bearnensis*. He compared his new genus with *Altaspiratella*, but considered it different because of the presence of an umbilicus (which is incorrect for the type species, *A. elongatoidea*), the absence of a twisted columella and a modified lip. A twisted columella is present in *A. elongatoidea* and the apertural lip of this species is at least thickened, as discussed above. Thus, there are no criteria justifying a differentiation of *Altaspiratella* and *Plotophysops*, and I consider the latter a junior subjective synonym of the former (Janssen, 1990b). Hodgkinson *et al.* (1992, p. 13) accepted this conclusion.

Kunz (1996, p. 164) studied some specimens from Gan by SEM and also described the short subsutural crests in the apical part of the shells (second protoconch whorl). This was compared with similar crests occurring in the Peraclididae (Pseudothecosomata).

Distribution – Apart from the occurrences at Gan, *Altaspiratella bearnensis* is also present in North Sea Basin Ypresian deposits. Such occurrences were not yet known to Janssen & King (1988), but specimens of *A. bearnensis* were since recognised from the London Clay, divisions C(?), D and E (Eocene, Ypresian) from several locations: BMNH not registered/1, Warden Point, Sheppey, leg. D.J. Ward, January 1978, found in a mixed sample referred to in Cooper (1984, p. 8), also containing *Heliconoides mercinensis* (Watelet & Lefèvre, 1885), *Limacina taylori* Curry, 1965, and *L. tutelina* Curry, 1965 (London Clay Formation, Division C or D); RGM 229 301-303/36, RGM 229 362/1, London, Highgate, Highgate Archway exposure, leg./don. C. King (London Clay Formation, division E, unit 3; see King, 1981, p. 39); RGM 286 639/6, Warden Point, Sheppey, collected *ex situ* from foreshore gravels by A. Lawson, donated by S. Tracey, 1 June 1996 (London Clay Formation, Division D); RGM 286 640/5, Creeksea near Burnham-on-Crouch (England, Essex), collected *ex situ* (foreshore sample) by A. Lawson, donated by S. Tracey, 1 June 1996 (London Clay Formation, Division D); RGM 286 641/5, Burnham-on-Crouch (England, Essex), Cliff Reach, collected *ex situ* by A. Lawson, donated by S. Tracey, 1 June 1996 (London Clay Formation, Division D); RGM 515 553/1 juvenile specimen, Warden Point, collected *ex situ* in foreshore gravels by D.J. Ward, January 1978, don. 1986.

The British specimens of *A. bearnensis* invariably have their aperture damaged, as all shells are filled with pyrite, which makes the lip easily break off. Still, it is obvious that they reach larger dimensions than the specimens from Gan, with which they seem to be identical in all other respects.

Hodgkinson *et al.* (1992, p. 13) recorded *A. bearnensis* from two localities in Texas (U.S.A.), which, contrary to all European occurrences of this species, have a Lutetian age (Weches Formation, NP 15). Their specimens differ morphologically from typical *A. bearnensis* by a slender shape (apical angle 31°) and absence of the slight peripheral angularity. The apertural reinforcements, however, seem to agree with *A. bearnensis* (presence of an internal ridge and a basal notch). Obviously, this is a later development of *A. bearnensis*, probably in need of a new name.

Unfortunately I have not been able to compare the material of *A. "elongatoides"* from New Zealand, published by Beu & Maxwell (1982, p. 44). These authors just mention the name, without description or illustration, from the Heretaungan and Manaorapan Stages, which, according to Harland *et al.* (1982, p. 36), correlate with the European Ypresian.

***Altaspiratella multispira* (Curry, 1982)**

Pl. 2, figs. 6-10.

v. 1982 *Plotophysops multispira* Curry n. sp., p. 42, pl. 1, fig. 10a-c.

Type locality – Gan (Tuilerie), Eocene, Middle-Late Ypresian, Marnes de Gan, NP12/13.

Type material – BMNH GG. 21256/1, holotype, Curry, 1982, pl. 1, fig. 10a (Pl. 2, fig. 6 herein); BMNH GG. 21257/2, paratypes, Curry, 1982, pl. 1, fig. 10b-c (Pl. 2, figs. 7-8 herein).

Description – Only fragments are available of this species. Shell sinistral, elongately cylindrical, when complete *c.* 4.5 times higher than wide (see reconstruction, Pl. 2, fig. 10), apical angle 10°. The adult shell has 6 relatively high and convex whorls, slowly and gradually increasing in diameter, separated by incised and very oblique sutures. Aperture oval, pointed above, rounded below, with well developed reinforcement structures, consisting of an internally thickened apertural margin, which is bent outward. Columella similarly thickened, warped and with a distinct torsion. The basal part of the aperture bears a projecting tooth where apertural margin and columella meet. There is no umbilicus.

Material examined – **Gan (Bosdarros):** RGM 396 613/13, leg. A.W. Janssen, 28 August 1990. **Gan (Tuilerie):** BMNH PITG25496/1, damaged specimen from unsorted sample; BMNH PITG25502/1, damaged specimen from unsorted sample, no paratypes, all D. Curry collection; JRP/1 (Pl. 2, fig. 9a-b); RGM 396 601/22, leg. A.W. Janssen, 1981-1990; RGM 396 608/1, leg./don. C. Dolin, 1983. Middle-Late Ypresian.

Discussion – A related species, *Altaspiratella gracilens* Hodgkinson, 1992 (*in* Hodgkinson *et al.*, 1992, p. 14, pl. 1, figs. 4, 5), from the Ypresian-Lutetian of the U.S.A. (Texas, Louisiana), is morphologically intermediate between *A. bearnensis* and the present species. It is similarly an elongate, almost cylindrical species, but the shape of the shell is somewhat less slender, with slightly convex tangents along the spire, and the structures

of the aperture seem to be different. The type specimens of *A. gracilens*, as illustrated by Hodgkinson *et al.*, are poorly preserved.

Distribution – *Altaspiratella multispira* is known exclusively from two Ypresian localities in Gan.

Genus *Currylimacina* A.W. Janssen, 2003

Type species – *Skaptotion cossmanni* Curry, 1982 (Eocene, Ypresian).

Currylimacina cossmanni (Curry, 1982)

Pl. 4, figs. 1-7; Pl. 5, figs. 1-3.

*v. 1982 *Skaptotion cossmanni* Curry n. sp., p. 39, pl. 1, fig. 8a-c.

. 1992 *Skaptotion? reklawensis* Garvie, new species; Hodgkinson *et al.*, p. 23, pl. 7, figs. 1-4.

. 2003 '*Skaptotion*' *cossmanni* Curry, 1982: Janssen, p. 166.

Type locality – Gan (Tuilerie), Eocene, Middle-Late Ypresian, Marnes de Gan, NP12/13.

Type material – BMNH GG. 21253/1, holotype, Curry, 1982, pl. 1, fig. 8a-b (Pl. 4, fig. 1a-b herein); BMNH GG. 21254/1 juvenile, paratype, Curry, 1982, pl. 1, fig. 8c (Pl. 4, fig. 2a-d herein), BMNH PITG25487/9 specimens, most of them damaged, many fragments, paratypes, all D. Curry collection.

Description – Shell sinistral, spherical, consisting of four convex whorls, initially in a low cone, but progressively enclosing the earlier whorls, which results in a globose, more or less nautiloid shell with a deep apical 'umbilicus' in which the initial whorls sometimes are still visible. The lower, real umbilicus is very deep and narrow. Faint, somewhat opisthocline growth lines are present, especially well visible on the younger whorls. The shell has a microornament of a dense collabral striation (Pl. 5, fig. 3), following the course of the incremental lines. The aperture is large, reniform, and produced both above and below the penultimate whorl. Only in completely adult specimens (such as the holotype) is the apertural margin slightly thickened internally.

Material examined – **Gan (Tuilerie)**: RGM 396 594/1, broken after drawing (Pl. 4, fig. 5), RGM 396 595/1 juvenile, (Pl. 4, fig. 6), RGM 396 596/1 (Pl. 4, fig. 3a-c), RGM 396 597/1 juvenile (Pl. 4, fig. 4a-d), RGM 569 451/1 juvenile (Pl. 5, fig. 1), RGM 569 454/1 (Pl. 5, fig. 2a-b), all leg. A.W. Janssen, 1981-1990; SMF 332773/3, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – *Skaptotion? reklawensis* Garvie (*in* Hodgkinson *et al.*, 1992, p. 23, pl. 7, figs. 1-4) from the Reklaw and Weches formations in Texas (U.S.A.) was considered to be dextral by its author, which is incorrect. In a sample of four specimens, received March 2001 from Christoffer Garvie, from the Reklaw Formation, Marquez Shale Member of Taylor Branch, Texas, U.S.A. (not the type locality), of Ypresian age, one almost

adult specimen distinctly shows its sinistral initial whorls. The same is clear for some specimens illustrated here from Gan (Pl. 4, figs. 2c, 3a, 4b; Pl. 5, fig. 2a-b) and The Netherlands (Pl. 4, fig. 7a-b). The American specimens agree in all respects with the topotypical material from Gan (also in the presence of the microornament; Pl. 5, fig. 3) and, consequently, *Skaptotion reklawensis* is here considered a junior subjective synonym of *Currylimacina cossmanni*. Curious, again, is the occurrence of this species in the Lutetian Weches Formation. The same was found (see above) for *Altaspiratella bearnensis* or a closely related form.

Distribution – Apart from the type locality in France and the American occurrences referred to above, the present species is also known from the North Sea Basin: IJsselmuidentoren-I borehole (Overijssel, The Netherlands), depth 799.5-804.5 m below rotary table (RGM 397.060/1, pyritic internal mould, now almost completely dissolved in silicone oil); depth 829.0-833.6 m below rotary table (RGM 397 062/1, pyritic internal mould in silicone oil, Pl. 4, fig. 7a-b). Both specimens from the Ieper Clay Formation (Eocene, Ypresian), leg. P.A.M. Gaemers, don. September 1987.

Genus *Heliconoides* d'Orbigny, 1835

Type species – *Heliconoides inflata* (d'Orbigny, 1834) (Recent).

Discussion – In a discussion on genus level taxonomy of Limacnidae, Janssen (2003, p. 168) recognised six or seven genera in that family. Unornamented umbilicated limacnoid species were included in *Heliconoides*, in which the columella is simple or with torsion (but not in a three-dimensional spiral) and with a widened apertural margin or otherwise reinforced apertural structures. *Heliconoides* thus includes a wide range of shell shapes, varying from helical to discoidal; almost certainly this genus is polyphyletic. As is also demonstrated by the present paper, the knowledge on this group of pteropods to date is insufficient to unravel the evolutionary development. It may be expected that eventually *Heliconoides* will be split up in various separate genera.

***Heliconoides auriformis* (Curry, 1982)**

Pl. 6, figs. 1-5.

v. 1982 *Spiratella auriformis* Curry n. sp., p. 38, pl. 1, fig. 7a-b.

? 1992 *Limacina texana* Garvie and Hodgkinson, new species, Hodgkinson *et al.*, p. 20, pl. 4, figs. 3-6.

Type locality – Gan (Tuilerie), Eocene, Middle-Late Ypresian, Marnes de Gan, NP12/13.

Type material – BMNH GG. 21252/1, holotype, Curry, 1982, fig. 7 (Pl. 6, fig. 1a-b herein); BMNH PITG25488/3 isolated specimens, 10 specimens and 1 fragment mounted on card, paratypes, all D. Curry collection.

Description – Shell small (holotype H = 0.9 mm), sinistral, globular, with 2¾ whorls, rapidly increasing in diameter and attaching above the periphery of the foregoing

whorl. Spire above the body whorl depressed or slightly protruding, apex visible in a front view. Aperture large, elliptical and placed obliquely, reinforced by a relatively wide margin which is bent outward and slightly thickened. Base of the shell rounded, with a narrow umbilicus. Columella flexuous and twisted.

Some juvenile specimens (Pl. 6, figs. 4, 5) are, with some doubt, included in this species. They have the depressed apical side and apical spiral similar as in the holotype, but their shell is markedly shouldered.

Material examined – **Gan (Tuilerie)**: BMNH PITG25490/1, specimen found in sample identified *Spiratella* sp.; BMNH PITG25503/1 and 1 fragment, from unsorted sample, no paratypes, all D. Curry collection; RGM 396 585/1 (Pl. 6, fig. 2a-d), RGM 396 586/1 juvenile (Pl. 6, fig. 4a-c), RGM/1 juvenile, specimen lost (Pl. 6, fig. 5a-c), all leg. A.W. Janssen, 1981-1990; RGM 396 604/1 (Pl. 6, fig. 3a-c), leg./don. D. Merle, 1987; RGM 396 606/1 fragment, leg./don. C. Dolin, 1983; SMF 332774/2, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – This species is easily recognisable by its globose shape and large, widened aperture. Curry (1982) compared it with *Heliconoides tertiaria* (Tate), a species originally described from the Australian Miocene, which differs, however, by its planorboid apical plane and a different morphology of the apertural reinforcements (compare Janssen, 1995 and below). The present species closely resembles a species from the Late Ypresian Reklaw Formation in Texas, viz. *Heliconoides texana* (Garvie & Hodgkinson in Hodgkinson et al., 1992). That species has a very similar general shape, but admittedly reaches double the size of *H. auriformis* and its spire is more depressed.

Distribution – *Heliconoides auriformis* is exclusively known from its type locality.

***Heliconoides daguini* sp. nov.**

Pl. 6, figs. 6, 7.

Holotype – RGM 396 587/1 (Pl. 6, fig. 6), leg. A.W. Janssen, 1981-1990.

Type locality – Gan (Tuilerie).

Stratum typicum – Marnes de Gan (Eocene, Middle-Late Ypresian), NP12/13.

Derivatio nominis – Named after Fernand Daguin (1889-1948), who extensively described the geology of the western Aquitaine basin (Daguin, 1948) just before he died in an airplane crash.

Paratype – **Gan (Tuilerie)**: RGM 396 588/1 juvenile (Pl. 6, fig. 7a-c), leg. A.W. Janssen, 1981-1990. Middle-Late Ypresian.

Diagnosis – Large, planispiral *Heliconoides* species of 3½ whorls. Aperture large, semicircular, bent outward and with an internal margin-parallel ridge.

Description – For a *Heliconoides* species the shell is large (H = 3 mm, W = 4 mm). The shell has 3½ convex whorls that rapidly increase in diameter. The initial whorls are very slightly raised (Pl. 6, fig. 7a), but the body whorl hides the apical shell part in a straight frontal view (Pl. 6, fig. 6a). The aperture is large and semicircular, strongly protruding below the base of the penultimate whorl and only slightly raised above it. Apertural reinforcement structures consist of an internal margin-parallel ridge, whereas the narrow actual margin is bent outward. The ridge is connected with the columella which is widened into a columellar platform, with a notch just below the base of the penultimate whorl. The base of the shell is gradually rounded and has a distinct umbilicus which occupies about one sixth of the shell's diameter. The surface of the shell is smooth with difficultly visible, orthocone growth lines.

Discussion – Although there are just two specimens, it was decided to introduce a new taxon as the characteristics are peculiar. The large size distinguishes the present species from similar Eocene planispiral limacinids, such as *Heliconoides nitens* (Lea, 1833), *H. texana* (Garvie & Hodgkinson in Hodgkinson et al., 1992), *Limacina convolutus* Hodgkinson in Hodgkinson et al., 1992 or *L. wechesensis* Hodgkinson in Hodgkinson et al., 1992. Although more or less similar in general shape, these species lack any apertural reinforcement structures (*Limacina*) or these structures have an entirely different morphology.

Distribution – Exclusively known from Gan (Tuilerie).

Heliconoides hospes (Rolle, 1861)

Pl. 7, figs. 1-9.

- *v 1861 *Limacina hospes* Rolle, p. 3, pl. 1, fig. 1, 1a-b (non fig. 2 = *Adeorbis etruscus* Rolle).
- v. 1886 *Spirialis hospes* (Rolle); Kittl, pp. 69, 70, 72, pl. 2, fig. 39.
- . 1959 *Spirialis hospes* (Rolle); Iorgoiescu, p. 29, pl. 9, fig. 6a, b.
- . 1966 *Spirialis hospes* (Rolle); Gheorghian et al., pp. 8, 15, pl. 1, fig. 1a-c; pl. 3.
- v. 1984b *Limacina hospes* Rolle, 1861; Janssen, p. 69, pl. 2, fig. 1a-d.
- v. 1991a *Limacina hospes* Rolle, 1861; Zorn, p. 20, pl. 1, figs. 4-6.
- v. 1991b *Limacina hospes* Rolle, 1861; Zorn, p. 99, pl. 2, figs. 1-7, pl. 10, fig. 5, pl. 11, fig. 1.
- v. 2005b *Heliconoides hospes* (Rolle, 1862); Janssen, p. 79.

Type locality – Mecklenburg (Germany), Oligocene, Chattian, reworked boulders of Sternberger Gestein.

Type material – Holotype, NMV 1859.XIV.233 (re-illustrated in Janssen, 1984b, pl. 2, fig. 1).

Description – Shell sinistral, one and a half times wider than high, with almost 3 moderately convex whorls, together forming a more or less depressed cone. Aperture large, higher than wide, apertural margin distinctly widened. Narrow umbilicus present.

Material examined – **Bélus (Marcon)**: MNHN A32085/1 (Pl. 7, fig. 2a-d), MNHN PL 6600/4 juveniles(?); **Peyrehorade (Peyrère)**: MNHN PL 6602/3 juveniles(?); MNHN PL

6626/5 juveniles(?) (separated from sample of 11 specimens, see *Heliconoides linneensis*); MNHN unnumbered/5 juveniles(?), MNHN A32092/1 juvenile(?) (Pl. 7, fig. 5a-d); RGM 541 404/1 (Pl. 7, fig. 8a-b), RGM 541 405/17 juveniles(?), leg. A.W. Janssen, 10 June 1981; **Peyrehorade (Tauziède)**: MNHN PL 5897/1 juvenile(?); **Saint-Etienne-d'Orthe (Larti-gaou)**: RGM 541 414/1 (Pl. 7, fig. 1a-d), RGM 541 415/1 juvenile(?), leg. A.W. Janssen, 1984-1990; **Saint-Etienne-d'Orthe (Verdun)**: MNHN A32086/1 damaged (Pl. 7, fig. 4a-b); MNHN A32087/1 specimen(?) (Pl. 7, fig. 3a-b), MNHN PL 6598/5 juveniles(?); **Saint-Paul-lès-Dax (Abesse)**: MNHN A32088/1 juvenile(?) (Pl. 7, fig. 9); **Saint-Paul-lès-Dax (Bezoye)**: MNHN PL 6599/1 juvenile(?), 1 fragment(?); **Saint-Paul-lès-Dax (Estoti)**: MNHN A32089/2 juveniles(?) (Pl. 7, fig. 6a-b, 7a-c). Chattian.

Discussion – Quite a number of Aquitaine specimens of Chattian age resemble this species closely, albeit that most of them are either juvenile or damaged. In some the shell is almost planispiral. Such specimens (Pl. 7, fig. 3a) are indicated with a query above.

The available specimens from the Aquitaine Basin differ from those typical of the North Sea Basin in having only $2\frac{3}{4}$ -3 whorls, instead of $3\frac{3}{4}$. They reach almost the same size, however, as their whorls increase more rapidly in diameter. Also, their shells are relatively wider, as the spire is more depressed. Conversely, the apertural features are practically identical and, as only few adult specimens are at hand, I see no reason to introduce a new species.

Distribution – *Heliconoides hospes* was originally described from Late Oligocene boulders, known as 'Sternberger Gestein', the age of which was recently discussed in Janssen (2005b). In the North Sea Basin, *Heliconoides hospes* is recorded from many localities in Germany, Denmark, The Netherlands and Belgium. The species occurs in the Rupelian and Chattian. The specimens recorded herein from Aquitaine are the first from outside the North Sea Basin. The Saint-Etienne-d'Orthe marls are dated NP25 (Sturbaut *in* Zorn & Janssen, 1993, p. 61) which is also true for several other cited outcrops, dated (by means of planktonic foraminifera or nannoplankton) as zones P22 and NP25 (see Müller & Pujol, 1979; Cahuzac, 1980; Cahuzac *et al.*, 1995), meaning that there is no significant difference in age between the North Sea and Aquitaine basin occurrences.

Heliconoides inflata (d'Orbigny, 1834)

Pl. 7, figs. 10, 11.

- * 1834 *A(lanta)* [sic] *inflata* d'Orb.; d'Orbigny, pl. 12, figs. 16-19.
- . 1835 *Atlanta* (*Heliconoides*) *inflata* d'Orb.; d'Orbigny, p. 174.
- . 1880 *Embolus rostralis* Souleyet (*Spirialis*); Seguenza, p. 277.
- v. 1887 *Spirialis tertiaria*, Tate spec. nov., p. 196 (*partim*, only pl. 20, fig. 12a-c; includes *Heliconoides tertiaria*).
- . 1925 *Spirialis miostralis* Kautsky nov. spec., p. 202.
- ?v 1934 *Limacina inflata* (d'Orbigny); Collins, p. 179, pl. 7, figs. 3-5 (*partim*, non figs. 6-8 = *Limacina imitans*).
- . 1967 *Limacina* (*Thilea*) *inflata* (Orbigny, 1836); van der Spoel, 1967, p. 50, figs. 17, 18.
- v. 1990a *Limacina inflata* (d'Orbigny, 1836); Janssen, p. 14, pl. 2, figs. 5-7, pl. 3, fig. 11, pl. 10, fig. 2.
- . 2003 *Heliconoides inflata* (d'Orbigny, 1836); Janssen, p. 168.

- v. 2004b *Heliconoides inflata* (d'Orbigny, 1836); Janssen, p. 110, pl. 1, figs. 4-6.
- v. 2007a *Heliconoides inflata* (d'Orbigny, 1836) type B; Janssen, p. 151, pl. 2, figs. 1-3, pl. 21, figs. 1-3.
- v. 2007b *Heliconoides inflata* (d'Orbigny, 1836); Janssen, p. 60, pl. 21, figs. 1-3.

Type locality – '... dans l'Océan atlantique et dans le grand Océan, sur une zone de 36 degrés nord et au sud de la ligne, ou de 1440 lieues marines, dans la largeur des grands océans du globe' (d'Orbigny, 1835, p. 175) (Recent).

Type material – BMNH 1854.12.4.35, cat. nr. 61. About 82 specimens in bad condition (dry collection, originally alcohol) (van der Spoel, 1976, p. 188).

Description – Shell small, sinistral, planorboid, apical plane concave, with the nucleus slightly elevated. There are three convex whorls, gradually increasing in diameter. Proximal half of body whorl with an internal falciform structure, produced anteriorly into a thickened subperipheral belt, appearing at the apertural margin as a rostrum, as the shell walls above and below the belt are extremely fragile and usually broken. Aperture large, produced both above and below the penultimate whorl. Columella thickened and often with a slight central notch. The base of the shell is umbilicate.

Material examined (with preserved apertural structures = *Heliconoides inflata*; juveniles = *Heliconoides inflata*?) – **Orthez (Le Paren)**: MNHN PL 12618/3 juveniles, MNHN A32090/1 juvenile (Pl. 7, fig. 12); RGM 516 563/1 juvenile, leg./don. J. van der Voort, 1997; RGM 541 304/11 juveniles, RGM 541 313/1 juvenile (Pl. 7, fig. 14a-d), leg. A.W. Janssen, 1979, 1981, 1986; RGM 541 310/8 juveniles, leg. F.A.D. van Nieulande, 26 July 1988, don. April 1989; **Salles**: MHB/7 juveniles, leg. unknown, 'aus *Cardita jouanneti*'; **Salles (Larieux)**: RGM 541 315/many juveniles, leg./don. F.A.D. van Nieulande, 17 July 1984. Serravallian.

Saint-Martin-de-Hinx (Secat): BRS 16446M/64, leg. B.G. Roest, 16 June 1987; MNHN PL 3350/49, MNHN A32091/1 (Pl. 7, fig. 11a-c) retaining apertural structures; RGM 395 402/many, two of these retaining apertural structures, leg. A.W. Janssen, 30 July 1984; RGM 541 051/many juveniles, RGM 541 052/2 fragments, retaining apertural structures, leg. A.W. Janssen, 1 August 1985; **Saubrigues (Jean-Tic)**: BRS 16521M/17, leg. B.G. Roest, 16 June 1987; RGM 541 379/2 juveniles, leg. A.W. Janssen, 8 June 1981; SMF 332775/3, largest specimen with preserved apertural structures, leg. R. Janssen; **Saubrigues (Tauziets)**: ABH 8Sb1/3 fragments with apertural structures preserved, c. 350 juveniles, leg. A.W. Burger, 11 May 1992; MNHN PL 4803/8; RGM 541 348/31 juveniles, leg. A.W. Janssen, 1979, 1981; RGM 569 475/13 and many fragments, leg. H.J. Mulder, 2007, don. October 2008; SMF 332776/12, some specimens retaining apertural structures, leg. R. Janssen, 8 June 1981. Langhian.

Corbleu (Carro): BRS 16702M/1 juvenile, leg. B.G. Roest, 17 June 1987; **La Brède (Moras)**: SMF 332777/1, apertural structures not preserved, K. Jung collection, 1883-1885; **Léognan**: MHB/8, 'aus Gastropoden', apertural structures not preserved; RGM 541 344/10, apertural structures not preserved, leg. unknown, from sediment contents of gastropods in old collection; **Léognan (Coquillat)**: BMNH PITG25520/3, preserving apertural structures; BMNH PITG25521/30 juvenile or damaged; both D. Curry collection; **Martillac (Barreau)**: BRS 14629/20, several retaining apertural structures, leg. B.G.

Roest, 9 May 1986; RGM 541 346/2, retaining apertural structures, leg. B.G. Roest, 9 May 1986, don. May 1997; **Martillac (Barreau 1)**: RGM 541 345/10, 5 of which retaining apertural structures, leg. A.W. Janssen, 6-7 August 1984; **Martillac (vigne)**: MNHN PL 11618/1; **Mérignac**: RGM 541 347/19, three retaining apertural structures, leg./don. F.A.D. van Nieulande, 20 July 1980; **Saucats**: MHB/2 juveniles, leg. unknown, 'aus *Cassiss*'; **Saucats (Coquillière)**: BRS 14990M/6, leg. B.G. Roest, 8 May 1985; RGM 541 331/138, four of which retaining apertural structures, leg./don. H.P.J. Keukelaar; RGM 541 333/136, four retaining apertural structures, leg./don. F.A.D. van Nieulande, July 1981; **Saucats (Coquillière-A 1)**: RGM 541 328/8, RGM 541 329/1, retaining apertural structures (Pl. 7, fig. 10a-b), leg. J. Gunst, 1982, don. F.A.D. van Nieulande; **Saucats (Coquillière-A2)**: RGM 541 332/4, apertural structures not preserved, leg./don. F.A.D. van Nieulande; **Saucats (Coquillière-A3)**: RGM 541 330/3, apertural structures not preserved, leg. J. Gunst, 1982, don. F.A.D. van Nieulande; **Saucats (Coquillière-A4)**: RGM 429 724/3, one retaining apertural structures, leg. A.W. Janssen, 21 and 24 July 1984; **Saucats (Lagus)**: MNHN PL 8374/10 more or less damaged/juvenile specimens (one of which retaining apertural reinforcements); **Saucats (Péloua)**: RGM 227 555/4 juveniles, leg./don. D. Gourgues, 1984; RGM 541 338/12 juveniles, leg./don. F.A.D. van Nieulande, July 1980; **Saucats (Pont-Pourquey)**: MNHN PL 11671/2 juveniles; RGM 541 340/12, no apertural structures preserved, leg./don. F.A.D. van Nieulande, July 1980); SMF 332778/1, apertural structures not preserved, leg. R. Janssen, 19 July 1978. Burdigalian.

La Brède: RGM 541 342/10, apertural structures not preserved, leg. J. Gunst, July 1982, don. F.A.D. van Nieulande; **Meilhan (Vives)**: MNHN PL 6637/11; RGM 516 559/3, apertural structures not preserved, leg./don. J. van der Voort; RGM 569 424/many, apertural structures not preserved, leg. S. Mermuys, 2006, don. 2007; **Saint-Paul-lès-Dax (Mainot)**: MHB/1, 4 juveniles, apertural structures not preserved, leg. unknown, 'aus Gastropoden'; **Saucats (Larley)**: MNHN PL 3991/7 mainly juvenile specimens. Aquitanian.

Damaged or juvenile specimens = '*Heliconoides* sp. (*inflata* or *tertiaria*)' – **Saint-Jean-de-Marsacq (Lahitet-1)**: MNHN PL 3664/5 juveniles; MNHN PL 6635/1 damaged; MNHN ex PL 3665/1 juvenile; **Saint-Jean-de-Marsacq (Pinot?)**: MHB/c. 70 juveniles (or damaged), apertural structures not preserved, 'aus Gastropoden'; **Saint-Jean-de-Marsacq (Pinot)**: RGM 541 384/many juveniles, leg./don. G. Garding, 3 July 1996; RGM 541 382/2 and 1 fragment, apertural structures preserved, leg./don. G. Garding, 3 July 1996; **Saint-Paul-lès-Dax (Cabanes)**: ABH 8Sp1/16 juveniles, 8Sp2/60 juveniles, leg. A.W. Burger, 15-16 June 2002; MHB/1, 3 juveniles, 'aus Gastropoden'; MNHN A32093/1 (Pl. 7, fig. 13), MNHN PL 6636/7 juveniles; RGM 541 353/120, apertural structures not preserved, leg. S. Mermuys, 2003-2004, don. November 2006; RGM 541 370/3, leg. A.W. Janssen, 1979-1987; SMF 332779/14 juveniles, leg. R. Janssen, 9 June 1981. Burdigalian.

Discussion – For extensive synonymy of Recent occurrences see van der Spoel (1967, p. 50). The relatively few specimens from the Aquitaine Basin with well-defined apertural reinforcements all seem to belong to type B, as defined in Janssen (2004b), in which the peripheral belt starts on earlier whorls and the falciform thickening is not developed. Specimens of *Heliconoides tertiary* (see below) are almost impossible to distinguish from the present species if the apertural features are not

present (juvenile or damaged specimens), which is the case in the greater part of the available samples. Their whorls increase slightly slower in diameter and the aperture hardly or not reaches above the penultimate whorl (compare Janssen, 1990a, pl. 3, figs. 8a and 11a). However, in a large sample a reliable identification is strongly hampered or impossible, because of overlapping variability. In the Aquitaine Basin, undoubtedly recognisable specimens of the two species, *H. inflata* and *H. tertiaria*, are found co-occurring in few localities only, viz. Saint-Jean-de-Marsaq (Lahitet-1 and Pinot) and Saint-Paul-lès-Dax (Cabanes), all of Burdigalian age. In the Mediterranean area, however, both species occur during Burdigalian and Langhian, so both can be expected during the entire time interval of the Aquitaine area. Accordingly, specimens not retaining apertural structures were identified as '*Heliconoides inflata?*' from localities where *H. tertiaria* is absent, and as '*Heliconoides sp. (inflata/tertiaria)*' if these species were found co-occurring.

The taxon *Spirialis miostralis* Kautsky, 1925, was introduced from Late Burdigalian/Langhian ('Hemmoorian' in local chronostratigraphy) rocks in northern Germany, North Sea Basin, without an illustration. The description, however, is such that the species is easily recognisable among the Miocene North Sea Basin limacinids. Kautsky did not describe any special apertural reinforcement structures in the material he had at hand and, indeed, virtually all North Sea Basin populations yield only specimens in which such structures are not developed. In the collection of the Geological Survey of Denmark, Copenhagen, however, I unexpectedly located a sample of *H. miostralis* from Gram-Enderupskov (borehole DGU 141.196, depth 54 m below surface; Arnum Formation), in which a number of specimens demonstrate well-developed apertural structures (Pl. 8, fig. 1a-c), strongly resembling those of Recent *Heliconoides inflata* (d'Orbigny, 1834), viz. with a internal falciform thickening in the second half of the body whorl, produced anteriorly into a distinct subperipheral belt or rostrum.

Once these features were discovered they could occasionally also be traced in specimens from other localities in the North Sea Basin. Even the specimen from Winterswijk-Miste (The Netherlands), illustrated in Janssen (1984a, pl. 20, fig. 3a-b, subperipheral belt not indicated), on closer investigation has this belt clearly developed. This feature was not mentioned in the description, indicating that at the time such structures were not expected to occur and were overlooked. It seems that such apertural reinforcements in the Miocene North Sea Basin populations develop only in the most adult or even senile specimens.

Kautsky compared his material with *Spirialis rostralis* Eydoux & Souleyet, 1840, which is a recognised synonym of what is now called *Heliconoides inflata*. He did not write, however, about the apertural reinforcement structures of the latter, but just compared the shapes of both species. It now appears that *H. miostralis* and *H. inflata* are distinctly related and the former should, no doubt, be considered ancestral to the latter.

The differences between specimens of *Heliconoides miostralis*, with completely developed apertural morphology, and *H. inflata* are very small indeed. In the North Sea Basin the whorls of *H. miostralis* commonly increase slightly faster in diameter, resulting in a somewhat wider aperture. The transition between its lower apertural margin and the columellar side is commonly more angular and the aperture protrudes more strongly above the penultimate whorl. In larger material from various localities,

however, the distinction between *H. miostralis* and *H. inflata* becomes vague and difficult to maintain. Therefore, it is more logical to consider both as belonging to one and the same species *H. inflata* and, if required, preserve the name *miostralis* for the North Sea Basin form at infraspecific level. This also agrees better with the occurrences in the Miocene of Australia (Janssen, 1990a) and the Caribbean (Janssen, 1999a), showing a more typical morphology, closely agreeing with Recent *H. inflata*. The disappearance of the taxon from the North Sea Basin during the later Miocene and Pliocene no doubt was caused by climatic changes, as *H. inflata* nowadays is distributed only in tropical and subtropical seas.

Distribution – Late Oligocene, North Sea Basin; Early and Middle Miocene, North Sea Basin, Aquitaine Basin, Mediterranean, Caribbean, south Australia; Pliocene, Mediterranean, Philippines, Japan; Pleistocene/Recent, tropical and subtropical seas worldwide.

***Heliconoides linneensis* Janssen, 2008a**

Pl. 8, figs. 2-6.

*v 2008a *Heliconoides linneensis* Janssen sp. nov., p. 70, figs. 1-7.

Type locality – Saint-Etienne-d’Orthe (Lartigaou). Oligocene, Chattian, Marnes de Saint-Etienne-d’Orthe Formation, zone NP25 (Steurbaut *in* Zorn & Janssen, 1993, p. 61; Cahuzac *et al.*, 1995).

Type material – Holotype RGM 541 416 (Pl. 8, fig. 2a-c) and paratypes as listed below.

Description – The shell is sinistral, small, slightly higher than wide (height of holotype 0.92 mm, width 0.86 mm) and nearly spherical in shape. The protoconch is not clearly separated from the teleoconch. The nucleus has a diameter of *c.* 45 µm and has a granulated to honeycomb microornament (Janssen, 2008a, fig. 7b). There are somewhat more than three, rarely three and a half, moderately convex whorls, together forming a low cone with convex tangents. The body whorl is gradually rounded and has a narrow umbilicus. Close to the apertural margin an obliquely vertical, slightly curved swelling in the shell wall forms a reinforced rim. At this place the shell wall has a micro-ornament of irregularly arranged pustules (Janssen, 2008a, fig. 6b). The shell wall in front of this rim is very fragile and broken in practically all specimens.

Material examined (all paratypes, if not stated otherwise) – **Bélus (Marcon)**: MNHN A32071/17 and 1 (illustrated Janssen, 2008a, fig. 2a-b; Pl. 8, fig. 3a-b herein); MNHN A32072/2 fragments, P. Lozouet collection; **Orthevielle (Tauzia)**: MNHN A32073/1 fragment; **Peyrehorade (Peyrère)**: MNHN A32074/1 (illustrated Janssen, 2008a, fig. 3a-c; Pl. 8, fig. 4a-c herein), MNHN A32075/5; RGM 541 403/2, leg. A.W. Janssen; **Peyrehorade (Tauziède)**: MNHN A32076/5, 1 fragment; **Saint-Etienne-d’Orthe (Église A)**: MNHN A32077/8 and 10 damaged; **Saint-Etienne-d’Orthe (Église B)**: MNHN A32078/18; **Saint-Etienne-d’Orthe (Église C)**: MNHN A32079/2 fragments, P. Lozouet collection; **St Etienne d’Orthe (Hondelatte)**: RGM 541 457/2

fragments, leg. A.W. Janssen; **Saint-Etienne-d'Orthe (Lartigaou)**: BRS 16336/11; RGM 541 417/1 (illustrated Janssen, 2008a, fig. 6a-b), RGM 541 418/1 (illustrated Janssen, 2008a, fig. 7), RGM 541 419/88, leg. A.W. Janssen, 1984-1990, RGM 541 449/3, leg./don. A.C. Janse; SMB unnumbered/22 (no paratypes), leg. S. Mermuys, July 2006; **Saint-Etienne-d'Orthe (Verdun)**: MNHN A32080/6 and 27; **Saint-Paul-lès-Dax (Bezoye)**: MNHN A32081/3 juveniles; **Saint-Paul-lès-Dax (Estoti)**: MNHN A32082/1 (illustrated Janssen, 2008a, fig. 5a-c; Pl. 8, fig. 6a-c herein); **Saint-Paul-lès-Dax (Lestrilles)**: MNHN A32083/1 (illustrated Janssen, 2008a, fig. 4a-b; Pl. 8, fig. 5a-b herein). Chattian.

Saint-Paul-lès-Dax (Cabanes): SMF 332780/2 (no paratypes), leg. R. Janssen, 9 June 1981. Earliest Burdigalian.

Discussion – This species is quite common in the Chattian rocks of the Adour area, but it was also found in the earliest Burdigalian of Saint-Paul-lès-Dax (Cabanes). The two specimens do not look reworked.

A closely related species is *Heliconoides vanderweideni* Janssen, 2004a (p. 14, pl. 3, figs. 17a-b, 18a-c), introduced from the Chattian/Aquitanian Lower Globigerina Limestone Formation of the Maltese Archipelago. It differs from the present species in being more globular, with more convex whorls and the apertural rim is interrupted at two thirds of its height.

Distribution – Exclusively known from Late Oligocene ('Chattian of the Adour area') and earliest Burdigalian deposits in the Aquitaine Basin.

***Heliconoides merlei* sp. nov.**

Pl. 3, fig. 3; Pl. 8, figs. 7-9.

v. 1982 *Spiratella* sp.: Curry, p. 37, pl. 1, fig. 2a-c.

Holotype – BMNH GG. 21247a, specimen illustrated in Curry (1982, pl. 1, fig. 2b; Pl. 8, fig. 7a-d herein).

Type locality – Gan (Tuilerie).

Stratum typicum – Marnes de Gan (Eocene, Middle-Late Ypresian), NP12/13.

Derivatio nominis – Named after Dr Didier Merle (MNHN), who wrote his Ph.D. (Merle, 1986) on the mollusc fauna of the Gan locality and donated specimens from that locality for the RGM collections.

Paratypes – **Gan (Tuilerie)**: BMNH GG. 21247b/1 (illustrated Curry, 1982, pl. 1, fig. 2a) (Pl. 8, fig. 8a-d herein), BMNH PITG25491/10 juveniles, BMNH PITG25493/2 juveniles from sample identified *Spiratella mercinensis*, all D. Curry collection; RGM 396 850/1 juvenile, Pl. 8, fig. 9a-b, RGM 541.542/2 juveniles, RGM 569.460/1 juvenile (Pl. 3, fig. 3), all leg. A.W. Janssen, 1981-1990; SMF 332781/2 juveniles, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Diagnosis – Shell small, sinistral, almost planispiral, with a depressed rounded shape, resembling a flat *Umbonium*. Aperture large, with a widened apertural margin, the upper part of which is almost straight in juvenile specimens.

Description – Shell small, sinistral, in adult state slightly more than twice as wide as high (H = 0.56 mm, W = 1.28 mm) and with a very low-conical spira, its shape resembling a flattened *Umbonium*, with a just protruding apex. There are three whorls (reconstruction) initially attaching just above the periphery of the preceding whorl, but increasingly higher towards the aperture. In juvenile specimens (Pl. 8, figs. 8a, 9a), the upper margin of the aperture is straight and almost horizontal, with a rather abrupt transition into the abaxial apertural margin. In the adult state, the aperture is much wider than high and its margin is somewhat bent outward as a reinforcement structure. The base of the shell is flattened and has a distinct umbilicus occupying about one sixth of the shell's diameter.

Discussion – This species is insufficiently known. Apart from a very fragmentary adult shell (Curry, 1982, fig. 2b; holotype, Pl. 8, fig. 7a-d herein), just a few juvenile specimens are available. It has, however, a quite remarkable shape and cannot be mistaken for any other known thecosome pteropod. Distantly similar is '*Planorbis*' *andersoni* Gardner (1927, p. 377, figs. 36, 37) from the Middle Eocene of Texas, of which only the holotype is known; this species was also illustrated as '*Skaptotion*' *andersoni* (Gardner) by Hodgkinson *et al.* (1992, p. 22, pl. 6, figs. 2-4). That specimen, however, is relatively more thickset, reaches a larger dimension (W = 2.2 mm), its apical plane is distinctly depressed and it is unknown if the species develops apertural reinforcements.

Distribution – *Heliconoides merlei* is only known from its type locality.

***Heliconoides mermuysi* sp. nov.**

Pl. 9, figs. 2, 3.

Holotype – RGM 541 350 (Pl. 9, fig. 2a-d), leg. S. Mermuys, 2003-2004, don. November 2006.

Type locality – Saint-Paul-lès-Dax (Cabanes).

Stratum typicum – Miocene, Early Burdigalian, N5 zone; reefal and shelly coarse sands, coastal facies, Falun de Cabanes.

Derivatio nominis – The new species is named after Mr Stef Mermuys, of Bergschenhoek (The Netherlands), who collected and donated part of the type material.

Paratypes – **Saint-Paul-lès-Dax (Cabanes):** ABH 8Sp2/2 juveniles (1 lost), leg. A.W. Burger, 15-16 June 2002; MNHN A32084/1 (Pl. 9, fig. 3a-c), 1 juvenile; RGM 541 351/3, RGM 569 413/1, leg. S. Mermuys, 2003-2004, don. November 2006; RGM 541 369/1, leg. A.W. Janssen, 1979-1987; SMF 332782/4, K. Jung collection, 1883-1885; SMF 332783/2, leg. R. Janssen, 9 June 1981. Early Burdigalian.

Diagnosis – *Heliconoides* with a flattened shell, *c.* 1½ times wider than high, and three whorls in a regular spiral. Aperture circular, with a clearly separated external reinforcement rim.

Description – The shell is small (diameter close to 1 mm), depressed conical, about one and a half times wider than high, and has three convex whorls in a regular spiral. The whorls attach slightly above the periphery of the preceding whorl. The aperture is large, almost circular, slightly indented by the penultimate whorl. The apertural margin is somewhat widened and bears a clearly separated external reinforcement rim. The base of the shell has a wide umbilicus (about one quarter of the shell's diameter) in which the two preceding whorls are visible.

Discussion – The shape of this species closely resembles *Heliconoides hospes* (see above), but in that species the apertural margin is simply widened, without a reinforcement rim. Also, *H. tertiaria* is similar, but its body whorl is higher and the spire is planorboid, not depressed conical.

Distribution – This new species so far is only known from the type locality.

Heliconoides nemoris (Curry, 1965)

Pl. 9, figs. 4, 5

- v. 1965 *Spiratella nemoris* Curry sp. nov, p. 362, figs. 17a-b (not 16a-b = *S. mercinensis*).
- v. 1982 *Spiratella nemoris* Curry; Curry, p. 37, pl. 1, fig. 5a-b.
- ? 1992 *Limacina nemoris* (Curry); Hodgkinson *et al.*, p. 18, pl. 3, figs. 9, 10.

Type locality – Bramshaw, Hampshire (UK); Upper Bracklesham Beds (Eocene, "Auversien" = late Lutetian).

Type material – Holotype, BMNH GG. 7100, reillustrated herein (Pl. 9 fig. 4a-e); several paratypical specimens referred to by Curry (1965).

Description – Shell small ($H = c.$ 1 mm), conical, just slightly higher than wide. The shell has four whorls, the first one and a half of which are planispiral, which make the apex look blunt. The whorls are rather convex, separated by incised sutures, and increase gradually in width. Aperture relatively large, occupying slightly more than half the shell height, semicircular, columella straight, not thickened in its middle part (holotype). Apertural margin internally reinforced by a narrow ridge (Pl. 9, fig. 4e). Margin oblique to the shell's vertical axis (lateral view, Pl. 9, fig. 4d).

Material examined – **Biarritz**: BMNH GG. 21268/1 (illustrated by Curry, 1982, pl. 1, fig. 5a-b) (Pl. 9, fig. 5a-b herein); BMNH PITG25512/12. This locality (Marnes des Bains) is Priabonian (NP19-20 zones; Mathelin & Sztrákos, 1993).

Discussion – In the original description (Curry, 1965), the apertural margin was described as 'slightly expanded in the adult shell', which, however, could not be ac-

knowledge on the holotype, in which, on the contrary, the apertural margin demonstrates the presence of an internal ridge, not mentioned by Curry. Because of this reinforcement I transfer the species to the genus *Heliconoides*.

The specimens from Biarritz in the BMNH collection, referred to by Curry (Pl. 9, fig. 5a-b herein), are filled with pyrite, which prevents observation of the characteristics of the inner apertural margin. Some of them are larger than the holotype and have slightly less convex whorls.

Distribution – Apart from the occurrence at Biarritz, *Heliconoides nemoris* is known from the late Middle to early Late Eocene of the London, North Sea and Paris basins (Janssen & King, 1988, fig. 188). Specimens referred to with this name from Middle and ‘undifferentiated’ Eocene deposits in the U.S.A. (Hodgkinson *et al.*, 1992, p. 18, pl. 3, figs. 9, 10) remain under 1 mm shell height and do not have the blunt apex of the European specimens. Hodgkinson *et al.* (1992, text-fig. 3) indicate the occurrence of their specimens in NP16, which is Late Lutetian/Early Bartonian.

***Heliconoides paula* (Curry, 1982)**

Pl. 3, fig. 2; Pl. 9, fig. 6.

v. 1982 *Spiratella paula* Curry n. sp., p. 38, pl. 1, fig. 6a-b.

Type locality – Gan (Tuilerie), Eocene, Middle-Late Ypresian, Marnes de Gan, NP12/13.

Type material – Holotype BMNH GG. 21251/1, Curry (1982, pl. 1, fig. 6a-b; Pl. 9, fig. 6 herein); BMNH PITG25492/7, paratypes, all D. Curry collection.

Description – Very small (H = 0.7 mm), sinistral shell of conical shape, just slightly higher than wide, consisting of 4½ convex whorls in a regular spiral. The height of the body whorl equals 4/5th of the total shell height. The aperture is oval, slightly higher than half the shell height. The apertural margin is strongly sigmoid (lateral view) and distinctly thickened, continuous into the columella. Base of the shell gradually rounded, umbilicus virtually absent.

Material examined – **Gan (Tuilerie)**: type specimens as specified above, furthermore: BMNH PITG25504/1 juvenile and 1 fragment, from unsorted sample, no paratypes, D. Curry collection; RGM 396 600/1, 1 def., RGM 569 453/1 (Pl. 3, fig. 2), both leg. A.W. Janssen, 1981-1990; SMF 332784/2, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – This rather elegant species is easily recognisable by its small size and sigmoid, thickened apertural margin.

Distribution – Only known from the type locality.

Heliconoides pyrenaica sp. nov.

Pl. 3, fig. 4; Pl. 9, fig. 7.

- v. 1982 *Spiratella mercinensis* (Watelet & Lefèvre); Curry, p. 36, pl. 1, fig. 1a-b. (*non* Watelet & Lefèvre, 1885).

Holotype – BMNH GG. 21266/1, Curry, 1982, pl. 1, fig. 1a-b (Pl. 9, fig. 7a-b herein).

Type locality – Gan (Tuilerie).

Stratum typicum – Marnes de Gan (Eocene, Middle-Late Ypresian), NP12/13.

Derivatio nominis – Named after the department of Pyrénées-Atlantiques, the administrative unit in which the type locality is situated.

Paratypes – **Gan (Tuilerie)**: BMNH PITG25494/1 fragment, 12 juvenile specimens, D. Curry collection; RGM 569 455/1 damaged, 4 juvenile specimens, RGM 569 456/1 juvenile (Pl. 3, fig. 4), all leg. A.W. Janssen, 1981-1990. Middle-Late Ypresian.

Diagnosis – *Heliconoides* of planorboid shape, with three convex whorls. Body whorl widening rapidly. Aperture large, upper margin not reaching above penultimate whorl. Apertural margin reinforced by an internal ridge, continuous with the columella.

Description – Shell small, H = 1.1 mm, W = 1.5 mm. There are three convex whorls of which the last one increases especially rapidly in diameter, resulting in a planorboid shape, with the upper margin of the large aperture in line with the apical plane, not reaching above the penultimate whorl. The large aperture is lunate, produced downward. Its margin is reinforced by an internal ridge connected with the lower part of the columella. In front of this ridge a narrow, extremely thin and fragile further part of the shell wall is present, which is irregularly broken. The columella is rather solid, with a slight swelling below the base of the foregoing whorl. The base of the shell is gradually rounded, with a narrow umbilicus.

Discussion – The holotype is the only available more or less complete specimen. Several juvenile specimens, yet without the apertural structures, can be recognised by their relative shell height. A fragment in the BMNH collection also shows the apertural reinforcement.

The holotype was illustrated by Curry (1982) as '*Spiratella mercinensis* (Watelet & Lefèvre, 1855' [*sic*]). It does not agree in several respects with that species, as known from the Paris Basin Ypresian (compare Watelet & Lefèvre, 1885, p. 102, pl. 5, fig. 2a-c). A specimen of the real *H. mercinensis*, from the Ypresian of Saint-Gobain (Paris Basin), is illustrated herein for comparison (Pl. 9, fig. 1a-b). The differences in proportions are clear at first glance; *H. pyrenaica* is considerably higher with a more rounded aperture. Also, the apertural structures are utterly different; in *H. mercinensis* the inner apertural ridge is strongly recurved backward in the middle to a more or less v-shaped sinus, which makes the upper and lower parts of the aperture look projecting. The '2 ou 3

proéminences obtuses', mentioned in Curry's (1982, p. 36) description, are irregularly broken remnants of the fragile extreme apertural margin.

Very similar is a specimen illustrated by Hodgkinson *et al.* (1992, p. 21, pl. 5, figs. 1-3) under the name of *Limacina wechesensis* Hodgkinson. That specimen, however, has a differently shaped aperture, without reinforcements, and a wider umbilicus. Its age is Lutetian.

Distribution – Only known from the type locality.

***Heliconoides tertiaria* (Tate, 1887)**

Pl. 10, figs. 1-3

- *v. 1887 *Spiralis tertiaria* Tate, spec. nov., p. 196 (partim, non pl. 20, fig. 12a-c = *Heliconoides inflata*).
- v. 1897 *Limacina tertiaria*, Tate (sp.); Harris, p. 19 (partim?).
- v. 1899 *Limacina tertiaria*, Tate; Tate, p. 260.
- 1903 *Limacina tertiaria*, Tate; Dennant & Kitson, p. 94.
- 1965 *Spiratella tertiaria*; Curry, p. 368.
- 1982 *Spiratella tertiaria* Tate; Curry, p. 38.
- 1982 *Spiratella tertiaria* (Tate); Bernasconi & Robba, p. 215
- v. 1990a *Limacina tertiaria* (Tate, 1887); Janssen, p. 19, pl. 3, figs. 1-10, pl. 4, figs. 1-6, pl. 11, figs. 1-2.

Type locality – Muddy Creek near Hamilton, Otway Basin, Tyrenderra Embayment, Victoria, Australia; 'lower beds' = Muddy Creek Formation (Miocene, Balcombian to Bairnsdalian) (Langhian–Tortonian).

Type material – Lectotype SAM T 239 (Janssen, 1990a, p. 21, pl. 3, fig. 1) and 12 paralectotypes, SAM 238/5-6, SAM P29782-4.

Description – Shell small, sinistral, planorboid, with *c.* 2¾ convex whorls, rapidly and gradually increasing in diameter. Apical plane concave, first whorl slightly elevated, but usually invisible in a frontal view of adult specimens. Aperture large, circular, margin reinforced by a ridge, in front of which the whorl is widened. Columella usually with a distinct central notch. Base of shell with a relatively narrow umbilicus, occupying about one sixth of the shell diameter.

Material examined – **Saint-Jean-de-Marsacq (Lahitet-1)**: MNHN A32094/4 (Pl. 10, fig. 2a-b), MNHN 3664/1; MNHN A32095/1 (Pl. 10, fig. 3a-b); **Saint-Jean-de-Marsacq (Pinot)**: RGM 429 263/2, 16 juveniles, RGM 541 482/2 retaining apertural structures, leg. F.A.D. van Nieulande, July 1996, don. October 1996; RGM 516 562/1, RGM 541 495/1 juvenile, leg./don. J. van der Voort, 22 June 1997; RGM 541 383/20, leg./don. G. Garding, 3 July 1996; **Saint-Paul-lès-Dax (Cabanes)**: RGM 541 352/1 (Pl. 10, fig. 1a-b), RGM 569 412/1, leg. S. Mermuys, 2003-2004, don. November 2006; RGM 541 368/1, leg. A.W. Janssen, 1979-1987; SMF 332785/6, K. Jung collection, 1883-1885; SMF 332786/1, O. Boettger collection, ex K. Jung, 1883-1885. Burdigalian.

Discussion – Juvenile or damaged specimens not retaining the apertural features cannot with any certainty be distinguished from juvenile *Heliconoides inflata* (see above).

Such specimens were labeled *Heliconoides inflata?* in localities where only that species was found or as '*Heliconoides* sp. (*inflata/tertiaria*)' in localities where both species occur with certainty.

Distribution – The species was originally described from the Miocene of southern Australia. A closely related, if not identical species, *Heliconoides ferax* (Laws, 1944), is known from the Altonian (= Langhian) of New Zealand. Further, *H. terciaria* occurs at many Miocene (Aquitanian to Langhian) localities in the central Mediterranean (Malta, Sicily, Italia, Sardinia; RGM collections). This is the first European extra-Mediterranean record. All outcrops cited above from Aquitaine, however, are of Burdigalian age.

Genus *Limacina* Bosc, 1817

Type species – *Limacina helicina* (Phipps, 1774) (Recent).

Remarks – The taxon *Munthea* van der Spoel, 1967 (p. 37), was introduced as a subgenus of *Limacina* for three Recent species, viz. *L. bulimoides* (d'Orbigny, 1836), *L. 'cochlostiloides'* Tesch, 1907, and *L. trochiformis* (d'Orbigny, 1834), but without designation of a type species. According to art. 13.3 ICZN, therefore, *Munthea* is not an available name. Janssen (2003, p. 165) referred to *Munthea* van der Spoel, 1967, and designated *Limacina trochiformis* as type species. This fulfills arts. 13.1.2 and 13.3 of the Code, but not art. 16.1.

To make the 'new' name *Munthea* gen. nov. available, I here refer to van der Spoel's (1967) description and designate *L. trochiformis* as its type species. For the time being, however, this is a purely academic question, as I consider *Munthea* to be a junior synonym of *Limacina* Bosc, 1817. Whenever a new nomenclature will be necessary for the Limacinidae, the name *Munthea* will at least be available. I thank Philippe Bouchet (MNHN), who drew my attention to this situation (in litt., March 2006).

Limacina bulimoides (d'Orbigny, 1834)

Pl. 3, fig. 5; Pl. 10, fig. 4-5.

- * 1834 *A(lanta)* [sic] *bulimoides*, d'Orbigny, pl. 24, figs. 36-38.
- . 1836 *Atlanta bulimoides* d'Orb; d'Orbigny, p. 179.
- . 1967 *Limacina* (*Munthea*) *bulimoides* (Orbigny); van der Spoel, p. 53, fig. 21.
- . 1977 *Limacina bulimoides* (d'Orbigny); Bé & Gilmer, p. 764, pl. 3, fig. 4a-d.
- . 1983 *Limacina bulimoides* (d'Orbigny); Shibata & Ujihara, p. 158, pl. 43, figs. 3, 4.
- . 1983 *Limacina trochiformis* (d'Orbigny); Shibata & Ujihara, p. 158, pl. 43, fig. 2 (*non* d'Orbigny).
- . 1986 *Limacina bulimoides* (d'Orbigny); Shibata, p. 124.
- . (1996) *Limacina bulimoides* (d'Orbigny); Kunz, p. 64, pl. 2.
- v. 1998 *Limacina bulimoides* (d'Orbigny); Janssen, p. 99, pl. 1, figs. 6-8.
- v. 2007a *Limacina bulimoides* (d'Orbigny, 1836); Janssen, p. 151, pl. 15, figs. 3-5.
- v. 2007b *Limacina bulimoides* (d'Orbigny, 1836); Janssen, p. 62, pl. 1, figs. 8, 9, pl. 22, figs. 2, 3.

Type locality – ...'commune aux deux grands Océans. Elle occupe aussi une très-grande surface, puisque nous l'avons rencontrée sur 34 degrés au nord et au sud de l'Équateur, équivalent à une largeur de 1280 lieues marines, dans la zone torride et tempérée des mers'' (d'Orbigny, 1836, p. 179).

Type material – Gray (1854) listed syntypes of many species described by d'Orbigny, but the species '*Atlanta (Heliconoides) bullinoides*, d'Orb.' [sic] (Gray, 1854, p. 7) is not marked B.M., indicating that syntypes were not received for the BMNH collection. Van der Spoel (1976, p. 264) also did not find syntypical specimens in the MNHN collection.

Description – See van der Spoel (1967, p. 53).

Material examined – **Saucats (Coquillière)**: RGM 541 326/20 juveniles, leg./don. H.P.J. Keukelaar; RGM 541 327/5 juveniles, RGM 541 547/1 juvenile (Pl. 10, fig. 4), RGM 541 548 /1 (Pl. 3, fig. 5a-b), all leg./don. F.A.D. van Nieulande, July 1981; **Saucats (Coquillière-A 1)**: RGM 541 325/5 juveniles, leg. J. Gunst, 1982, don. F.A.D. van Nieulande; **Saucats (Pont-Pourquey)**: RGM 541 341/3 juveniles, leg./don. F.A.D. van Nieulande, July 1980. Burdigalian.

La Brède: RGM 541 343/11 juveniles, leg. J. Gunst, July 1982, don. F.A.D. van Nieulande. Aquitanian.

Discussion – For extensive synonymy of Recent occurrences see van der Spoel (1967, p. 53). The few specimens recovered from several localities in the Aquitaine Basin are all juvenile or severely damaged, and therefore difficult to compare with the Recent species *Limacina bulimoides*, with which they agree in proportions. One of the larger available specimens is compared (Pl. 10, fig. 4) with an equally sized Recent specimen (Pl. 10, fig. 5), which demonstrates that especially the early whorls in the Miocene shell are slightly more convex.

Distribution – *Limacina bulimoides* is widely distributed in the Recent fauna of tropical and subtropical seas. Pliocene specimens from the Caribbean, the Mediterranean and the Philippines agree more closely with the Recent form than the Miocene specimens recorded here.

Limacina gormani (Curry, 1982)

Pl. 3, figs. 6-8; Pl. 10, figs. 6-8; Pl. 11, fig. 1; Pl. 12, figs. 1-2.

*v. 1982 *Spiratella gormani* Curry n. sp., p. 37, pl. 1, fig. 4a-e.

? 1992 *Limacina pygmaea* (Lamarck); Hodgkinson *et al.*, p. 19, pl. 3, figs. 14, 15 (*non* Lamarck?).

. (1996) *Limacina gormani* (Curry, 1981); Kunz, p. 159, pl. 28, figs. 1-4.

. (1996) *Praeperaclis gormani* (Curry, 1981); Kunz, p. 161.

Type locality – Gan (Tuilerie), Marnes de Gan, Middle-Late Ypresian, NP12/13.

Type material – Holotype BMNH GG. 21249/1, illustrated Curry (1982, fig. 4a-b; Pl. 10, fig. 6a-d herein), BMNH PITG25489/130 paratypes (only c. 80 paratypes, however, were mentioned by Curry, 1982). The two paratypes illustrated in Curry (1982, fig. 4c-d) could not be recognised among the available specimens.

Description – Near-spherical limacinid, when adult higher than wide (H = 1.68, W = 1.32 mm, holotype), but juvenile specimens markedly wider than high and with a dis-

tinct peripheral carina. Body whorl large, occupying 9/10th of the shell height. The whorls attach at the periphery of the preceding whorl, which makes the carina invisible in larger specimens. The suture is shallow. The periphery and base of the body whorl are rounded when adult, a very narrow umbilicus is present (Pl. 3, fig. 7), but covered in larger specimens by the recurved columella, which may be slightly thickened in its middle. The apertural margin is not reinforced. Growth lines are inconspicuous. On the early whorls an ornament of short radial crests is present along the abapical side of the suture. These crests are almost invisible with a light microscope, but clearly seen in SEM-images (Pl. 3, fig. 8a-b; Pl. 11, fig. 1b).

In one juvenile aberrant specimen, a distinct spiral ridge is present on the second and third whorl (Pl. 11, fig. 1a-b).

Material examined – **Gan (Bosdarros)**: RGM 396 614/38, leg. A.W. Janssen, 28 August 1990; **Gan (Tuilerie)**: BMNH PITG25505/17 juvenile specimens, from unsorted sample, no paratypes, BMNH PITG25497/14 juvenile specimens, from unsorted sample, no paratypes, all D. Curry collection; RGM 396 589/1 (Pl. 10, fig. 7a-c), RGM 396 590/1 juvenile (Pl. 12, fig. 2a-c), RGM 396 591/1 juvenile (Pl. 12, fig. 1a-c), RGM 396 592/1 juvenile (Pl. 10, fig. 8a-c); RGM 396 593/many, RGM 541 316/1 (Pl. 3, fig. 8a-b), RGM 541 421/1 (Pl. 3, fig. 7), RGM 541 550/1 (Pl. 3, fig. 6), RGM 569 452/1 juvenile (aberrant specimen) (Pl. 11, fig. 1a-b), all leg. A.W. Janssen, 1981-1990; RGM 396 603/4 juveniles, leg./don. D. Merle; RGM 396 607/1 juvenile, leg./don. C. Dolin, 1983; SMF 332787/24, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – Curry (1982, pl. 1, fig. 4e) gave a reconstruction of a fully adult specimen. In his drawing the apertural margin seems to be thickened, which is not actually so. Also, the flexuous shape of the margin could not be recognised in the material before me. None of the many available specimens has its apertural margin really preserved and growth lines are not visible.

Kunz (1996, p. 159, pl. 28, figs. 2, 3 b) was the first to observe the presence of the short and regular subsutural crests, and concluded that this species should be classified in the Pseudothecosomata, Peraclididae. He suggested a new genus for this species, *Praeperaclis*, which name, however, is not available, as his paper remained unpublished. The occurrence alone of subsutural crests, invisible as they are in light microscopy, does not convince me of the validity of a new taxon and the columellar portion of the shell has not the slightest resemblance with Peraclididae. I therefore retain *L. gormani* in the Thecosomata, Limacinoidea.

Specimens illustrated by Hodgkinson *et al.* (1992) as *Limacina pygmaea*, from the Stone City and Cook Mountain Formations, Wheelock Marl Member (Texas, U.S.A.), closely resemble *L. gormani* and, judging from the illustrations, I would not hesitate to include them in the present species. Curiously, however, the age of these deposits is considered to be Bartonian (Hodgkinson *et al.*, 1992, text-fig. 1), which makes their identity unlikely.

Distribution – Apart from the occurrences at Gan, France, a single doubtful specimen was recovered from the Ieper Clay Member (Ypresian) of the IJsselmuiden borehole-I; 843-848 m-RT (The Netherlands) (RGM 397 063).

Limacina pygmaea (Lamarck, 1805)

Pl. 12, figs. 3-5.

- * 1805 *Ampullaria pygmaea* ..., Lamarck, p. 30.
- . 1806a *Ampullaria pygmaea*; Lamarck, pl. 61, fig. 6a, b.
- . 1824 *Ampullaria pygmaea*. Lamk.; Deshayes, p. 141.
- . 1837 *Ampullaria pygmaea*. Lamk.; Deshayes, pl. 17, figs. 15, 16.
- . 1881 *Spirialis Bernayi*, de Laubrière, p. 377, pl. 8, fig. 5.
- . 1885 *Spirialis pygmaea*, Lamarck, sp.; Dollfus & Ramond, p. 40, pl. 3, fig. 1a-d.
- . 1885 *Spirialis Bernayi*, de Laubrière; Dollfus & Ramond, p. 41, pl. 3, fig. 2.
- . 1885 *Spirialis parisiensis*, Watelet & Lefèvre, p. 101, pl. 5, fig. 3a-c.
- . 1885 *Ampullaria pygmaea* Desh. [sic]; Zittel, p. 312, fig. 459.
- . 1892 *Spirialis pygmaea* (Lamk.); Cossmann, p. 7, pl. 2, figs. 26-28.
- . 1892 *Spirialis Bernayi*, de Laub.; Cossmann, p. 8, pl. 2, fig. 25.
- . 1910 *Spirialis pygmaea* Lam.; Pezant, p. 158, pl. 13, fig. 1a, b.
- . 1913 *Spirialis Bernayi* Laub.; Cossmann, p. 238.
- . 1913 *Spirialis pygmaea* (Lamk.) var. *Bernayi* de Laubrière; Cossmann, p. 238.
- . 1913 *Spirialis pygmaea* (Lamk.) var. *Pezanti* (nov. var., 1913); Cossmann, p. 238.
- . 1913 *Spiratella pygmaea* (Lamck.); Cossmann & Pissarro, pl. 60, fig. 1-1.
- v. 1965 *Spiratella pygmaea* (Lamarck); Curry, p. 362, figs. 18a, b, 19
- . 1979 *Spiratella pygmaea* (Lamarck); Curry & Rampal, p. 23, fig. 1a, b.
- v. 1982 *Spiratella pygmaea* (Lamarck); Curry, p. 37, pl. 1, fig. 3a, b.
- non 1992 *Limacina pygmaea* (Lamarck); Hodgkinson *et al.*, p. 19, pl. 3, figs. 14, 15 (= *Limacina* aff. *gormanii*).
- v. 2007 *Limacina pygmaea* (Lamarck, 1805) ?; Janssen *et al.*, p. 165, fig. 11.

Type locality – ‘Chaumont’ (= Chaumont-en-Vexin, Oise, France; Paris Basin). Eocene, Lutetian.

Type material – The whereabouts of the syntypes is unknown.

Description – Shell small, sinistral, naticoid, slightly wider than high to somewhat higher than wide. There are about four whorls in a regular spiral, which in the Gan material is usually flattened, hardly or not visible in a frontal view. Aperture semicircular, apertural margin not reinforced, columella with a clear thickening in the middle. Umbilicus narrow, occupying one seventh of the shell’s diameter.

Material examined – **Gan (Bosdarros)**: RGM 396 615/4 (poorly preserved), RGM 396 616/2, leg. A.W. Janssen, 28 August 1990; **Gan (Tuilerie)**: BMNH GG. 21258/2, illustrated Curry (1982, pl. 1, fig. 3a, b; Pl. 12, figs. 3, 4 herein); RGM 396 849/1, leg. A.W. Janssen, 1981-1990 (Pl. 12, fig. 5); SMF 332788/1, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – Especially in the Lutetian of the Paris Basin, this species is found with variable height of the spire. In the typical form the spire is slightly elevated and even more so in forma *bernayi* de Laubrière, 1881. In forma *pezanti* Cossmann, 1913, the spire is flattened, hardly or not protruding above the body whorl. Most specimens from Gan belong to this latter form, but there are two poorly preserved specimens (RGM 396 616) that have their spire more elevated, agreeing with the typical form of this species.

Distribution – The Gan localities are the only occurrences known in Ypresian rocks. This species is known from numerous localities of Lutetian age in the Paris Basin. Cossmann (1922, p. 156) also recorded a single specimen from Le Bois-Gouët (Loire-Atlantique, France). From the North Sea Basin, the species is known from Middle Eocene localities in England, Belgium and The Netherlands (RGM collections). Janssen *et al.* (2007) found a doubtful specimen in Lutetian concretions from Denmark.

The specimens recorded by Hodgkinson *et al.* (1992) do not belong to this species, but seem to be related to *Limacina gormani* (see above). *Spiratella pseudopygmaea* Eames, 1952 (p. 150, pl. 6, fig. 146a-b), based on juvenile specimens from the Eocene of India/Pakistan, might be related or even identical.

Limacina valvatina (Reuss, 1867)

Pl. 12, figs. 6-12.

Selected synonyms:

- *v 1867 *Spiralis valvatina* Reuss, p. 32, 146, pl. 6, fig. 11a, b.
- v 1968 *Spiratella valvatina* (Reuss 1867); Rasmussen, p. 243, pl. 27, figs. 1-3, 11.
- . 1969 *Spiralis valvatina* Reuss, 1867; Hiltermann, p. 189, pl. 1, fig. 3.
- . 1972 *Spiratella valvatina* (Reuss, 1867); Nordsieck, p. 18, 125, pl. 32, fig. 219.
- v 1972 *Spiratella valvatina* (Reuss, 1867); Janssen, p. 61, text-figs. 31-40, pl. 11, fig. 10.
- . 1977 *Spiratella valvatina* (Reuss, 1867); Jakubowski & Musial, p. 116, fig. 5a-c.
- v 1984a *Limacina valvatina* (Reuss, 1867); Janssen, p. 381, pl. 20, figs. 1a, b, 2a, b.
- v 1984b *Spiralis valvatina* Reuss, 1867; Janssen, p. 72.
- . 1984 *Limacina*; Backeljau, p. 73, 74, fig. 5 (upper left, lower middle) (*partim*).
- v 1989 *Spiratella praerangi praerangi* Tembrock sp. n., p. 244, fig. 6a, b.
- v 1989 *Spiratella praerangi weinbrechti* Tembrock ssp. n., p. 244, fig. 7a-c.
- v 1989 *Spiratella (Heterofusus) lueneburgensis* Tembrock sp. n., p. 244, fig. 9a, b
- v 1990c *Limacina valvatina* (Reuss, 1867); Janssen, p. 85, text-figs. 7-9.
- v 1993 *Limacina valvatina* (Reuss, 1867); Janssen & Zorn, p. 179, pl. 1, figs. 4-11, pl. 2, figs. 1-11, pl. 3, figs. 1-12 (with extensive Paratethys synonymy).
- v 1995 *Limacina cf. valvatina* (Reuss, 1867); Janssen, p. 25, pl. 1, fig. 11.
- v 1999b *Limacina valvatina* (Reuss, 1867); Janssen, figs. 7-9.
- v 2002 *Limacina valvatina*; Gürs & Janssen, p. 124, pl. 2, fig. 2a-c.

Type locality – Wieliczka, Poland; Wieliczka Formation (Miocene salt rock, ‘Badenian’ = Langhian).

Type material – Lectotype (Janssen, 1984b) and 6 paralectotypes in NMV 1867.VII.42.

Description – In its typical form, this species has the ‘ideal’ *Limacina*-shape; a regularly conical spire, approximately as wide as high, straight tangents along the whorls, a semicircular aperture, a not reinforced apertural margin and a narrow umbilicus. The Aquitaine specimens are all small to very small, the largest specimen (Pl. 12, fig. 7) reaching just 0.75 mm. They show a slight variability in H/W-ratio, some are slightly higher than wide, some are relatively wider. Apparently exclusively juvenile specimens were found.

Material examined – **Orthez (Le Paren)**: RGM 541 305/1 juvenile (Pl. 12, fig. 11a-d), RGM 541 306/9 juveniles, RGM 541 314/1 juvenile (Pl. 12, fig. 12a-d), leg. A.W. Janssen,

1979, 1981, 1986; RGM 541 311/5 juveniles, leg. F.A.D. van Nieulande, 26 July 1988, don. July 1989; RGM 569 425/1, leg. S. Mermuys, 2006, don. 2007. Serravallian.

Saubrigues (Jean Tic): BRS 16520M/2 juveniles, leg. B.G. Roest, 16 June 1987; **Saubrigues (Tauziets):** ABH/8Sb2/1 damaged specimen, leg. A.W. Burger, 11 May 1992. Langhian.

Léognan: MHB/2, 'aus Gastropoden', as *Spiratella* (*Spiratella* b) *praerangi praerangi* Tembrock, 1989; **Léognan (Coquillat):** BMNH PITG25522/1 damaged juvenile, D. Curry collection; **Saint-Jean-de-Marsacq:** MHB/3 juveniles, 'aus Gastropoden', as *Spiratella* (*Spiratella* b) *praerangi praerangi* Tembrock, 1989; **Saint-Jean-de-Marsacq (Pinot):** RGM 429 264/2, leg. F.A.D. van Nieulande, July 1996, don. October 1996; RGM 541 385/34 juveniles, RGM 541 551/1 (Pl. 12, fig. 10), both leg./don. G. Garding, 3 July 1996; **Saint-Paul-lès-Dax (Cabanes):** ABH 8Sp2/1 juvenile, leg. 15-16 June 2002; RGM 541 354/10, RGM 541 552/1 (Pl. 12, fig. 7), leg. S. Mermuys, 2003-2004, don. November 2006; **Saucats:** MHB/1 (Pl. 12, fig. 8) 'aus Cassis', as *Spiratella* (*Spiratella* b) *praerangi praerangi* Tembrock, 1989; **Saucats (Coquillière):** RGM 541 334/1, leg./don. F.A.D. van Nieulande; RGM 541 335/1 Pl. 12, fig. 9), leg./don. F.A.D. van Nieulande, July 1981; RGM 541 336/2, leg./don. H.P.J. Keukelaar; **Saucats (Péloua):** RGM 541 339/1, leg./don. F.A.D. van Nieulande, July 1980. Burdigalian.

Meilhan (Vives): MNHN A32096/1 juvenile? (Pl. 12, fig. 6); Aquitanian.

Discussion – For extensive synonymy see Janssen & Zorn (1993, p. 179). *Limacina valvatina* is a common pteropod in the North Sea and central Paratethys basins, occurring from the Late Oligocene (Chattian) to the late Middle Miocene ('Langenfeldian' = Serravallian). They reach their largest sizes in the 'Badenian' (= Langhian) of the Paratethys (Janssen & Zorn, 1993) with a shell height to over 2 mm. Especially during the Langhian/Serravallian of the North Sea Basin and Paratethys, *L. valvatina* develops rapidly in two directions, one with a very high shell, *L. gramensis* (Rasmussen, 1968), with a shell height to over 3 mm and a H/W-ratio over 110, and on the other hand to forms with a depressed to planorboid shell shape, namely *L. ingridae* Janssen, 1989, *L. wilhelminae* Janssen, 1989, and *L. atlanta* Mörch, 1874, the latter species continuing during the Pliocene (Gürs & Janssen, 2002).

Distribution – Apart from the North Sea Basin and central Paratethys, *Limacina valvatina* is known from the Langhian of northern Italy and Sicily, and from the Chattian/Aquitanian to Langhian of Malta (Janssen, 2004a and unpublished, RGM collections). In Aquitaine, it occurs during the Early and Middle Miocene, up to the Serravallian. The Mediterranean occurrences, like those from Aquitaine, merely represent small specimens. Obviously, this species preferred somewhat cooler water.

Specimens identified as *Limacina* aff. *gramensis*, recorded by Janssen (1990a, p. 11) from five localities in southern Australia, are all juvenile, but only one of these has a H/W-ratio over 110, which is considered a reliable discriminating parameter to distinguish between *L. valvatina* and *L. gramensis* (Janssen & Zorn, 1993, p. 169). Most other specimens have a lower H/W-ratio, agreeing with *L. valvatina*. The available material from Australia is too scarce and too juvenile to conclude on a specific identity.

Limacina? vegrandis sp. nov.

Pl. 11, figs. 2-5; Pl. 12, fig. 13.

Holotype – RGM 396 598/1 (Pl. 12, fig. 13a-d).*Type locality* – Gan (Tuilerie).*Stratum typicum* – Marnes de Gan (Eocene, Middle-Late Ypresian), NP12/13.*Derivatio nominis* – *L. vegrandis* (adj.), insignificant, after the very small size of the specimens.*Paratypes* – **Gan (Tuilerie)**, BMNH PITG25498/4, from unsorted sample; BMNH PITG25506/5, from unsorted sample, all D. Curry collection; RGM 396 599/9, RGM 541 533/1 (Pl. 11, fig. 2a-b); RGM 541 534/1 (Pl. 11, fig. 3), RGM 569 457/1 (Pl. 11, fig. 4), RGM 569 458/1 (Pl. 11, fig. 5a-b), all leg. A.W. Janssen, 1981-1990. Middle-Late Ypresian.*Diagnosis* – Shell extremely small, with 1¼ globose whorls, rapidly increasing in diameter. Aperture circular with a strongly concave columellar side. Body whorl with short subsutural crests.*Description* – Shell sinistral, extremely small (H = 0.34 mm, W = 0.44 mm, holotype). There are just 1¼ whorls that increase rapidly in diameter and especially in height; the inflated body whorl equals total shell height. Aperture large and circular, occupying 9/10th of total shell height, with a very concave columellar side. Apertural margin not reinforced, obliquely situated (lateral view). Base gradually rounded and with a very narrow umbilicus, in which some crests are occasionally visible (Pl. 11, fig. 2b). Also, some short subsutural crests are sometimes seen on the upper side of the last half whorl. The nucleus shows a microornament of irregular pitting (Pl. 11, fig. 5b).*Discussion* – Considering the number of available specimens it seems very likely that the shells are fully grown. They represent a species unknown to date and their small size makes them incomparable to any known holoplanktonic gastropod. The presence of subsutural crests resembles similar structures present in species of the pseudothecosomatous genus *Peracle*, but also, like *Limacina gormani* (see above), the columellar structures do not bear a resemblance to any species of that genus. There is some resemblance, both in size and shape, with the pseudothecosomatous genus *Cymbulia* (compare Janssen, 2007a, pl. 22, figs. 4-9, Late Holocene Red Sea specimens). These shell forms, however, are relatively wider, have a large umbilicus and no subsutural crests. Therefore, the species is included in the genus *Limacina* with a query.*Distribution* – Only known from the Gan locality.

***Limacina* sp. 1**

Pl. 12, fig. 14.

Description – Relatively large species (H = 2.14 mm, W = 1.62 mm), high conical, with straight tangents along the almost flat whorls. Nucleus and first whorl missing. Apical angle *c.* 60°. The body whorl occupies 7/10th of the shell height. Aperture relatively small, squarish. Apertural margin damaged, but apparently not reinforced. Growth lines indistinct, but clearly prosocline. Umbilicus present, but very small.

Material examined – **Gaas (Lagouarde)**: MNHN A32097/1 (Pl. 12, fig. 14a-b). Rupelian.

Discussion – Apparently this is an undescribed species, in the combination of size and shape unlike any other pteropod. Unfortunately, just a single specimen is available, insufficient to introduce a new taxon.

***Limacina* sp. 2**

Pl. 13, figs. 1, 2.

Description – Two specimens from the Aquitaine Chattian do not agree with any of the other limacinids. Both are conical, higher than wide (the smaller one more so than the larger) and both are apparently juvenile. They have rather convex whorls. They might even represent two different species.

The larger specimen (Pl. 13, fig. 2) resembles *Limacina valvatina* (see above), but as it is the only specimen of Late Oligocene age, I think it better to include it in open nomenclature.

Material examined – **Pontonx (Mineur)**: MNHN A32098/1 juvenile (Pl. 13, fig. 1); **Saint-Paul-lès-Dax (Estoti)**: MNHN A32099/1 (Pl. 13, fig. 2). Chattian.

Limacinidae sp. 1.

Pl. 13, figs. 3-5.

Description – Three juvenile or damaged specimens represent one or two unidentified, most probably yet undescribed limacinid species. All three are distinctly wider than high, two have a very slightly elevated spire (Pl. 13, figs. 3a, 4a), the third is planorboid (Pl. 13, fig. 5a).

Material examined – **Gaas (Espibos, level 7)**: SMF 332789/1, leg. R. Janssen, 18 July 1978; **Gaas (Lagouarde)**: MNHN A32100/1 juvenile (Pl. 13, fig. 5a-c); MNHN A32101/2 juveniles (Pl. 13, figs. 3a-c, 4a-b). Rupelian.

Discussion – These specimens either represent *Heliconoides* or *Limacina* species, or even both, which can only be decided when more and more complete/adult specimens will be available.

Limacinidae sp. 2

Pl. 13, fig. 6.

Description – A single, badly damaged specimen, missing a quarter of its body whorl and without the columellar side of the aperture visible, does not agree with any of the other limacinid species from Gan. Its diameter is 1.16 mm, its height 0.42 mm. There are 3½ rather convex whorls in a regular spiral, together building a low cone with slightly convex tangents. The base of the shell is gradually rounded, with an umbilicus occupying c. one fifth of the shell's diameter.

Material examined – **Gan (Tuilerie)**: RGM 396 609/1 (Pl. 13, fig. 6a, b), leg./don. C. Dolin, 1983. Middle-Late Ypresian.

Discussion – Presumably this also is an undescribed species, belonging either to *Heliconoides* or *Limacina*.

Superfamily Cavolinioidea Gray, 1850
Family Creseidae Curry, 1982
Genus *Camptoceratops* Wenz, 1923b

Type species – *Camptoceratops priscus* (Godwin-Austen, 1882) (Eocene, Ypresian).

Discussion – The name of the type species is often given as *Camptoceratops prisca*. According to Greek dictionaries I find Gr. κέρας - *kerat-* (*keras*) “horn” + Gr. ὄψη- *ops* “face”) (both masculine), and therefore the ending of the name should also be masculine: *C. priscus*.

Camptoceratops was introduced by Wenz (1923b) as a new genus for *Camptoceras priscum* Godwin-Austen, 1882. Like Godwin-Austen, Wenz considered *Camptoceratops 'prisca'* to be a freshwater mollusc, related to the genus *Isidora* Ehrenberg, 1831. It was only Curry (1965, p. 360) who recognised it as a pteropod and discussed its relationship with the North American genus *Bovicornu* Meyer, 1886 (type species *B. eocenense* Meyer, 1886, by monotypy), suggesting that both might be considered synonyms.

Hodgkinson *et al.* (1992, p. 24), after discussing earlier opinions that *Bovicornu* might be synonymous with *Euchilotheca* Fischer, 1882 (Collins, 1934, p. 165; van Winkle Palmer, 1947, p. 464) or with the caecid genus *Meioceras* Carpenter, 1858 (Dall, 1892, p. 302; Cossmann, 1912, p. 155), concluded that *Bovicornu* and *Camptoceratops* should not be considered synonyms. The main differences are the absence of apertural reinforcements in *Bovicornu* and the more inflated shell in *Camptoceratops*. Additionally, the shell in *Bovicornu eocenense* is clearly twisted in a much wider spiral in which the whorls do not touch each other, whereas its larval shell has distinctly separated protoconchs 1 and 2. I agree with this determination and consider *Camptoceratops* an independent euthecosomatous genus in the Creseidae.

The aperture of *Camptoceratops priscus* is remarkably similar to that of the limacinid species *Altaspiratella multispira* (Curry, 1982, p. 42) (see above). Both species have a thickened apertural margin with a distinct tooth-like projection at its base. A similar, although less developed projection is found in *A. bearnensis*. These three species co-occur in the

Gan assemblage and together suggest a series of species in which the spire of the shell becomes more and more uncoiled, making the impression as if this is an evolutionary sequence, leading from Limacinoidea-Limacinidae to Cavolinioidea-Creseidae.

Camptoceratops is considered to be a creseid genus by all authors. But how misleading this is appeared in a unambiguous way to myself, after having drawn the lectotype and an additional specimen of *C. priscus*. Without realising that cavolinoid species are usually illustrated aperture up, I had imprudently drawn them in the limacinoid way, aperture down, with the result that in Plate 13, where they are positioned according to current usage, these specimens erroneously seem to be illuminated from lower right, whereas all further specimens are drawn in light from upper left. This illustrated once more clearly that *Camptoceratops* demonstrates characteristics of both Limacinoidea and Cavolinioidea.

It remains curious to find these forms co-occurring, realising that the latest-Paleocene limacinoid species *Heliconoides mercinensis* is the oldest pteropod known. If that species is to be considered the ancestral species from which all now known pteropods descended, the development must have been extremely rapid. In the Ypresian, the three mentioned species, resembling a transition from limacinoids to cavolinoids, occur contemporaneously, together with a well-developed creseid, viz. *Euchilotheca ganensis*.

A development of the many pteropod species present in the Ypresian Gan assemblage from the single Late Paleocene *H. mercinensis* seems quite unlikely, leading to the conclusion that other (Late) Paleocene pteropod species might still be unknown. A transitional form between *H. mercinensis* and *Altaspiratella*-forms has not been found yet.

Bovicornu takes a morphological position in between *Camptoceratops* and *Creseis*. Several further creseid pteropods show remnants of an original spiralisation, such as *Euchilotheca elegans* Harris, 1894, as illustrated by Curry (1965, fig. 2b). One could also interpret the oblique dorsal furrow present in *Styliola* to be a remnant of original coiling.

***Camptoceratops priscus* (Godwin-Austen, 1882)**

Pl. 5, figs. 4-6; Pl. 13, figs. 7-15.

- v. 1882 *Camptoceras priscum*, Godwin-Austen n. sp., p. 220, pl. 5, figs. 1-5.
- v. 1882 *Camptoceras priscum* Godwin-Austen var. *obtusum*, p. 220, pl. 5, figs. 6, 7.
- . 1923a *Camptoceratops prisca prisca* (Godwin-Austen) [sic]; Wenz, p. 1680.
- . 1923a *Camptoceratops prisca obtusa* (Godwin-Austen) [sic]; Wenz, p. 1680.
- . 1923b *Camptoceras prisca* (Godwin-Austen); Wenz, p. 117.
- v. 1965 *Camptoceratops prisca* (Godwin-Austen); Curry, p. 360, figs. 7-10, pls. 16, 17.
- . 1979 *Camptoceratops priscum* (Godwin-Austen); Curry & Rampal, p. 23, fig. 1c, d.
- v. 1981 Steinkerne, 7 mm; linksgewunden [= 'internal moulds, 7 mm, sinistral']; Gürs & Gürs, pl. 19, fig. 7.
- v. 1982 *Camptoceratops prisca* (Godwin-Austen); Curry, p. 42, pl. 1, fig. 11a, b.
- . 1988 *Camptoceratops prisca*; Janssen & King, p. 359, fig. 188.
- . 1992 *Camptoceratops americanus* Garvie, new species, in Hodgkinson *et al.*, p. 25, pl. 7, figs. 13-15.

Type locality – Island of Sheppey, near Sheerness, higher level of cliffs, about halfway between East End Lane and Hensbrook, Kent, England. Ypresian.

Type material – Lectotype (Curry, 1965, pl. 16c; herein reillustrated Pl. 13, fig. 7) in BMNH G. 459, on a septarian nodule containing many paralectotypes. The counterpart of this slab is in the British Geological Survey Museum, Keyworth, Nottinghamshire, registration no. GSM.101138 (Curry, 1965, pl. 17).

Description – Shell height to over 7 mm, width c. 1.8 mm, elongate, shaped as a widely open spiral of some $3\frac{1}{2}$ - 4, apparently sinistral (but presumably ultra-dextral) coils. Initial shell part almost straight, usually with a rounded tip (Pl. 13, fig. 15), but sometimes with a clearly separated somewhat globular protoconch-1 (Pl. 13, figs. 9, 10, 12, 13), and hardly separated protoconch-2, transverse section circular. Aperture oblique to the shell's axis, its margin reinforced with a thickened lip slightly bent outward. The abapical part of the margin bears a prominent tooth.

Material examined – **Gan (Bosdarros)**: RGM 396 617/34, leg. A.W. Janssen, 28 August 1990; **Gan (Tuilerie)**: BMNH GG. 7109/1 (illustrated Curry, 1965, p. 365, fig. a-c) (Pl. 13, fig. 11a-b), BMNH GG. 21248/1 (illustrated Curry, 1982, pl. 1, fig. 11a; Pl. 13, fig. 14a-c herein), BMNH PITG25483/72 specimens/fragments, BMNH PITG25507/15, from unsorted sample, BMNH PITG25499/10, from unsorted sample, all D. Curry collection; RGM 396 582/1 (Pl. 13, fig. 8a-c), RGM 396 583/1 (Pl. 13, figs. 9, 10), RGM 396 584/many, RGM 541 555/1 juvenile (Pl. 13, fig. 15), RGM 541 556/1 juvenile (Pl. 5, fig. 5), RGM 541 557/1 juvenile (Pl. 5, fig. 6a-b); RGM 569 447/1 juvenile (Pl. 13, fig. 12), RGM 569 448/1 juvenile (Pl. 13, fig. 13) (specimen lost), RGM 569 459/1 fragment (Pl. 5, fig. 4), all leg. A.W. Janssen, 1981-1990; RGM 396 610/17, leg./don. C. Dolin, 1983; SMF 332790/18, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – See discussion of the genus above. The species *Camptoceratops americanus* Garvie in Hodgkinson *et al.*, 1992 (p. 25, pl. 7, figs. 13-15), described from the North American Early Eocene, resembles the present species closely, but, according to its author may be distinguished from *C. priscus* by “the far greater development of the reflected outer lip and lack of a broad tooth or rostrum” (p. 25). Considering that the largest specimen of *C. americanus* remains below a height of 3 mm, which is less than half the size of adult *C. priscus*, these shells are obviously immature (or damaged) individuals. The severely damaged apertural part of both the illustrated holotype and paratype of *C. americanus* suggests “a far greater development” of the outer lip, which is not necessarily true for adult undamaged shells. That an apertural tooth or rostrum is absent is quite logical in such specimens. Therefore, *C. americanus* is interpreted here as a junior synonym of *C. priscus*, at least until adult specimens with preserved apertural features are available.

Distribution – The distribution in the London Clay Formation of the London Basin is extensively given by Bristow *et al.* (1980, pp. 266, 272-274, fig. 3) and King (1981, pp. 124, 125, 132, figs. 13, 15, 16, 44, 45; 1984, p. 143, fig. 10). The species is known from the North Sea Basin in Belgium (Ieper Clay Formation, Mont Panisel Formation, Aalter Sand Member, Egem Sand Member), The Netherlands (Opende-1 NAM borehole, 757-933 m-RT; Rotterdam E55 borehole, unpublished; Ypresian; RGM collection) and Germany (Katharinenhof, Fehmarn: ‘London Ton’, Gürs & Gürs, 1981; Plön, borehole D51, depth

150.0 m, 'Unter Eozän', Janssen & King, 1988; RGM collections). In the United States *Camptoceratops americanus* is recorded from the top of zone NP13 and the base of zone NP14 (Ypresian).

Genus *Creseis* Rang, 1828

Type species – *Cleodora (Creseis) virgula* Rang, 1828 (Recent).

Remarks – *Creseis* is known to occur from the Middle Eocene onwards (Hodgkinson *et al.*, 1992) and survives in the Recent fauna with four species. Most taxa are characterised by a smooth conical shell (only in *C. berthae* and *C. chierchiaie* is an annulated ornament present) with circular transverse section, differing in apical angle and degree of curvature of the teleoconch, and in the morphology of their protoconchs, that is a more or less clearly separated protoconch-1 and -2. The tip of the protoconch commonly is rounded or slightly pointed. The lack of more pronounced morphological characteristics makes distinguishing the various species difficult.

Apart from several names originally or subsequently included in *Creseis*, but nowadays assigned to other genera, the taxa maintained in *Creseis* and their known ranges are:

<i>Creseis aquensis</i> Benoist, 1889	-	Early Miocene
<i>Creseis berthae</i> A.W. Janssen, 1989	-	Early Oligocene
<i>Creseis chierchiaie</i> (Boas, 1886)	-	Miocene-Recent
<i>Creseis clava</i> (Rang, 1828)	-	Recent
<i>Creseis conica</i> Eschscholtz, 1829	-	Recent
<i>Creseis corpulenta</i> (Meyer, 1887)	-	Late Eocene-Late Oligocene
<i>Creseis cylindrica</i> Hodgkinson <i>in</i> Hodgkinson <i>et al.</i> , 1992	-	Middle Eocene
<i>Creseis dussertiana</i> Bourguignat, 1868	-	Pliocene
<i>Creseis ebla</i> (de Gregorio, 1890)	-	Eocene?
<i>Creseis gagei</i> Gripp, 1922	-	Pliocene
<i>Creseis hastata</i> (Meyer, 1886)	-	Late Eocene-Early Oligocene
<i>Creseis letourneuxi</i> Bourguignat, 1868	-	Pliocene
<i>Creseis nimba</i> (de Gregorio, 1890)	-	Eocene?
<i>Creseis olteanui</i> Stancu, 1978	-	Middle Miocene
<i>Creseis riedli</i> Tauber <i>in</i> Sieber, 1958	-	Middle Miocene
<i>Creseis simplex</i> (Meyer, 1886)	-	Middle Eocene
<i>Creseis spina</i> (Reuss, 1867)	-	Middle Miocene
<i>Creseis virgula</i> (Rang, 1828)	-	Recent

Several of these taxa are doubtful. *Creseis aquensis* is an enigmatic, insufficiently described taxon that has never been illustrated (see below), and *C. berthae* might not be a pteropod (or even a mollusc) at all and could belong to the Annelida. *Creseis dussertiana* and *C. letourneuxi* are exclusively known from the original description accompanied by rather poor illustrations; they remain inscrutable. The names *C. ebla* and *C. nimba* are based on incomplete material, and the types are lost. Hodgkinson *et al.*

(1992, p. 7), following Collins (1934), rightly discarded these two taxa from the list of valid pteropod species. *Creseis gageliana*, only known from the first description, syntypes unavailable, resembles *Creseis* in shape, but has an obvious flattening of the shell in the apertural half, unlike any other species in this genus. I consider it doubtful if this really is a pteropod. *Creseis riedli* has never formally been described and is a *nomen nudum*. Finally, the taxa *C. hastata* and *C. spina* are synonymised in the present paper. Therefore, from the existing, above mentioned 18 taxa only nine are to be considered valid.

Measurements of creseid protoconchs are basically according to Zorn (1991b, p. 108, fig. 7B).

***Creseis antoni* sp. nov.**

Pl. 5, fig. 7; Pl. 14, figs. 1, 2.

Holotype – RGM 541 400 (Pl. 14, fig. 1), leg. A.C. Janse, don. May 2007.

Type locality – Gaas, Espibos.

Stratum typicum – Falun de Gaas, level 6 with *Oostrombus*; Oligocene, Rupelian.

Derivatio nominis – This new species is named after Mr Anton C. Janse, of Brielle, The Netherlands, who collected and donated the type specimens, and who contributed to this paper in other ways as well.

Diagnosis – Straight conical shell, circular transverse section, apical angle approximately 12-14°, protoconch-1 heart-shaped, protoconch-2 hardly discernable.

Description – Straight *Creseis* species, largest specimen with a shell height of 2.4 mm and a width at the aperture of 0.56 mm. The teleoconch is elongated conical with a circular transverse section and an apical angle of *c.* 12-14°. The larval shell consists of a heart-shaped protoconch-1 (H = 0.12 mm) with a rounded tip, separated by a clear constriction. Protoconch-2 is hardly or not distinguishable, poorly separated from the teleoconch at *c.* 0.5 mm from the apex. There is no surface ornament and growth lines are hardly visible.

Paratypes – **Gaas (Espibos, level 6)**: RGM 541 399/1 (Pl. 5, fig. 7a-b), RGM 541 401/1 (Pl. 14, fig. 2). Rupelian.

Discussion – *Creseis antoni* co-occurs at its type locality with *C. spina* (see below), which has an utterly different larval shell with a cylindrical protoconch-1 and a swollen, clearly separated protoconch-2. At Gaas the teleoconch of all specimens of the latter species have a distinctly smaller apical angle.

A related, maybe even identical species was described and illustrated by Hodgkinson *et al.* (1992, p. 28, pl. 9, figs. 10, 11) from a borehole on the Nova Scotian shelf as *Creseis* sp. A. It has a curved shell with a slightly smaller, but also heart-shaped protoconch-1 (H = 0.10 mm) and a more clearly separated protoconch-2 than *C. antoni*. The

age of the American specimens is uncertain because of downhole contamination, but they are most probably Eocene.

Distribution – Only known from the type locality.

Creseis aquensis* Benoit, 1889 *nomen dubium

- * 1889 *Creseis Aquensis* Benoit, p. 33.
- 1932 *Creseis aquensis* Benoit; Peyrot, p. 471.
- 1933 *Creseis aquensis* Benoit; Peyrot, p. 21.

Type material – Incomplete specimens, according to Benoit, were housed in the Muséum de Dax (Duverger collection). In the quite chaotic collections of this Museum at Dax no specimens could be located (visited 19 June, 1981). Benoit stated this species to originate from the Early Burdigalian (his 'Langhien inférieur') "faluns" of the Adour Basin.

Discussion – Benoit (1889, p. 33) introduced this name "simplement pour mémoire et pour attirer l'attention sur cette curieuse forme ...", just comparing it with *Creseis fuchsi* 'Rittl.', from which it would differ by its smooth surface with just some weak striations (growth lines?). Its shell height was said to be *c.* 15 mm, with the lower part recurved forward, ending in a rather sharp and elongated point. *Creseis fuchsi* Kittl, 1886, however, is not a pteropod, but a freshwater gastropod of the genus *Orygoceras* (compare Stancu, 1978, p. 338).

Peyrot (1933) did not find anything that might belong to *Creseis aquensis*. It is suggested that this taxon is a *nomen dubium*.

***Creseis corpulenta* (Meyer, 1887)**

Pl. 14, fig. 3.

- * 1887 *Styliola corpulenta* Meyer n. sp., p. 9, pl. 2, fig. 16.
- v. 1982 *Creseis cf. corpulenta* (Meyer); Curry, p. 44, pl. 1, fig. 15a, b.
- 1992 *Creseis corpulenta* (Meyer); Hodgkinson *et al.*, p. 26, pl. 8, figs. 7-9.

Type locality – Jackson, Riverside Park, Hinds Co, Mississippi, U.S.A. (Moody's Branch Formation, late Bartonian/early Priabonian, NP17).

Type material – Holotype USNM 638879, illustrated by Hodgkinson *et al.* (1992, pl. 8, figs. 7, 8).

Description – Shell small (H = 3.3 mm, W = 1.0 mm, holotype; H = 2.72 mm, W = 1.16 mm, specimen illustrated herein), conical, straight or slightly curved. Apical angle 22° (20-24°), transverse section circular to very slightly elliptical. Protoconch not preserved in the specimens studied for the present paper, but, according to Meyer (1887) and Hodgkinson *et al.* (1992, pl. 8, figs. 7, 8), with a rounded tip followed by a swelling similar to that of *Creseis hastata*. An indication of such a swelling is just retained in two of the specimens in the Curry collection.

Material examined – **Biarritz**: BMNH GG. 2.265/1 (illustrated Curry, 1982, pl. 1, fig. 15a-b) (Pl. 14, fig. 3a-c herein); BMNH PITG25511/3 specimens, some fragments, and BMNH PITG25513/1 on matrix, represent the four additional specimens from this locality, referred to by Curry (1982). Priabonian (NP19-20 zones).

Discussion – For further synonymy see Hodgkinson *et al.* (1992, p. 26). *Creseis corpulenta*, according to Hodgkinson *et al.* (1992), occurred during the Middle/Late Eocene to Late Oligocene (NP 17-24/25?) and thus its presence in the Late Eocene rocks of Biarritz is unexceptional. Curry (1982) apparently included the species in open nomenclature because of the absence of a protoconch, but the wide apical angle makes it quite probable that these few specimens indeed represent this species. In the specimen illustrated (Pl. 14, fig. 3c), it can just be seen that the swelling of protoconch-2 has indeed been present.

The specimens agree with compared samples from the type locality and from Little Brazos River (Early Bartonian, Crocket Formation, Wheelock Member; U.S.A., Texas) (RGM 396 458 and 396 463, leg./don. F. Riedel and K. Bandel, respectively).

Distribution – Bartonian to Chattian of Mississippi, Louisiana (Hodgkinson *et al.*, 1992) and Texas. The Biarritz occurrence is the only one known from Europe.

***Creseis roesti* sp. nov.**

Pl. 5, figs. 8-10; Pl. 14, figs. 4, 5.

Holotype – **Martillac (Barreau)**: RGM 569 470 (ex BRS 14630M/1) (Pl. 14, fig. 4a-e), leg. B.G. Roest, 9 May 1984, don. June 2008.

Type locality – Martillac (France, Gironde), Pas-de-Barreau, outcrop in streambed of brook, coordinates x = 369.250, y = 3271.250.

Stratum typicum – Falun de Léognan (Miocene, Early Burdigalian), infralittoral shelly sands with *Turritella terebralis* Lamarck, 1799, N5 and lower SBZ25 zones (cf. Cahuzac *et al.*, 2005).

Derivatio nominis – The new species is named after Mr Ben G. Roest, of Silvolde, The Netherlands, who collected and donated the holotype.

Paratypes – **St Jean-de-Marsacq (Pinot)**: RGM 541 387/4, leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Meilhan (Vives): RGM 569 416/70, RGM 569 417/1 (Pl. 14, fig. 5a, b), RGM 569 418-420/3 (Pl. 5, figs. 8a, b, 9a, b, 10), all S. Mermuys leg., 2006, don. 2007. Aquitanian.

Diagnosis – *Creseis* species strongly resembling the Recent *C. conica* Eschscholtz, 1829, but with a markedly narrower apical angle.

Description – Elongately conical shell, straight, very slightly curved or somewhat irregular (holotype), with an apical angle of only c. 6°. The transverse section is circular

all over the height of the shell. The larval shell has a rounded tip and is hardly or not separated from the teleoconch, initially perfectly cylindrical or with a very slightly swollen protoconch-1. A boundary between protoconch and teleoconch is difficult to see, also a separation between protoconch-1 and -2 is invisible in most specimens. A surface ornament is absent, but, especially in an apertural direction, some incremental lines may occur.

Discussion – The larval shell of this species resembles the Late Pleistocene to Recent *C. conica* so strongly that I suspect it to be its forerunner species, even if no Late Miocene or Pliocene connecting occurrences are known so far. The Recent species may be straight or slightly curved, but not irregularly curved as in some of the fossil specimens. The larval shell was not described or illustrated of the Eocene species *Creseis cylindrica* Hodgkinson in Hodgkinson *et al.*, 1992. Eight specimens (RGM 429 746) donated by C. Garvie (March 2001), from the type locality at Little Brazos Bluff (Texas; Bartonian, Cook Mountain Formation) are distinctly more slender than *C. roesti*, with a more pointed larval shell (but incomplete in all specimens). *Creseis cylindrica* is characterised by a slight internal thickening of the apertural margin in completely adult specimens. It is suggested to transfer this species to the genus *Euchilotheca* (see below).

Distribution – Late Aquitanian-Burdigalian, Aquitaine Basin, France.

***Creseis simplex* (Meyer, 1886)**

Pl. 14, figs. 6, 10-12.

- * 1886 *Styliola simplex*, Meyer n. sp., p. 78, pl. 3, fig. 10.
- v 1982 *Creseis* cf. *hastata* (Meyer); Curry, p. 43, pl. 1, fig. 14b, c (*partim, non* Meyer)
- . 1992 *Creseis simplex* (Meyer); Hodgkinson *et al.*, p. 28, pl. 9, figs. 4-9.

Type locality – Jackson, Hinds Co. (U.S.A., Mississippi), Moodys Branch Formation (Bartonian).

Type material – Holotype USNM 638841, reillustrated in Hodgkinson *et al.* (1992, pl. 9, figs. 4, 5), copied herein (Pl. 14, fig. 6).

Description – Elongately conical shell, apical angle of teleoconch c. 7-8°, straight or somewhat irregularly curved, transverse section circular. The tip of protoconch-1 is rounded and very slightly swollen, protoconch-2 is separated from the teleoconch by a barely visible constriction at c. 0.6 mm from the tip.

Material examined – **Biarritz**: BMNH PITG25515/1 specimen on matrix, preserving protoconch (Pl. 14, fig. 12); BMNH PITG25514/5 specimens on matrix, preserving protoconch; **Peyrehorade (Arribaouts)**: RGM 541 411/1 (Pl. 14, fig. 10a-b), RGM 541 413/2 (cf.), leg. A.W. Janssen, 29 September 1990. Priabonian.

Biarritz samples BMNH GG. 21262/1? (illustrated Curry, 1982, pl. 1, fig. 14c as *C. cf. hastata*) (Pl. 14, fig. 11 herein), BMNH PITG2.516/13 specimens on matrix, BMNH

PITG25517/9 isolated specimens, and BMNH PITG25510/many fragments, all D. Curry collection, and all without larval shells preserved, cannot be identified better than *Creseis simplex*? or *Creseis* sp., as they might include also *Creseis* sp. nov., described below.

Discussion – For additional synonymy see Hodgkinson *et al.* (1992, p. 28). *Creseis simplex* differs from *C. 'hastata'* (compare illustrations of holotypes in Hodgkinson *et al.*, 1992, pl. 9, figs. 4 and 1, 2, respectively, and copied herein Pl. 14, figs. 6, 7) by a distinctly less or even hardly swollen protoconch-2. Additionally, according to these authors (p. 28), *C. simplex* shows a wider variability in its H/W-ratio. The specimen from Peyrehorade (Arribaouts; Pl. 14, fig. 10a, b) has the larval shell shape of this species. Its H/W-ratio cannot be measured as the shell is compressed.

The specimen from the Biarritz Late Eocene, illustrated by Curry (1982, pl. 1, fig. 14c; Pl. 14, fig. 11 herein), looks very similar, but its larval shell is not preserved. In additional material from Biarritz in the BMNH Curry collection, 18 specimens are preserved on pieces of matrix. From six of these I could free the larval shells by cautious preparation. One such specimen is illustrated here (Pl. 14, fig. 12a, b). These specimens have the typical protoconch shape of *C. simplex*.

Specimens from Gan illustrated by Curry (1982, pl. 1, fig. 14d-e) as *C. cf. hastata* do not belong to one of these taxa, but to *Euchilotheca ganensis* (see below). *Creseis hastata* (Meyer, 1886) is here synonymised with *C. spina* (Reuss, 1867), see the discussion under that species, below.

Distribution – Lutetian and Bartonian of the U.S.A., as specified by Hodgkinson *et al.*, 1992, p. 28), Priabonian of Biarritz and Peyrehorade (France).

***Creseis spina* (Reuss, 1867)**

Pl. 14, figs. 7-9, 13, 14; Pl. 15, figs. 1-16.

- *v 1867 *Cleodora* (*Creseis*) *spina*, Reuss, p. 145, pl. 6, fig. 9.
- . 1886 *Styliola hastata* Meyer n. sp., p. 78, pl. 3, fig. 11.
- v. 1982 *Creseis hastata* (Meyer 1886); Lozouet & Maestrati, p. 183, fig. 8.
- v. 1984b *Cleodora* (*Creseis*) *spina* Reuss, 1867; Janssen, p. 66, pl. 1, figs. 1-2.
- . 1991b *Creseis spina* (Reuss, 1867); Zorn, p. 110, pl. 5, figs. 1-6, 13-18, 21; pl. 12, fig. 2.
- . 1992 *Creseis hastata* (Meyer); Hodgkinson *et al.*, p. 27, pl. 9, figs. 1-3.
- v. 1993 *Creseis spina* (Reuss, 1867); Janssen & Zorn, p. 190, pl. 6, figs. 5-7; pl. 7, figs. 2-4.

Type locality – Wieliczka, Poland; Wieliczka Formation (Miocene salt rock, 'Badenian' = Langhian).

Type material – Lectotype (Janssen, 1984b) and paralectotype in NMV 1867.VII.41 (Pl. 14, fig. 8a, b and 9, respectively). Holotype of *C. hastata* in USNM 644595, re-illustrated in Hodgkinson *et al.* (1992, pl. 9, figs. 1, 2), copied herein (Pl. 14, fig. 7).

Description – Shell elongately conical, straight or slightly curved dorsally, apical angle of early teleoconch variable between less than 5 to over 15°. Transverse section circular to very slightly dorso-ventrally depressed all over the teleoconch's height. Surface

smooth or with barely indicated growth lines that may be somewhat more distinct adaperturnally. Protoconch-1 initially cylindrical with a rounded tip, then gradually widening into a swollen protoconch-2, which is separated from the teleoconch by a distinct constriction.

Material examined – **Orthez (Le Paren)**: RGM 541 307/17, RGM 541 308/1 (Pl. 15, fig. 16), RGM 541 309/1 (Pl. 15, fig. 15), leg. A.W. Janssen, 1979, 1981, 1986; RGM 541 312/7, leg. F.A.D. van Nieulande, 26 July 1988, don. July 1989; **Salles (Moulin Ruiné)**: RGM 541 317/3 protoconchs, leg./don. F.A.D. van Nieulande, 17 July 1984. Serravallian.

Saint-Martin-de-Hinx (Secat): RGM 541 053/3, leg. A.W. Janssen, 1 August 1985. Langhian.

Saint-Jean-de-Marsacq (Pinot): RGM 429 265/3 damaged/fragments, leg. F.A.D. van Nieulande, July 1996, don. October 1996; RGM 541 386/27, RGM 569 409/1 (Pl. 15, fig. 13), RGM 569 428/1 (Pl. 15, fig. 14), leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Béhus (Marcon): MNHN A32102/1 (Pl. 15, fig. 7); **Saint-Etienne-d'Orthe (Lartigaou)**: RGM 541 420/1 (Pl. 15, fig. 6), leg. A.W. Janssen, 1984-1990; **Saint-Paul-lès-Dax (Abesse)**: MNHN A32103/1 (Pl. 15, fig. 12a, b); **Saint-Paul-lès-Dax (Estoti)**: MNHN A32104/4 (Pl. 15, figs. 8-11), P. Lozouet collection. Chattian

Gaas (Espibos): MNHN PL 5503/26, MNHN A32105/1 (Pl. 14, fig. 13a-c); **Gaas (Espibos, level 2)**: RGM 541 398/3, leg. A.W. Janssen, 1981; **Gaas (Espibos, level 6)**: RGM 541 392/8, RGM 541 393-397/5 (Pl. 15, figs. 1-5), leg./don. A.C. Janse, May 2007; SMF 332791/2, leg. R. Janssen, 18 July 1978; **Gaas (Espibos, level 7)**: SMF 332792/3, SMF 332793/10, both leg. R. Janssen, 18 July 1978; SMF 332794/1, leg. R. Janssen, 16 June 1981; **Gaas (Laguarde)**: MNHN A32106/1 (Pl. 14, fig. 14a-c). Rupelian.

Discussion – For further New World synonymy (*Creseis hastata*), see Hodgkinson *et al.* (1992, p. 27). *Creseis spina*, described from the Badenian (= Langhian) of the Central Paratethys, and *C. hastata*, introduced from the Rupelian of the United States, are both characterised by an elongated conical shell with very similar protoconchs. Among the Aquitaine pteropod material, specimens from many localities of Oligocene and Miocene age agree with this protoconch shape.

I was not successful in attempting to subdivide the French Oligo-Miocene populations into recognizable taxa by means of measurements of the larval shells (using the parameters defined by Zorn, 1991a). Measurements of protoconch height vary per locality, but do not show a gradual, time-related tendency. The same is true for diameters of protoconch-1 and -2, and the extremes within populations show wide overlaps.

The only characteristic in which a more or less time-connected parameter could be recognised is the apical angle of the early teleoconch, which seems to increase during the Miocene. Specimens of Miocene *Creseis spina* (lecto- and paralectotype, see Pl. 14, figs. 8, 9) are very variable (Zorn, 1991b) and demonstrate apical angles of the early teleoconch from almost 0° to over 14°. There are also considerable discrepancies in the French Miocene populations; specimens from Orthez (Serravallian) are distinctly more slender, agreeing with the Oligocene populations, than those from older populations

(Late Burdigalian-Langhian) from Saint-Jean-de-Marsacq and Saint-Martin-de-Hinx. The latter also have more slender protoconchs and might already represent transitional forms to *C. chierchiae* (Boas, 1886), but apparently more typical *C. spina* pertained until the Serravallian.

It must be concluded that such populations all belong to a single species, demonstrating variability according to locality. As *Creseis spina* is the oldest available name for this complex, it is concluded that this name should be applied here and that *C. hastata* is a junior subjective synonym. This was implicitly already concluded in Zorn (1991b, p. 112). The taxon *C. spina* herewith becomes one of the longest ranging pteropod species (Bartonian to Serravallian, roughly 30 Ma), comparable with the long range of another creseid pteropod species, viz. *Styliola subula* (Chattian to Recent, roughly 28 Ma).

Creseis spina seems to be the forerunner species of Recent *C. chierchiae*, the typical form of which is characterised by the presence of annulations on the teleoconch. *Creseis chierchiae* f. *constricta* Chen & Bé, 1964, co-occurring in Recent faunas, does not show such annulations and is known from the fossil record (Pliocene of the Philippines; Janssen, 2007b, p. 65, pl. 2, figs. 7, 8, pl. 23, figs. 3-6). Its average protoconch is more slender (see comparisons in Zorn, 1990, pl. 4, figs. 1-6 and 7-12) than in *C. spina*. Its teleoconch, with a wide apical angle varying between 17.5 and 22° (Zorn, 1991b, table 11), is not regularly conical, as in *C. spina*, but becomes adaperturally almost cylindrical.

Specimens from the Miocene (Batesfordian-Bairnsdalian = ~ Langhian-Serravallian) of South Australia, recorded by Janssen (1990a, p. 26) as *Creseis* cf. *chierchiae*, differ from *C. spina* slightly by a somewhat higher protoconch and an early teleoconch apical angle of more than 15°. Also, their adult shape (Janssen, 1990a, pl. 5, fig. 1a) tends to become cylindrical adaperturally, which points to *C. chierchiae*.

Distribution – Bartonian to Rupelian of the United States (Hodgkinson *et al.*, 1992, text-fig. 3); Rupelian to Serravallian of the Aquitaine Basin (this paper); Badenian (= Langhian) of the Central Paratethys (Zorn, 1991b; Janssen & Zorn, 1993; Bohn-Havas & Zorn 1994, p. 77). A very similar, but noticeably smaller, form occurring during the Burdigalian to Langhian of the central Mediterranean (Italy, Malta) merits a closer study (unpublished, RGM collections).

***Creseis tugurii* sp. nov.**

Pl. 15, fig. 17; Pl. 16, figs. 1, 2.

Holotype – RGM 569 410 (Pl. 15, fig. 17a-b).

Type locality – Saint-Paul-lès-Dax (France, Landes), outcrop at Moulin de Cabanes.

Stratum typicum – Falun de Cabanes; Miocene, Early Burdigalian, N5 zone; reefal and shelly coarse sands, coastal facies.

Derivatio nominis – The species is named after the famous locality of Moulin de Cabanes at Saint-Paul-lès-Dax (fr. 'Cabane' = cabin; L. *tugurium*, noun, neuter = cabin, *tugurii* = from the cabin).

Paratypes – **Saint-Paul-lès-Dax (Cabanes)**: RGM 541 355/5, RGM 569 411/1 (Pl. 16, fig. 1a, b), leg./don. S. Mermuys, 2003-2004, don. November 2006; RGM 541 372/1, RGM 569 415/1 (Pl. 16, fig. 2a, b), leg. A.W. Janssen, 1979-1987; SMF 332795/3, leg. R. Janssen, 16 June 1981. Early Burdigalian.

Diagnosis – Slender *Creseis*-species, apical angle of early teleoconch *c.* 7-8°. Larval shell very small, slightly pointed with a rounded tip, separated from the teleoconch by a constriction at *c.* 0.2 mm from the top. The constriction can be very indistinct or even completely absent.

Description – Shell at first glance very similar to *Creseis spina*, but with a basically differing larval shell. Protoconch-1 and -2 are not separated. The larval shell is very small, approximately twice as high as wide, its height being just *c.* 0.2 mm. In the holotype and several paratypes it is clearly separated from the early teleoconch by a constriction ($W = c. 0.08$ mm), but in other specimens this constriction is less distinct or even completely absent. The protoconch-1 bulb is slightly pointed adapically and has a rounded tip in almost all specimens. The apex is pointed in only one specimen (Pl. 16, fig. 2b). The apical angle of the early teleoconch is approximately 7-8°, the transverse section is circular.

Discussion – This new species, just as *Heliconoides mermuysi* and *Diacrolinia orbignyi*, is known exclusively from Moulin de Cabanes. This accentuates the peculiar character of the holoplanktonic mollusc assemblage of that locality, which is supported by the presence of *Vaginella victoriae* (apart from this locality in Aquitaine, only known from Australia) and *Johnjagtia moulinsii* (quite common at Moulin de Cabanes, but only known by its type specimen from the Early Burdigalian of Saucats-Église).

Distribution – Miocene, Early Burdigalian of Saint-Paul-lès-Dax (Cabanes).

Creseis sp. 1

Pl. 15, figs. 18, 19.

v 1982 *Creseis* cf. *hastata* (Meyer); Curry, p. 43, pl. 1, fig. 14a (*partim, non* Meyer).

Description – Elongately conical shell, apical angle of teleoconch *c.* 10°, straight (but only two juvenile shells are known), transverse section circular. The tip of protoconch-1 is clearly pointed, protoconch-2 is rather swollen, and separated by clear constrictions at *c.* 0.2 and 0.4 mm from the tip.

Material examined – **Biarritz**: BMNH PITG25518/2 juvenile specimens (Pl. 15, figs. 18, 19), probably including the one illustrated in Curry (1982). Priabonian.

Discussion – Many isolated fragments in the Curry collection from Biarritz, identified as *Creseis* cf. *hastata* (here with a query included in *C. simplex*, see above), apparently from washed sediment, include two apical fragments, one of which might be the specimen illustrated by Curry (1982, pl. 1, fig. 14a, but not recognisable with certainty).

Their protoconch-2 is clearly more swollen than in *C. simplex* and protoconch-1 has a pointed tip, whereas in both *C. 'hastata'* (= *C. spina*) and *C. simplex* the tip of the protoconch is rounded. So they certainly do not belong to either of these species. These two apical fragments seem to represent an undescribed species, but I refrain from introducing a new taxon.

Distribution – Only known from the Biarritz locality, of Priabonian age (NP19-20 zones).

***Creseis* sp. 2**
Pl. 15, figs. 20-24.

Description – Some specimens from Chattian localities differ markedly from the *Creseis spina*-complex by a different shape of the larval shell. In *C. spina* the transition of protoconch-1 to -2 always shows concave sidelines. In two specimens from Bélus (Marcon) (Pl. 15, figs. 20, 21) these sidelines are clearly convex, whereas in a specimen from Peyrère (Pl. 15, fig. 22) they are straight. In all these specimens, the top of the larval shell is considerably more pointed than it is in *C. spina*.

Material examined – **Bélus (Marcon)**: MNHN A32107/2 (Pl. 15, figs. 20, 21); **Peyrehorade (Peyrère)**: RGM 541 406/1 (Pl. 15, fig. 22a, b), leg. A.W. Janssen, 10 June 1981; **Saint-Etienne-d'Orthe (Lartigaou)**: RGM 569 471a-b/2 (Pl. 15, figs. 23, 24), leg. A.W. Janssen, 1984-1990. Chattian.

Discussion – The present specimens cannot be included in *Creseis spina* because of their utterly different larval shell. They almost certainly represent an undescribed species. Considering the differences in the shape of the protoconchs, it might even very well be that they represent two different taxa. With only these shells available a final conclusion or introduction of new taxa is not feasible.

Genus *Euchilotheca* Fischer, 1882

Type species – *Euchilotheca succincta* (Defrance, 1828) (Eocene, Lutetian).

Remarks – Three species in the genus *Euchilotheca* are currently known; the type *E. succincta* (Lutetian of the Hampshire Basin, England, and the Paris and Loire basins, France), *E. elegans* Harris, 1894 (Lutetian of the Hampshire Basin, England, and Paris Basin, France) and *E. ganensis* (Ypresian of southwest France).

***Euchilotheca ganensis* Curry, 1982**
Pl. 16, fig. 3; Pl. 17, figs. 1-7.

- *v 1982 *Euchilotheca ganensis* Curry n. sp., p. 43, pl. 1, fig. 12a-d.
v. 1982 *Creseis* cf. *hastata* (Meyer); Curry, p. 43, pl. 1, fig. 14d-e (*non* Meyer).

Type locality – Gan (Tuilerie), Eocene, Ypresian, Marnes de Gan.

Type material – BMNH GG. 21259/1, holotype (illustrated Curry, 1982, pl. 1, fig. 12a-b) (Pl. 17, fig. 1a-c herein); BMNH GG. 21260/1, paratype (illustrated Curry, 1982, pl. 1, fig. 12c-d) (Pl. 17, fig. 2a-b herein); BMNH PITG25484/5, paratypes, all D. Curry collection.

Description – Elongately conical shell (H of largest, the only known complete and adult specimen, 9.3 mm, W at aperture 1.3 mm; Pl. 17, fig. 6a-e) with circular transverse section. Initial part strongly resembling *Creseis* species larval shell of c. H = 0.7 mm, with clearly separated protoconch-1 and -2, but the latter less inflated than in *C. spina*. Tip of the protoconch rounded. The aperture is externally reinforced by a clear and well-defined ridge, the supposedly dorsal side of the apertural margin is higher than the ventral side. In lateral view, the aperture therefore is situated obliquely with respect to the shell's long axis. The surface of the teleoconch has no ornament, incremental lines are visible with difficulty.

Material examined – **Gan (Bosdarros)**: RGM 396 618/70, leg. A.W. Janssen, 28 August 1990; **Gan (Tuilerie)**: BMNH GG. 21261/1 fragment (illustrated Curry, 1982, pl. 1, fig. 14b, as *Creseis* cf. *hastata*) (Pl. 17, fig. 5 herein), BMNH GG. 21263/2 (illustrated Curry, 1982, pl. 1, fig. 14d, e, as *Creseis* cf. *hastata*; Pl. 17, figs. 3, 4 herein), BMNH PITG25484/5, no paratypes, BMNH PITG25508/5 juveniles, from unsorted sample, no paratypes, BMNH PITG25500/9, from unsorted sample, no paratypes, all D. Curry collection; RGM 396 578/1 (Pl. 17, fig. 6a-e), RGM 396 579/1, RGM 396 580/1 (Pl. 17, fig. 7a, b), RGM 396 581/54, RGM 569 450/1 fragment (Pl. 16, fig. 3), all leg. A.W. Janssen, 1981-1990; RGM 396 602/33, leg. D. Merle, don. 1987; RGM 396 611/6, leg. C. Dolin, don. 1983; SMF 332796/14, leg. R. Janssen, 17 July 1978 and June 1981. Middle-Late Ypresian.

Discussion – The specimens from Gan (Tuilerie), identified as *Creseis* cf. *hastata* by Curry (1982), agree completely with the present species. In the quite abundant material available from Gan, most specimens are virtually straight, but some of them are a bit more irregular and there is a slight variability in the apical angle of the teleoconch. There is no trace of a weak sinistral coiling, as seen in the type of the genus. Among the many specimens there is also no indication for the presence of a septum. Curry (1965, p. 359) noted the presence of such a septum in a specimen of *E. succincta* with intact larval shell and had reason to believe that a septum is present “in most specimens”. At any rate this septum does not lead to a shedding of the larval shell, as it always does in *E. elegans* Harris, 1894, a species in which these features remain unknown.

In size and shape, *Euchilotheca ganensis* closely resembles a species described from the Middle Eocene of the U.S.A., *Creseis cylindrica* Hodgkinson in Hodgkinson *et al.*, 1992 (p. 27, pl. 8, figs. 10-14). It differs from *E. ganensis* only in that its apertural margin is not obliquely situated and only reinforced on the inside, instead of having the well-defined external rim of that species. As a thickened apertural margin is unknown in the genus *Creseis*, it might be advisable to transfer *C. cylindrica* to *Euchilotheca*.

Cheilospicata Hodgkinson, type and only known species *C. repanda* Hodgkinson in Hodgkinson *et al.*, 1992 (p. 26, pl. 8, figs. 1-4), from the Middle Eocene of Texas, seems to be closely related to *Euchilotheca*. It differs only by another development of the apertural flange. Its larval shell, however, is as yet unknown.

Distribution – Only known from the Ypresian of the two Gan localities.

Genus *Praehyalocylis* Korobkov in Korobkov & Macarova, 1962

Type species – *Praehyalocylis chivensis* Korobkov & Macarova, 1962 [= *Praehyalocylis annulata* (Tate, 1887)].

Remarks – Species of this genus differ from *Hyalocylis* Fol, 1875, by their straight (hardly or not curved) teleoconch, by their circular rather than elliptical transverse section and by not shedding the larval shell. See the discussion in Janssen (1990a, p. 31) on the various fossil representatives of *Praehyalocylis* and *Hyalocylis*. Most of the fossil species are insufficiently known, especially from their larval shells.

The name of this genus is based on the Recent genus *Hyalocylis*, which is derived from the greek word *hyalos*, meaning ‘glass’, ‘crystal glass’ or ‘transparent stone’, and (perhaps) *kylis*, which means ‘cup’, or *kylisis*, which means ‘rolling’. It is not a classical word (it does not appear in the standard lexicon of classical Greek), but a modern coinage. The gender is feminine. The commonly seen combination *Praehyalocylis maximus* is incorrect and has to be *P. maxima* (with thanks to Professor Joan Booth of Leiden University for this explanation).

***Praehyalocylis annulata* (Tate, 1887)**

Fig. 5.

- *v 1887 *Styliola annulata*, Tate spec. nov., p. 195, pl. 20, fig. 1.
- ? 1922 *Balantium* cf. *maximum* Ludwig; Oppenheim, p. 82, pl. 5, fig. 12 (*non* Ludwig?).
- . 1989 *Praehyalocylis cretacea* (Blanckenhorn, 1889); Squires, p. 444, figs. 2.1-2.5 (*partim, non* Blanckenhorn, only the Late Eocene occurrences).
- v. 1990a *Praehyalocylis annulata* (Tate, 1887); Janssen, p. 28, pl. 5, figs. 7-12.
- . 1992 *Praehyalocylis maximus denseannulatus* (Ludwig); Hodgkinson *et al.*, p. 30, pl. 10, figs. 1-5 (*pars, non* Ludwig).

Type locality – Adelaide, borehole (= Kent Town Bore), northeast Parklands, South Australia, depth 45.0-66.4 m (Ludbrook, 1973). Late Eocene, Aldingan (= Priabonian), ‘glaucinitic clayey sands’ = Blanche Point Banded marls and equivalents of the Blanche Point Transitional Marls and Tortachilla Limestone.

Type material – Lectotype (Janssen, 1990a, p. 30, pl. 5, fig. 7) and three paralectotypes (SAM 214) from the type locality; two paralectotypes (SAM 214, P29779-29780) from Aldinga Bay, Willunga Embayment, St. Vincent Basin, South Australia (Late Eocene, Aldingan, Blanche Point Formation, Gull Rock Member, clay with ‘*Turritella*’ *aldingae* Tate or ‘lower marl’).

Description – The only available specimen from Aquitaine is poorly preserved, compressed on a piece of matrix (Fig. 5). Preserved height of the specimen is 8.1 mm, its apical part is missing, W of apertural side c. 2.7 mm. There are some 20 annulations that are more close-set towards the aperture.

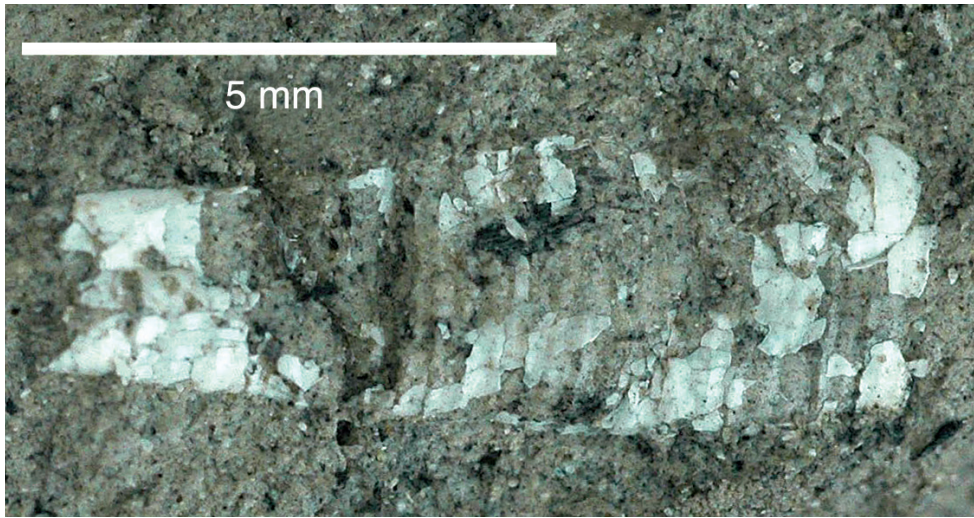


Fig. 5. *Praehyalocylis annulata* (Tate, 1887), from Peyrehorade (Arribaouts), RGM 541 410.

Material examined – **Peyrehorade (Arribaouts)**: RGM 541 410/1 (Fig. 5), leg. A.W. Janssen, 29 September 1990. Priabonian.

Discussion – For further synonymy, see Janssen (1990a, p. 28). The only available specimen from Aquitaine agrees, as far as can be decided, with the Australian type material of more or less the same age. Buonaiuto (1979, p. 329, figs. 489-500), in an unpublished thesis, described further material from the Australian Late Eocene. From his illustrations it is clear that *P. annulata* has a slightly curved and rather elongate initial teleoconch.

Squires (1989, p. 444, figs 2.1-2.5) also described the initial part of the teleoconch, which in his material is not curved, but extremely slender, and the sidelines of the early teleoconch are concave, which distinguishes this species from the Rupelian *Praehyalocylis maxima* (see below). Squires (1989) also included much younger specimens, of Oligocene and Miocene age in his description. These were not illustrated and probably represent other taxa.

Distribution – The Peyrehorade specimen represents the first record of this species from Europe. Apart from the Australian occurrences, *Praehyalocylis annulata* is known from Late Eocene deposits in Uzbekistan (*P. chivensis* Korobkov, 1966), as *P. cretacea* from Washington and Oregon, U.S.A. (Squires, 1989), and as *P. 'maximus' denseannulatus* from Texas (Hodgkinson *et al.*, 1992).

Praehyalocylis maxima (Ludwig, 1864)

Pl. 17, figs. 8-10.

* 1864 *Tentaculites maximus* Ludwig, p. 316.

. 1864 *Tentaculites maximus*, var. *dense-annulatus* Ldwg.; Ludwig, p. 318, pl. 50, fig. 21, 21a, b.

- . 1864 *Tentaculites maximus*, var. *laxe-annulatus* Ldwg.; Ludwig, p. 319, pl. 50, fig. 22, 22a, b.
- . 1889 *Tentaculites maximus* Ludw. var. *densecostatus* [sic]; Blanckenhorn, p. 601, pl. 22, figs. 10, 11.
- . 1889 *Tentaculites maximus* Ludw. var. *laxecostatus* [sic]; Blanckenhorn, p. 601.
- . 1893 *Creseis perspectiva* Futterer nov. sp., p. 11, fig. 3.
- . 1909 *Tentaculites (Creseis) maximus* Ludw.; Spandel, p. 225, pl. 2, fig. 14.
- . 1909 *Creseis perspectiva*; Spandel, p. 229.
- . 1913 *Creseis maxima* Ludw. sp.; Koert, p. 176, pl. 7, figs. 2-4.
- . 1921 *Creseis maxima* (Ludwig); Wenz, p. 113, pl. 11, fig. 38.
- . 1921 *Creseis perspectiva* Futterer; Wenz, p. 113.
- non 1922 *Balantium* cf. *maximum* Ludwig; Oppenheim, p. 82, pl. 5, fig. 12 (= *Praehyalocylis annulata*?).
- v. 1928 *Creseis maxima* (Ludwig); Zinndorf, p. 54, pl. 5, fig. 8.
- . 1932 *Creseis maxima* (Ludwig); Wenz, p. 38.
- . 1932 *Creseis perspectiva* Futterer; Wenz, p. 38.
- non 1940 *Styliola maxima* (Ludwig); Zittel, *raricostata* Noszky nov. var., p. 51, 73, pl. 2, fig. 32 (= *Creseis berthae* Janssen, 1989?).
- non 1940 '*Tentaculites*' *maximus* Ludw.; Staesche & Hiltermann, pl. 51, figs. 11-14 (= *Creseis berthae* Janssen, 1989).
- . 1962 *Praehyalocylis maximus* Ludwig, *P. maximus* var. *dense-annulatus* Ludw., *P. maximus* var. *laxe-annulatus*, *P. maximus* var. *densecostatus* [sic] Ludw.; Korobkov in Korobkov & Macarova, p. 86, pl. 3, figs. 9-13.
- non 1969 *Tentaculites maximus* Ludwig; Boekschoten, p. 45, pl. 3, fig. 6 (= *Creseis berthae* Janssen, 1989).
- . 1971 *Creseis maxima denseannulata* (Ludwig, 1864); Kuster-Wendenburg, p. 103, pl. 1, figs. 1, 2, 3?
- . 1971 *Creseis maxima laxeannulata* (Ludwig, 1864); Kuster-Wendenburg, p. 103, pl. 2, figs. 1, 2.
- . 1973 *Creseis maxima laxeannulata* (Ludwig, 1864); Kuster-Wendenburg, p. 154, pl. 8, figs. 125, 125₁.
- . 1973 *Creseis maxima maxima* (Ludwig, 1864); Kuster-Wendenburg, p. 153, pl. 8, figs. 124, 124₁.
- . 1982 *Creseis maxima maxima* (Ludwig, 1864); Kuster-Wendenburg, p. 111.
- . 1982 *Creseis maxima laxeannulata* (Ludwig, 1864); Kuster-Wendenburg, p. 111.
- . 1982 *Creseis maxima* (Ludwig 1864); Lozouet & Maestrati, p. 182, fig. 7.
- ? 1989 *Praehyalocylis cretacea* (Blanckenhorn, 1889); Squires, p. 444 (*partim*, non Blanckenhorn, not the Oligocene and Miocene occurrences).
- non 1992 *Praehyalocylis maximus denseannulatus* (Ludwig); Hodgkinson *et al.*, p. 30, pl. 10, figs. 1-5 (= *P. annulata*).
- . 2000 *Praehyalocylis laxeannulata* (Ludwig, 1864); Moths, p. 40, pl. 13, fig. 10
- v. 2004 *Praehyalocylis laxeannulata* (Ludwig 1864); Gürs & Janssen, p. 201.

Type locality – Hipping near Nierstein, mine shaft (Germany, Rheinland-Pfalz; Oligocene, Rupelian).

Type material – Ludwig's syntypes were lost during World War Two (Kuster-Wendenburg, 1971, p. 103). Neotypes (Kuster-Wendenburg, 1971, pp. 103-104, pl. 1, fig. 1 and pl. 2, fig. 1) of *Creseis maxima denseannulata* and *C. maxima laxeannulata* are in the Paläontologisches Institut der Universität Mainz, Germany, registration numbers PIM F 2424 and PIM F 2426, respectively. Kuster-Wendenburg (1973) chose the neotype of *C. maxima denseannulata* to be also the neotype of the nominal subspecies *C. maxima maxima*, by declaring *C. maxima denseannulata* an objective synonym.

Description – Regularly conical, creseiform shell with an apical angle of c. 15° with a small, clearly separated, more or less heart-shaped protoconch (H = 0.12 mm, W = 0.08 mm; Pl. 17, fig. 9a). The teleoconch has straight sidelines and a circular transverse section. It is initially smooth, but soon distinct annulations appear, the number of which

varies greatly. Sometimes they are thin and very close-set, f. *maxima* (Ludwig) (= *denseannulata*); sometimes stronger and clearly spaced, f. *laxeannulata* (Ludwig). Specimens commonly occur with stepwise increasing diameter of the teleoconch, f. *perspectiva* (Futterer). Fully grown specimens may reach a shell height of over 20 mm (Rupelian, Mayence Basin).

Material examined – **Gaas** (no further details): SMF 332797/1 (Pl. 17, fig. 10), K. Jung collection, 1883-1885; **Gaas (Lagouarde)**: MNHN A32108/2 (Pl. 17, figs. 8, 9a, b), P. Lozouet collection. Rupelian.

Discussion – Just a few specimens are known from Aquitaine. The specimen in coll. SMF (Pl. 17, fig. 10) shows the distinct stepwise increasing diameter and thus belongs to f. *perspectiva*. The larger of two specimens from Gaas (Lagouarde; MNHN collection) (Pl. 17, fig. 9a, b) combines characters of the typical form such as dense annulations, but also has an indication of a stepwise increasing diameter at one place. The other specimen (Pl. 17, fig. 8) is too juvenile.

The history of this species' nomenclature is quite confusing. Part of the misunderstanding started through the introduction by Ludwig (1864) of three names for only two different forms. Ludwig (1864, p. 316) stated that he named the large pteropod specimens from the Oligocene marine clays of the Mayence Basin '*Tentaculites maximus*'. In the same paper (pp. 318-319) he distinguished two varieties in the material available to him, which he named '*Tentaculites maximus*, var. *dense-annulatus*' and '*Tentaculites maximus*, var. *laxe-annulatus*'. The discriminating characteristic, also expressed in the names, is a much more widely spaced annulation in the latter. In spite of the fact that the syntypes of '*laxe-annulatus*' were found in a stratigraphically lower level, not together with '*dense-annulatus*', Ludwig considered both forms so closely similar ('stimmen ... so nahe überein') that he could only interpret them as varieties. His drawings (Ludwig, 1864, pl. 50, figs. 21 and 22, respectively) illustrate the differences between the two taxa clearly.

Blanckenhorn (1889, p. 601) quoted Ludwig's paper, but referred to the two Oligocene taxa, rather sloppily, as '*Tentaculites maximus* v. *densecostatus* Ludwig' and '*T. v. laxecostatus* Ludwig'. He illustrated two specimens (pl. 22, figs. 10, 11) from the Oligocene of Hohenkirchen (Germany), using the name '*T. maximus* v. *densecostatus* Ludwig' for both. These illustrations indeed resemble the form with close-set annulations, the specimen in his figure 11 additionally showing a stepwise increasing shell diameter at about half shell height. Von Koenen (1892, p. 992), who obviously did not know Ludwig's paper, also used that incorrect name. Even Spandel (1909, p. 225, pl. 7, fig. 3), although citing Ludwig's 1864 paper, referred to specimens with Blanckenhorn's inattentive names. The illustration of a specimen from Offenbach a.M. is indicated only as '*Tentaculites (Creseis) maximus* Ludw.', but distinctly shows the '*dense-annulatus*' ornament.

In 1893 Futterer (p. 11, fig. 3) introduced a related form from Oligocene sedimentary rocks near Heidelberg (Germany) with the name *Creseis perspectiva*, clearly differing from the two forms described by Ludwig by a repeatedly stepwise increasing teleoconch diameter. Very similar specimens were described by Koert (1913, p. 176, figs. 2-4) from several boreholes in northern Germany. Obviously, Koert was unaware of Futter-

er's paper as he indicated his specimens as '*Creseis maxima* Ludw. sp. var. *denseannulata*' (his fig. 3) and '*Creseis maxima* Ludw. sp. var. *laxeannulata*' (his figs. 2 and 4). The specimen of fig. 3 indeed shows a denser ornament of annulations (although not so clearly differing as in Ludwig's figures), but all three specimens have the stepwise increasing shell diameter, as described by Futterer.

Wenz (1921, pl. 11, fig. 38) illustrated a specimen from the Mayence Basin, as '*Creseis maxima* Ludwig' that agrees with Ludwig's 'var. *dense-annulatus*' by its dense annulations. In 1932 Wenz (p. 38) united the two varieties of Ludwig under the name *Creseis maxima* (Ludwig) and considered *C. perspectiva* a separate species. Zinndorf (1928, pl. 5, fig. 8) applied the name '*Creseis maxima*' to specimens from Oligocene clays. His illustration is not clear, but the sample is still available in SMF and here reillustrated (Fig. 6). The two specimens preserved on the clay tablet differ strongly in density of the annulations and represent both varieties described by Ludwig, which demonstrates beyond doubt that both occur contemporaneously. These two specimens do not show the stepwise increasing diameter.

In 1962 Korobkov (*in* Korobkov & Macarova, p. 84) introduced the genus *Praehyalocyliis* in which he included, apart from the Eocene type species *P. chivensis* Korobkov & Macarova, 1962 (= *Praehyalocyliis annulata*, see above), several further taxa including '*P. maximus*'. The illustrations of Ludwig and Blanckenhorn are copied in Korobkov & Macarova's paper and, curiously, the 'var. *densecostata* Ludwig' was maintained next to the 'var. *laxe-annulatus*' and 'var. *dense-annulatus*'.

The three poorly preserved specimens from the 'Niemtschitzer Schichten', of Late Eocene age, described by Oppenheim (1922, p. 82, pl. 5, fig. 12) as *Balantium* cf. *maximum*, most probably belong to *Praehyalocyliis annulata*.

Kuster-Wendenburg (1971, pp. 103-104), in her study of Rupelian pteropods of the Mayence Basin, still used the genus *Creseis* and maintained this name in later papers (Kuster-Wendenburg, 1973, 1982). In 1971 (p. 103) she wrote to have been unable to trace Ludwig's type specimens, which most probably did not survive World War Two. For that reason she decided to designate neotypes for the taxa '*Creseis maxima denseannulata*' and '*Creseis maxima laxeannulata*'. The neotype locality is the same for both, that is, Bodenheim (Germany; so-called 'Fischschiefer', Rupelian).

In her 1973 paper, Kuster-Wendenburg changed the naming of the two forms, to avoid the fact that three names were available for two taxa. She indicated the form so far recorded as *C. maxima denseannulata* in this and a later paper (1982) as *C. maxima maxima*, listing '*denseannulata*' among the synonyms, by which action she established which of the two taxa is the nominal subspecies.

The neotype of *Creseis maxima denseannulata*' (= *C. maxima maxima*; Kuster-Wendenburg, 1971, 1973) agrees with Ludwig's illustration of that taxon indeed, but that of '*laxeannulata*' (Kuster-Wendenburg, 1971, pl. 2, fig. 1) distinctly differs from Ludwig's description and illustration in having the stepwise increasing shell diameter, not indicated in the original drawing of Ludwig. Kuster-Wendenburg was of the opinion that Ludwig only had compressed specimens available, preserved on tablets of clay, in which the stepwise increasing diameter is concealed.

Study of compressed specimens preserved on clay tablets from the same locality as the neotypes (Bodenheim), housed in SMF, however, show such 'steps' clearly (Fig. 7). From this material it is clear that specimens with dense and more spaced annulations



Fig. 6. *Praehyalocylis maxima* (Ludwig, 1864) from Offenbach am Main, Mayence Basin (Germany, Rheinland-Pfalz), 'Pumpwerk nahe d. Kaiser', clay tablet illustrated by Zinndorf (1928, pl. 5, fig. 8). Oligocene, Rupelian, 'Fischschiefer'. SMF 332798, Dr K. Völzing leg., 25 September 1904.

occur together, as do specimens with and without the steps.

These observations lead me to the conclusion that we are dealing with a single Rupelian species, in which three forms can be distinguished; two of them with a regularly increasing shell diameter (*maxima* = *denseannulata*, with crowded annulations, and *laxeannulata*, with spaced ornament) and one with the stepwise increasing diameter (*perspectiva*). The neotype, however, of *laxeannulata* belongs distinctly to the *perspectiva*-form. To consider both *denseannulata* and/or *laxeannulata* as subspecies of '*Creseis*' *maxima*, as Kuster-Wendenburg (1971, 1973, 1982) did, is incorrect, as they obviously do not differ in geographical and/or stratigraphical distribution.

For several Mayence Basin occurrences of *P. maxima* (Weinheim-Trift, Bodenheim), calcareous nannoplankton studies revealed the NP23 zone (Kuster-Wendenburg, pers. comm., 2008). In her 1971 paper (p. 101, fig. 1) Kuster-Wendenburg also gave an overview of localities in Germany, all of Rupelian age.

Distribution – The specimens from the Rupelian of Gaas recorded herein are the first from the Aquitaine Basin. *Praehyalocylis maxima* is known from the Rupelian in the Mayence and North Sea basins, and was also recorded from the Rupelian of the Étampes area, Paris Basin (Morigny, Ormoy-la-Rivière; Lozouet & Maestrati, 1982). A fragmentary specimen of the f. *perspectiva* is RGM 228 540 from the Rupelian of Saint-Hilaire (Étampes area, France, Essonne department). Specimens of Oligocene age from the northwest U.S.A., recorded (but not illustrated) by Squires (1989) as *P. cretacea* (Blanckenhorn), might also belong to *P. maxima*. Gürs & Janssen (2004) discussed the occurrence of *P. maxima* (as *P. laxeannulata*) in the North Sea Basin, concluding a short term invasion into the basin, which they named the '*P. laxeannulata* Event', occurring in the early part of zone NP23.

Genus *Styliola* Gray, 1850

Type species – *Styliola recta* Lesueur ms = *Styliola subula* (Quoy & Gaimard, 1827) (Recent).

Styliola subula (Quoy & Gaimard, 1827)

Pl. 16, fig. 4; Pl. 18, fig. 1.

Synonymy and description – See Janssen (1990a, p. 32, pl. 5, figs. 13-19, pl. 6, figs. 1-9; 1999a, p. 18, pl. 3, figs. 7-9; 2007b, p. 73, pl. 3, figs. 1-4, pl. 24, figs. 2, 3).

Neotype locality – Canary Islands, south of Palma, 28° 26' N, 17° 51' W, bottom sample, sea depth 503 m (Late Holocene-Recent).

Type material – Neotype (Janssen, 1999a, p. 19, text-fig. 3), RMNH 57267.

Material examined – **Saint-Martin-de-Hinx (Secat)**: MNHN unnumbered/1 apical fragment, P. Lozouet collection. Langhian.

Saint-Paul-lès-Dax (Cabanes): RGM 541 373/1 (Pl. 18, fig. 1), leg. A.W. Janssen, 1979-1987. Burdigalian.

Bélus (Marcon): MNHN PL 6582/2 fragments; MNHN PL 6590/11; **Saint-Etienne-d'Orthe (Église A)**: MNHN PL 6591/4 apical fragments; **Saint-Etienne-d'Orthe (Église C)**: MNHN PL 10442/5 apical fragments, MNHN/unnumbered, 21 and 12 apical fragments, P. Lozouet collection; RGM 395.403/2 juveniles, 2 apical fragments, leg. A.W. Janssen, 30 July 1984; **Saint-Etienne d'Orthe (Hondelatte)**: RGM 541 458/16 apical fragments, 24 fragments, leg. A.W. Janssen, 24 September 1990; **Saint-Etienne-d'Orthe (Lartigaou)**: RGM 229 961/1 fragment (illustrated Zorn & Janssen, 1993, pl. 4, fig. 6), RGM 541 422/many apical fragments, RGM 541 423/many fragments retaining furrow, RGM 541 424/1 apical fragment (Pl. 16, fig. 4a-b), RGM 541 425/1 apical fragment, all

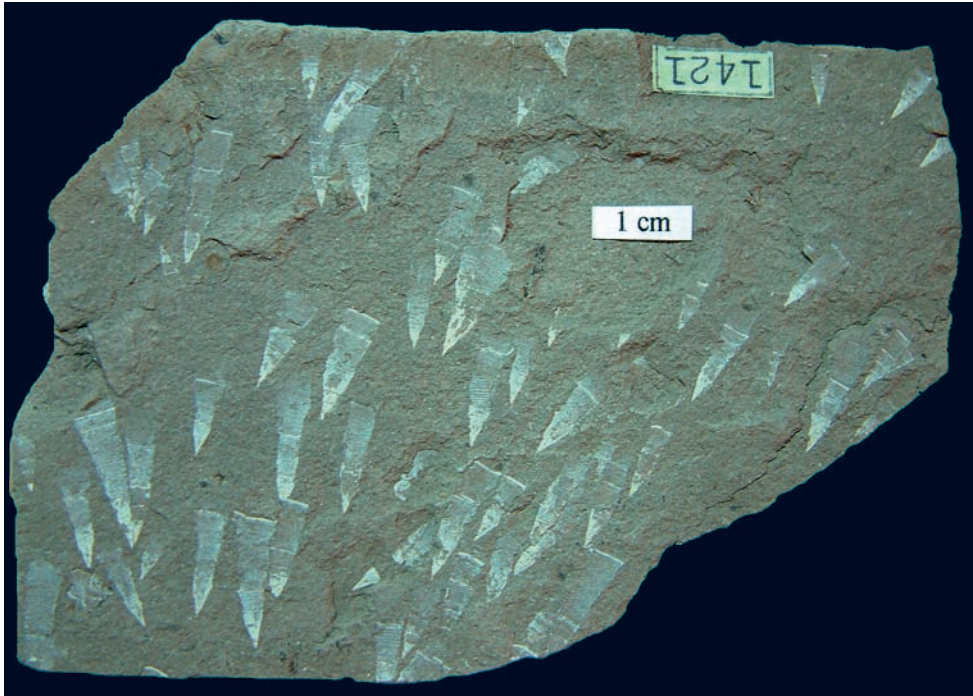


Fig. 7. *Praehyalocylis maxima* (Ludwig, 1864) from Bodenheim, Mayence Basin (Germany, Rheinland-Pfalz). Oligocene, Rupelian, 'Fischschiefer'. SMF 327481, H. Neuenhaus collection, ex Th. Crececius.

leg. A.W. Janssen, 1984-1990; SMB unnumbered/35 fragments, leg. S. Mermuys, July 2006; **Saint-Paul-lès-Dax (Estoti)**: unnumbered/7 fragments; MNHN unnumbered/10 fragments, both P. Lozouet collection; **Saint-Paul-lès-Dax (Lestrilles)**: MNHN PL 6614/1 apical fragment. Chattian.

Discussion – This species is not at all rare at the various Chattian localities of Saint-Etienne-d'Orthe, but all specimens are severely crushed, and only apical shell fragments and small fragments retaining the dorsal fold are recognisable. Zorn & Janssen (1993, p. 64, pl. 4, fig. 6) indicated these as *Styliola?* sp. These specimens are considered to belong to Late Oligocene to Recent *S. subula*. Compared to other occurrences of fossil *S. subula* there are, admittedly, some slight differences. The Chattian material discussed here has, in general, a somewhat wider protoconch-1 and the onset of the dorsal fold occurs at a slightly wider diameter of the shell. However, the shape of protoconch-1 in Recent samples includes specimens closely resembling the Saint-Etienne-d'Orthe shells. Vice versa, some slender specimens from that locality cannot be distinguished from Recent specimens, so there seems to be no reason for a taxonomical separation. From Miocene localities in Aquitaine surprisingly only a few specimens have been recorded.

The morphology of apical shell fragments of the present species quite closely resembles that of *Spoelia torquayensis* and even *Vaginella tricuspidata*, which makes identi-

fication of a larger number of specimens hazardous, needing extensive comparisons with more adult specimens retaining their larval shell, in which the small apical angle of the specimens is decisive.

Distribution – Late Oligocene of the North Sea Basin, Late Oligocene to Miocene in southwest France, Miocene-Pliocene of South Australia, Japan and the Mediterranean, Late Miocene-Pliocene of Indonesia, Early Pliocene of Portugal, Early to Middle Pliocene of the Caribbean, Pliocene of the Philippines, Holocene-Recent: worldwide in tropical and subtropical seas.

Family Praecuvierinidae A.W. Janssen, 2006

Genus *Praecuvierina* A.W. Janssen, 2005a

Type species – *Praecuvierina lura* (Hodgkinson in Hodgkinson *et al.*, 1992).

***Praecuvierina lura* (Hodgkinson in Hodgkinson *et al.*, 1992)**

- * 1992 *Cuvierina lura* Hodgkinson, new species, in Hodgkinson *et al.*, p. 32, pl. 11, figs. 11-15.
- . 2007 *Praecuvierina lura* (Hodgkinson, 1992); Lozouet & Le Renard, p. 2, pl. 1, figs. 1-3.

Discussion – Material of this species has not been made available to me. Lozouet & Le Renard (2007, p. 2, pl. 1, figs. 1-3) recorded 13 specimens from the Lutetian of Peyrehorade (Trompe).

Family Cuvierinidae Gray, 1840

Genus *Cuvierina* Boas, 1886

Type species – *Cuvierina columnella* Rang, 1827 (Recent).

Subgenus *Cuvierina sensu stricto*

***Cuvierina* (*Cuvierina*) *paronai*? Checchia-Rispoli, 1921**

Pl. 16, fig. 5; Pl. 18, figs. 2-5.

For the real *Cuvierina paronai* see:

- * 1921 *Cuvierina Paronai* Checchia-Rispoli, p. 6, figs. 1, 1a, b.
- v. 1995 *Cuvierina paronai* Checchia-Rispoli, 1921; Janssen, p. 44, pl. 3, figs. 7-10.

Type locality – San Nicola Varano (Italy, Gargano, Foggia), Lago di Varano Formation. The age of this formation is disputed, and is variously referred to as Langhian (Checchia-Rispoli, 1921), Serravallian (Sirna, 1968), Late Tortonian (D'Alessandro *et al.*, 1979) and Late Serravallian to Tortonian (D'Alessandro & Robba, 1980). The pteropod assemblage found at this locality unmistakably points to a Langhian age.

Type material – The whereabouts of the type specimens is unknown.

Description – Five specimens were found that are, with more or less certainty, considered to belong to *Cuvierina paronai*. An apertural fragment (Pl. 18, fig. 2a-b) from Saint-Paul-lès-Dax (Cabanes) has the typical triangular shape with an internal thickening and distinct longitudinal microornament. Two specimens from Saint-Martin-de-Hinx (Secat) and one from Saint-Jean-de-Marsacq (Pinot) are larval shells with protoconch (Pl. 18, figs. 3, 5). A conical specimen with circular transverse section from Saucats (Coquillière) (Pl. 18, fig. 4) seems to represent a juvenile specimen, without its protoconch and no sign of a septum.

Material examined – **Saint-Martin-de-Hinx (Secat)**: RGM 395 405/1 protoconch (Pl. 16, fig. 5), leg. A.W. Janssen, 30 July 1984, RGM 541 055/1 protoconch (Pl. 18, fig. 5a-b), leg. A.W. Janssen, 1 August 1985; **Saubrigues (Jean Tic)**, SMF 332800/2 larval specimens retaining protoconch. Langhian.

Saint-Jean-de-Marsacq (Pinot): RGM 541 388/1 protoconch (Pl. 18, fig. 3a, b), leg./don. G. Garding, 3 July 1996; **Saint-Paul-lès-Dax (Cabanes)**: RGM 541 356/1 fragment (Pl. 18, fig. 2a-c), leg. S. Mermuys, 2003-2004, don. November 2006; **Saucats (Coquillière-A 1)**: RGM 541 337/1 (Pl. 18, fig. 4), leg. J. Gunst, 1982, don. F.A.D. van Nieulande; Burdigalian.

Discussion – The Burdigalian specimens, especially those from Cabanes, predate the earliest known *Cuvierina* species from Europe, which is the Mediterranean/Paratethyan *C. paronai* Checchia-Rispoli, 1921, the oldest certain specimens of which (from Malta, RGM collection) are dated ‘Burdigalian/Langhian-transition’. The available specimens could very well belong to that species, but do not allow a definite identification.

Zorn (1991b, p. 132, pl. 9, figs. 3, 4) noted the presence of longitudinal microornament in specimens from Bad Vöslau (Austria; ‘Badenian’ = Langhian), contrary to the original description of Checchia-Rispoli (1921) in which the specimens are described as smooth. That, however, is quite logical as the material from Gargano, described by that author, is preserved as internal moulds only.

Distribution – In the Mediterranean Langhian/Tortonian, *Cuvierina paronai* is a common pteropod species, known from Italy (northern Italy, Gargano, Salento, Sicily, Sardinia), Malta and Cyprus (RGM collections). The present specimens, if belonging to this species, represent the first Atlantic records.

Genus *Ireneia* A.W. Janssen, 1995

Type species – *Ireneia tenuistriata* (Semper, 1861) (Oligocene, Chattian).

Discussion – *Ireneia* was classified hitherto in the family Cuvierinidae (Janssen, 1995) because of the presence of a longitudinal microornament as found in several *Cuvierina*-species, an internally thickened apertural margin, the more or less triangular shape of the aperture and the absence of lateral carinae. The earliest species of this genus is the type, *I. tenuistriata* (Semper, 1861) (see Janssen, 1995, p. 48, pl. 4, fig. 3), known from the earliest Eochattian in Germany.

Recently, however, a new, slightly younger *Ireneia*-species was described from the North Sea Basin's Late Oligocene (latest Eochattian), viz. *I. striatocarinata* Piehl, 2007 (p. 99, pl. 1, fig. 1a, b, text-fig. 3). In this very elongate species, clear lateral carinae are present in the apical half of the shell, strongly reminiscent of the genus *Vaginella*, which so far was included in the family Cavoliniidae. A relatively strong dorso-ventral flattening towards the aperture and the shape of the aperture in adapical view, showing a central dorsal swelling, similarly suggest an affinity with *Vaginella*, whereas its protoconch and microornament are typical for *Ireneia*.

This reopens the question as to whether or not *Vaginella* should be included in the Cuvierinidae. Rampal (1996, 2002) considered *Vaginella* to be ancestral to *Cuvierina*, but gave no argument in support of this point of view. Considering the morphological features of *I. striatocarinata*, one would be inclined to accept a common ancestor for *Vaginella* and *Ireneia*, in which case the latter should be a descendant of the former, as *Vaginella* ranges from the Rupelian onwards (see below), while *Ireneia* is known since the Late Oligocene only. The earliest known *Ireneia* species (= *I. tenuistriata*) does not show affinities with *Vaginella*. Further the ontogenetical development of *Vaginella* includes metamorphosis (Janssen, 1985b; see also below under *Vaginella*), during which the larval shell rapidly transforms into the full-grown shape. Such a shell-metamorphosis is exclusively known in the Cavoliniidae.

Ireneia calandrellii? (Michelotti, 1847)

- ? 1889 *Vaginella Calandrellii* [sic] (Michtt.); Benoist, p. 30, pl. 2, fig. 5a-c.
- ? 1932 *Vaginella Calandrelli* Michelotti; Peyrot, p. 473.
- ? 1932 *Vaginella calandrelli* [sic] Mich.; Peyrot, pl. 18, figs. 31, 32.
- ? 1933 *Vaginella Calandrelli* Michelotti; Peyrot, p. 23.
- ? 1933 *Vaginella calandrelli* [sic] Mich.; Peyrot, pl. 18, figs. 31, 32.

For *I. calandrellii sensu stricto* see:

- v. 1995 *Ireneia calandrellii* (Michelotti, 1847); Janssen, p. 49, pl. 4, figs. 4-6.

Type locality – ‘Colli Torinesi’, Piemonte, Italy, unknown deposit of Early-Middle Miocene age.

Type material – Neotype (Janssen, 1995, p. 50, pl. 4, fig. 4a-c), Dipartimento di Scienze della Terra, Torino, Italy (Bellardi & Sacco collection), BS 007.06.003.

Description and synonymy – See Janssen (1995).

Material examined – In the collection of the Musée d'Histoire naturelle at Bordeaux, where, according to Benoist (1889), the specimen from Saucats-Péloua, illustrated by him and also by Peyrot, was kept, unfortunately it is missing. Peyrot (1932) also referred to specimens from Saucats (Moulin de l'Église), Léognan (Thibaudeau; Degrange-Touzin collection) and Léognan (Coquillat; Neuville collection); all these localities are of Burdigalian age. The only samples identified as *I. calandrellii* that I have been able to locate in the Degrange-Touzin collection, housed in MBB, are a specimen from

Saucats (Église) and an almost unrecognisable fragment from Saucats (Péloua), both belonging to *Vaginella depressa*. The specimen from Peyrehorade (Peyrère), recorded by Peyrot (1932, p. 474), is included here in *Vaginella chattica* (see below).

Discussion – Judging from the description and illustration by Benoist (1889), his specimen from Péloua indeed resembles *I. calandrellii*, especially so by the apparent lack of lateral carinae, as mentioned by Benoist (p. 30 “manque de carène latérale à l’extrémité de la partie inférieure”). Peyrot (1932, p. 473) described these as “Les renforcements latéraux du test sont plus minces que chez *V. depressa*”. His illustrations are insufficient to recognise the species, but lateral carinae do not occur in *I. calandrellii*. In the absence of any specimen, the occurrence of this species in the Aquitaine Miocene has to remain doubtful.

Distribution – *Ireneia calandrellii* is known from various Italian localities dated as ‘Aquitanian to Serravallian’ (but most probably Late Burdigalian-Langhian only) (Janssen, 1995). The species was recognised in the Miocene of New Zealand (Janssen, 2006) and Chile (leg./don. S. Nielsen, Hamburg; RGM 516 556).

***Ireneia nieulandei* A.W. Janssen, 1995**

Pl. 18, fig. 6.

* 1995 *Ireneia nieulandei* Janssen sp. nov., p. 170, pl. 14, figs. 4, 5.

v. 2006 *Ireneia nieulandei* A.W. Janssen, 1995; Janssen, p. 79, figs. 10, 11.

Type locality – Saucats (Coquillière), level A 1. Miocene, Early Burdigalian, Falun de Pont-Pourquey.

Type material – Holotype, RGM 393 138; leg. F.A.D. van Nieulande, July 1981; don. 1994, illustrated Janssen (1995, p. 170, pl. 14, fig. 4a-c). Paratypes: **Saint-Paul-lès-Dax (Cabanes)**: MNHN A32109/2 juveniles; MNHN A32110/1 (Pl. 18, fig. 6a-e); **Santa Cruz, Patagonia, Argentina**: BMNH G. 12030/2, from ‘Eo-Oligocene, Santa Cruz Formation’), see Janssen (1995, p. 172).

Description – Shell large (holotype H = 20.8 mm, H of the illustrated paratype MNHN PL 6632 = 16.6 mm), conical tubular, straight or nearly so (the holotype is slightly asymmetric in ventral view). The protoconch is absent in the full-grown specimens, but could be studied in a juvenile paratype. There is no apical spine. A slight inflation is present, but there is no sharp boundary with the teleoconch. In the apical shell the transverse section is circular; towards the aperture it becomes slightly elliptical and flattened on the ventral side, the dorso-ventral diameter being slightly less than the shell width. Initially, the apical angle (ventral view) of the shell is c. 20°. From mid-height onwards the side lines are almost parallel. In lateral view the shell is somewhat flattened towards the aperture, as a result of which both ventral and dorsal sides are a little convex over their entire length, the ventral slightly more so than the dorsal. The ventral apertural margin is straight to very slightly convex and remains lower than the more strongly curved dorsal margin. The shape of the aperture in adapical view is more or less triangular, with a gradually curved

dorsal part and an almost straight ventral rim. Internally the aperture is reinforced by a slightly thickened shell wall.

The shell's surface has rather distinct growth lines, especially well visible in low angle light. They run parallel to the apertural margin and therefore have an oblique course on the sides. The apertural two thirds of the shell are completely covered with a microornament of incised longitudinal lines. These are visible under a 10-25 × magnification, especially where light reflects on the shell's surface.

Non-type material examined – **Léognan (Château de France)**: MBB/2, Ph. Rocher collection (larger specimen H = 11.5 mm, protoconch missing); **Saucats (Coquillière)**: ACP/1 (H = 14.2 mm, protoconch missing). Burdigalian.

Distribution – *Ireneia nieulandei* is now known from the Burdigalian of Aquitaine, from the 'Eo-Oligocene' of Santa Cruz, Patagonia, and from the Miocene (Otaian) of New Zealand.

Genus *Johnjagtia* A.W. Janssen, 2005a

Type species – *Cleodora (Creseis) moulinsii* Benoist, 1874a (Miocene, Burdigalian).

Johnjagtia moulinsii (Benoist, 1874a)

Pl. 16, figs. 6-9; Pl. 18, figs. 7-10.

*v. 1874a *Cleodora (Creseis) Moulinsii* Benoist (Nobis), p. 266.

1874a *Cleodora eburnea* (Ben.); Benoist, p. 460.

1874b *Cleodora eburnea*, Benoist; Benoist, p. cxxiv.

1884 *Creseis Moulinsii*, Ben.; du Boucher, p. 166.

1887 *Creseis Moulinsii* (Benoist); du Boucher, p. 148.

v. 1889 *Creseis Moulinsii* (Benoist); Benoist, p. 32, pl. 2, fig. 6a-b.

v. 1932 *Creseis Moulinsi* Benoist; Peyrot, p. 471.

v. 1933 *Creseis Moulinsi* Benoist; Peyrot, p. 21.

v. 2005a *Johnjagtia moulinsi*; Janssen, p. 41.

Type locality – The description of Benoist (1874a, p. 266) does not give the type locality, but in a table on p. 422 (fossil nr. 218) the species is mentioned from locality nr. 6, which refers to 'sable rose à *Arca Burdigalina*, carrière de Giraudeau' (near Moulin de l'Église), which is at Saucats (pp. 8 and 11). The accompanying fauna referred to indicates an age of Early Burdigalian. Benoist (1889, p. 33) referred again to the locality of the single specimen known to him as 'Saucats, à la carrière du moulin de l'Église'.

Type material – Holotype (Pl. 18, fig. 7), MBB, Benoist collection, found in box of *Cleodora* sp. = *Cleodora ortheziana* Benoist, 1889, whereas this latter specimen is missing.

Description – Elongated conical shell with an apical angle of c. 13°. The holotype is a juvenile or broken shell (H = 4.50 mm, W = 1.25 mm, dorso-ventral diameter 1.0 mm), but complete adult specimens reach a shell height of almost 9 mm and a width at the aperture of up to 1.9 mm. Transverse section initially circular, but towards the aperture

slightly dorso-ventrally flattened, especially on the ventral side. The protoconch is elongated oval, with a rounded or slightly pointed tip. It is separated from the teleoconch by a clear constriction at *c.* 0.16-0.17 mm from the apex. Incremental lines on the teleoconch are rather clear, straight on the ventral and curved adaperturally on the dorsal side. A distinct longitudinal furrow is present in the apical half of the shell, situated on the left-dorsal side of the shell, starting at a diameter of *c.* 0.6 mm and fading out at a diameter of *c.* 1.25 mm.

The surface of the apertural half of the shell is covered with a microornament of longitudinally incised lines, only visible ($\times 25$) at places where light reflects on the shell's surface. The aperture is oblique (lateral view), dorsally higher and curved, ventrally straight and reinforced by a distinct apertural rim. In adapical view the shape of the aperture is rounded on the dorsal side and straight or slightly concave ventrally to clearly reniform (Pl. 18, fig. 8a).

Just one of the few adult specimens has its protoconch preserved (Pl. 18, fig. 9d, e), so apparently the larval shell is not shed. There is no sign of a septum in all other specimens.

Material examined – **Saint-Paul-lès-Dax (Cabanes)**: ABH 8Sp1/3, ABH/8Sp2/10, leg. 15-16 June 2002; AJB/3; FSUB typothèque 25-4-11/1 (Pl. 18, fig. 8a-d), A. Cluzaud collection; MNHN PL 6629/27, MNHN A32111/1 specimen (Pl. 18, fig. 9d, e); MNHN unnumbered/3, MNHN unnumbered/2, both leg. Lozouet *et al.*; RGM 541 357/47, RGM 541 358/1, 541 359/1, 569 414/9, all leg. S. Mermuys, 2003-2004, don. November 2006; RGM 541 371/46, RGM 569 461-4/4 (Pl. 16, figs. 6-9), all leg. A.W. Janssen, 1979-1987; RGM 541 377/1 (Pl. 18, fig. 10a-d), leg./don. W. Groeneveld; SMF 332801/6, K. Jung collection, 1883-1885; SMF 332802-4/6 (in three samples), K. Jung collection, 1883-1885; SMF 332805-6/7 and 3, leg. R. Janssen, 10 June 1981. Early Burdigalian.

Discussion – This species is clearly related to the Cuvierinidae by the shape of its aperture and the presence of a longitudinal microornament, and especially resembles *Spoelia torquayensis*, from which it differs by the absence of lateral carinae and the possession of a dorso-lateral fold instead.

The holotype of *Johnjagtia moulinsii* was poorly illustrated in Benoist (1889, p. 32, pl. 2, fig. 6), with growth lines strongly exaggerated and the dorso-lateral fold not indicated, but mentioned in the description; ‘... un léger pli longitudinal’. The drawing misled Avnimelech (1945, p. 643) who considered it to belong to the genus *Hyalocylis*.

Peyrot (1932, p. 471) referred to the ‘type’ in the Benoist collection, but erroneously stated its locality as ‘Saucats (Péloua)’. The other specimen referred to by this author, from ‘La Brède (tranchée du ch. de fer)’ (locality of Aquitanian age), is still present in MBB (Duvergier collection). It is, however, not a pteropod, but part of a decapod chela.

Concerning the epitheton specificum, I keep the original spelling as *moulinsii*, in agreement with art. 33.4 of the International Commission on Zoological Nomenclature (1999). Benoist (1874a) apparently latinized the name of ‘l’honorable président de la Société Linnéenne’, after whom the species was named (Charles Des Moulins) to *moulinsius*, of which *moulinsii* is the genitive. So, the emendation (as *moulinsi*) made by Peyrot (1932) is invalid.

Cleodora eburnea was introduced in the same year as *C. moulinsii*, but Benoist himself

wrote (1874a, p. 460, *in errata*): ‘N° 218, ajoutez à la synonymie: *Cleodora eburnea* (Ben.). Compte Rendu Soc. Linn. Bord. 1873, p. 124’ (the latter published in 1874, cf. Benoist, 1874b; this p. cxxiv was effectively printed on 15 June 1874, as that is written on the corresponding part of the ‘Procès-Verbaux de la Soc. Linn. Bordeaux’).

Distribution – Apart from the holotype, which is from Saucats (Église), all known specimens of this species are from the Cabanes locality at Saint-Paul-lès-Dax, where it is common. Both localities are earliest Burdigalian.

Genus *Spoelia* A.W. Janssen, 1990a

Type species – *Spoelia torquayensis* A.W. Janssen, 1990a (Oligocene, Chattian).

Spoelia torquayensis A.W. Janssen, 1990a

Pl. 18, fig. 11; Pl. 19, figs. 1-6; Pl. 20, figs. 1, 2

*v. 1990a *Spoelia torquayensis* Janssen sp. nov., p. 42, pl. 7, figs. 1-5.

v. 2004a *Spoelia torquayensis* A.W. Janssen, 1990; Janssen, p. 16, pl. 3, figs. 23a-d, 24, 25a-c.

v. 2005a *Spoelia torquayensis* Janssen, 1990; Janssen, p. 29.

v. 2005b *Spoelia torquayensis* A.W. Janssen, 1990; Janssen, p. 79.

Type locality – Torquay, Bird Rock, Otway Basin, Victoria (Australia). Oligocene, ‘Janjukian’ (= Chattian), Torquay Group, Janjuk Formation.

Type material – Holotype (Janssen, 1990a, pl. 7, fig. 1; MVM P123408) and paratypes as specified in Janssen (1990a) from Spring Creek, Torquay (Australia), and from Saint-Etienne-d’Orthe (Église), Peyrehorade (Peyrère, Pl. 19, fig. 4a-d, fig. 5a-c) and Saint-Paul-lès-Dax (Estoti, Pl. 18, fig. 11a-c) (France). One paratype from this latter locality, MNHN PL 377/1 juvenile, registered as RGM 229 509, but returned to Paris (misunderstanding) and is now identified as *Vaginella tricuspidata*.

Description – See Janssen (1990a). Additional material collected after the first description of this species has shown that in completely adult specimens it is reinforced by a thickened rim or swelling all along the apertural margin (Pl. 19, fig. 1), similar to the one present in *Johnjagtia moulinsii*. The statement in the first description that the lateral carinae disappear “rather abruptly just before the aperture” is incorrect. In adult specimens, the carinae are situated in the apical half of the shell. Specimens showing the features of adult specimens are only known from Saint-Etienne-d’Orthe, where they could be collected on pieces of matrix.

Non-type material examined – **Bélus (Marcon)**: MNHN PL 6582/21 fragments, MNHN A32112/1 (Pl. 19, fig. 6a-c), this specimen has a carina on one side only; MNHN unnumbered/53 fragments, P. Lozouet collection; **Peyrehorade (Peyrère)**: MNHN PL 1840/4 fragments; SMF 332807-8/5 and 4, apical fragments, leg. R. Janssen, 9 June 1981; **Peyrehorade (Tauziède)**: MNHN PL 5896/17 fragments; **Pontonx (Mineur)**: MNHN PL 925/1 fragment; **Saint-Etienne-d’Orthe**: BRS 291190/1 juvenile, leg. B.G. Roest, 16 June 1987; **Saint-Etienne-d’Orthe (Église-A)**: MNHN unnumbered/2 fragments, P. Lozouet

collection; **Saint-Etienne-d'Orthe (Église B)**: MNHN PL 6583/10 fragments; **Saint-Etienne-d'Orthe (Église-C)**: MNHN unnumbered/1 damaged specimen, 5 and 44 apical fragments, all P. Lozouet collection; **Saint-Etienne d'Orthe (Hondelatte)**: RGM 541 459/18 protoconchs, 33 fragments, leg. A.W. Janssen, 24 September 1990; **Saint-Etienne-d'Orthe (Lartigaou)**: RGM 541 426/11, RGM 541 427/1 retaining apertural characteristic (Pl. 19, fig. 1), RGM 541 428/many apical fragments, RGM 541 429/many fragments, RGM 569 465-466/2 apical fragments (Pl. 20, figs. 1, 2a, b), all leg. A.W. Janssen, 1984-1990, RGM 541 450/1, leg./don. A.C. Janse; SMB unnumbered/28 fragments, leg. S. Mermuys, July 2006; **Saint-Etienne-d'Orthe (Lestelle)**: MNHN PL 5181/ 1 fragment; RGM 541 452/13, RGM 541 453/many fragments, leg. A.W. Janssen, 24 September 1990; **Saint-Etienne-d'Orthe (Verdun)**: MNHN, PL 6581/22, 19 fragments; MNHN unnumbered/1 fragment, P. Lozouet collection; **Saint-Paul-lès-Dax (Abesse)**: FSUB typothèque 51-4-27/1 (Pl. 19, fig. 2a-c), A. Cluzaud collection; MNHN PL 581/3 fragments; MNHN PL 749/2, 2 fragments; MNHN unnumbered/1 fragment, MNHN unnumbered/2 fragments, MNHN unnumbered/2 fragments, all P. Lozouet collection; **Saint-Paul-lès-Dax (Bezoye)**: MNHN PL 1368/4, 25 fragments, MNHN A32113/1 fragment (Pl. 19, fig. 3a, b); **Saint-Paul-lès-Dax (Estoti)**: ACP/1; MNHN PL 377/2 juveniles (originally these specimens were identified as paratypes (2 of 13) of *Spoelia torquayensis*, but checking the material in 2000 revealed that they cannot be identified with certainty); MNHN unnumbered/8 fragments, MNHN unnumbered/2 juveniles, MNHN unnumbered/8 fragments, all P. Lozouet collection;; **Saint-Paul-lès-Dax (Lestrilles)**: MNHN PL 6614/5 fragments. Chattian.

Discussion – Although the presence of the squarish lateral carinae is unmistakable and very typical for the species, rarely specimens are found possessing just one of these. An example is given (Pl. 19, fig. 6a-c), a specimen from Bélus (Marcon) in the MNHN collection.

The apical part of the shell is commonly just straight, but in some specimens there is a slight dorso-ventral curvature. A specimen in FSUB (A. Cluzaud's collection) (H = 6.50, W = 1.92 mm) from Saint-Paul-lès-Dax (Abesse) shows this feature clearly (Pl. 19, fig. 2c). Identifying dorsal or ventral side in this species is only possible if the aperture is retained.

Distribution – *Spoelia torquayensis* is now recorded from South Australia, and from the Aquitaine and North Sea basins, all of Chattian age. The species is not rare in the Lower Globigerina Limestone Member of Malta (Mediterranean), that used to be considered Aquitanian (Janssen, 2004a). Foresi *et al.* (2008) redated these rocks on the basis of planktonic foraminifera and calcareous nannoplankton as Chattian.

Cuvierinidae sp. nov.

Pl. 19, fig. 7.

Description – A single fragmentary specimen is available from the Saint-Paul-lès-Dax Chattian. Both apertural and apical parts are missing, the remaining height being no more than 1.5 mm. Its apical angle in frontal view is *c.* 29°. Transverse section is elliptical. An obvious, relatively wide furrow is present parallel to one side. Growth lines on the side with the furrow are more convex than on the other side of the shell, which I

therefore consider to be dorsal. In its apertural part, the surface of the specimen has distinct microornament, as in *Johnjagtia* or *Spoelia*.

Material examined – **Saint-Paul-lès-Dax (Abesse-B)**: MNHN A32114/1 (Pl. 19, fig. 7a-c), P. Lozouet collection. Chattian.

Discussion – This fragment cannot be related to any of the other Cuvierinidae known from Aquitaine. Its transverse section, because of the furrow, is reminiscent of *Styliola*, which has no microornament and a much narrower apical angle. This fragment apparently represents an as yet undescribed species.

Cuvierinidae sp. 1

Pl. 19, fig. 8

Description – Few specimens strongly resemble *Spoelia torquayensis* in general shape and microornament, but differ by the absence of the lateral carinae. Just fragmentary material is available, and nothing is known about the morphology of aperture and/or larval shell.

Material examined – **Bélus (Marcon)**, MNHN unnumbered/1 apical fragment, P. Lozouet collection; **Saint-Etienne-d’Orthe (Hondelatte)**: MNHN PL 6585/3 damaged specimens, **Saint-Etienne-d’Orthe (Verdun)**: MNHN A32115/1 damaged (Pl. 19, fig. 8a, b; MNHN unnumbered/1 apical fragment, P. Lozouet collection), **Saint-Paul-lès-Dax (Bezoye)**: MNHN unnumbered/1 apical fragment, P. Lozouet collection. Chattian

Discussion – A specimen of *Spoelia torquayensis* is known having just one of the lateral carinae (Pl. 19, fig. 6) and the present specimens may be aberrant shells of that species.

Cuvierinidae sp. 2

Pl. 19, figs. 9, 10.

Description – Two incomplete specimens from the Miocene of Saint-Paul-lès-Dax (Cabanes) are available. They are conical shells with a circular transverse section and an apical angle of *c.* 20°. In the largest of the two specimens, a clear microornament as in *Spoelia* or *Johnjagtia* is present (not indicated in the drawings). They occur with the species *Johnjagtia moulinsii*, but have a considerably wider apical angle and no trace of the dorso-lateral furrow. In the smaller specimen, the larval shell (Pl. 19, fig. 9d, e) is present. The tip is rounded, and protoconch-1 and -2 are separated by slight constrictions.

Material examined – **Saint-Paul-lès-Dax (Cabanes)**: MNHN A32116 and A 32117/2 juveniles (Pl. 19, figs. 9a-e, 10a-c), P. Lozouet collection. Early Burdigalian.

Discussion – These two specimens apparently represent a further cuvierinid species, but in the absence of more adult shells they can only be recorded in open nomenclature.

Family Cliidae Jeffreys, 1869

Remarks – See International Commission on Zoological Nomenclature (2006) for the correct spelling of the family name.

Genus *Clio* Linné, 1767

Type species – *Clio pyramidata* Linné, 1767 (Recent).

Remarks – Subgeneric names are sometimes applied to species of *Clio*, but for many taxa this is not (yet) possible, as the morphology of the larval shells is insufficiently well known. Therefore, I refrain from applying subgeneric names in the present paper.

The available material of this family from Aquitaine, with a few exceptions, consists of insufficiently well preserved specimens, predominantly apical shell fragments or isolated protoconchs which as a rule cannot be identified. Two Late Oligocene occurrences of better preserved specimens are introduced here as new species.

Clio lozoueti sp. nov.

Pl. 21, figs. 1-3.

Holotype – MNHN A32118/1 (Pl. 21, fig. 1a-e).

Type locality – Bélus (Marcon).

Stratum typicum – Grey to yellowish marls, with a few molluscs (Oligocene, Chattian).

Derivatio nominis – This unusual new species is named after Dr Pierre Lozouet (MNHN), who made a substantial part of the basic material for this paper available.

Diagnosis – A straight and extremely elongate *Clio*, dorso-ventrally compressed and with squarish lateral carinae. Larval shell with a rounded tip and separate protoconch-1 and -2.

Description – The shell is small ($H = 3.3$ mm) and extremely slender elongate. The apical angle is no more than $8-10^\circ$. Dorso-ventral diameter close to aperture half the shell width. Both sides of the shell are moderately convex, the dorsal side, recognisable by aperturally curved incremental lines, slightly stronger so than on the ventral side, and towards the aperture in some specimens with a somewhat produced centre. The larval shell consists of protoconch-1 and -2, clearly separated by constrictions. Protoconch-1 is elliptical ($H = 0.14$ mm, $W = 0.10$ mm), with a rounded tip. The constriction between protoconch-2 and the early teleoconch is at *c.* 0.35 mm from the tip. The dorso-ventral diameter of the early teleoconch is smaller than that of protoconch-2. Lateral carinae develop immediately behind the protoconch. They have a squarish transverse shape and continue until the aperture. There are no apertural reinforcements. The shape of the aperture in adapical view can be almost rhomboidal (Pl. 21, fig. 3a).

Paratypes – **Bélus (Marcon)**: MNHN A32119/8 and 1 (Pl. 21, fig. 2a-e); RGM 541 409/2, don. P. Lozouet, September 2000; **Peyrehorade (Peyrère)**: RGM 541 407/1 (Pl. 21, fig. 3a-c), leg. A.W. Janssen, 10 June 1981. Chattian.

Discussion – By its extremely slender and compressed shell shape, as well as by the presence of separate protoconchs-1 and 2, this species deviates from all described Cliidae. An equally slender, but not compressed species is *Clio ghawdextensis* (Janssen, 2004a), introduced from the Chattian/Early Miocene of the Maltese archipelago. In that species, however, two longitudinal lateral grooves are present and lateral carinae are absent. Its transverse section is elliptical. The protoconch of *C. ghawdextensis* is as yet unknown.

***Clio nielseni* A.W. Janssen, 1990c**

Pl. 21, fig. 4.

*v 1990c *Clio nielseni* Janssen sp. nov., p. 86, text-fig. 10, pl. 1, figs. 1-3.

Type locality – Mogenstrup, north of Skive, Jylland, Denmark, coastal cliff exposure. Oligocene, Chattian B, Vejle Fjord Formation, Brejning Clay Member.

Type material – Holotype, RGM 229 775a-b, paratypes from the type locality in MGUH 20 339-20 340 and RGM 229 776-778. Further paratypes are in the private collections of A.C. Janse, M.S. Nielsen and K.I. Schnetler.

Description – See Janssen (1990c). Three apical shell parts still preserving their protoconch are available from the Aquitaine Late Oligocene. The shell is strongly curved dorsally. The first indications of dorsal transverse ornament are present in the apertural part of the largest specimen (Pl. 21, fig. 4), as well as lateral carina with a squarish transverse section. The protoconch is globular. An apical spine is preserved in the two smaller specimens, which reluctantly are considered to belong to the same species.

Material examined – **Saint-Etienne-d’Orthe (Église C)**: MNHN unnumbered/2 apical fragments?; **Saint-Etienne-d’Orthe (Verdun)**, MNHN A32120/1 (Pl. 21, fig. 4a-c). Chattian.

Discussion – In all its characteristics, the illustrated specimen agrees with *C. nielseni* from the Danish Chattian. The absence of an apical spine is most probably the result of damage, as often seen in larval shells of *Clio*. It cannot be excluded that some of the other larval *Clio* shells described below from the Adour Late Oligocene belong to the present species.

Distribution – Apart from the type locality, *Clio nielseni* is also known from reworked Early Miocene boulders of so-called ‘Holsteiner Gestein’ from Damsdorf (Schleswig-Holstein, Germany) (RGM collections, leg./don. A. Montag). The specimen from Saint-Etienne-d’Orthe is the first record from outside the North Sea Basin.

***Clio ortheziana* (Benoist, 1889)**

Pl. 21, fig. 5

- * 1889 *Cleodora Ortheziana* Benoist, p. 27, pl. 2, fig. 3a-c.
- . 1932 *Cleodora ortheziana* Benoist; Peyrot, p. 471, pl. 18, figs. 33-35.
- . 1933 *Cleodora ortheziana* Benoist; Peyrot, p. 21, pl. 18, figs. 33-35.

Type locality – ‘... dans les sables argileux bleus de la métairie du Paren, aux environs d’Orthez’, France (Landes). Miocene, Serravallian, Falun à *Cardita jouanneti*, infralittoral facies.

Type material – According to Benoist (1889), the only known specimen (holotype) was housed in the ‘Muséum d’histoire naturelle de Bordeaux’. In the Benoist collection, in MBB, a box was present with a label stating ‘*Cleodora*, Orthez’ (seen May 1997), but erroneously containing the holotype of *Johnjagtia moulinsii* (see above). Unfortunately, the single known specimen of *Clio ortheziana* is missing.

Description – In the absence of any specimen, only the description and poor illustrations in Benoist (1889) and Peyrot (1932) are available. The description and drawings by Benoist are sometimes contradictory; his illustrations are copied herein (Pl. 21, fig. 5a-b).

This is a triangular species of *Clio* with concave sidelines (but straight according to the description) and a triangular transverse section, with convex dorsal and concave ventral side. Dorsally there are three equidistant radial ribs, of which the middle one is strongest, separated by wide intervals. The ventral side has a single, obtuse median rib. A transverse ornament is clearly indicated in the drawings, but according to the description the shell is ‘ornée de plis rugueux très faibles’, disappearing on the central rib.

Material examined – To date not a single specimen is available. It cannot be excluded that one or more of the juvenile Miocene *Clio* specimens described below belong to this species. However, such *Clio* protoconchs are not recorded yet from the type locality Orthez (Paren). Serravallian.

Discussion – Benoist (1889) compared his species with *Clio pyramidata* Linné, 1767, known from the Late Miocene onwards, and still abundantly occurring in tropical and subtropical seas. The main characteristics of Benoist’s specimen seem to agree with that species, but the strength of the radial ornament and presence of transverse riblets could also point to *Clio cuspidata* (Bosc, 1802), although that species is known only from the Pliocene onwards.

Distribution – Only recorded from the Orthez (Paren) locality.

***Clio vasconiensis* sp. nov.**

Pl. 16, figs. 10, 11; Pl. 21, figs. 6-8.

Holotype – RGM 541 430 (Pl. 21, fig. 6).

Locus typicus – Saint-Etienne-d’Orthe (Lartigaou).

Stratum typicum – Marnes de Saint-Etienne-d’Orthe (Oligocene, Chattian).

Derivatio nominis – Named after Gasconne (L. *Vasconia*), the region in southwest France where the type locality is situated.

Paratypes – **Saint-Etienne-d’Orthe (Église C)**: MNHN A32121/2 apical fragments, P. Lozouet collection; **Saint-Etienne-d’Orthe (Lartigaou)**: MNHN A32122/2, leg. A.W. Janssen, 1984-1990, don. June 2008; RGM 541 431/1 (Pl. 21, fig. 7a, b), RGM 541 432/4, RGM 541 433/16, RGM 541 434/many fragments, RGM 541 435/1 with tripled central rib (Pl. 21, fig. 8); RGM 541 436/1 with tripled central rib, RGM 541 437/1 apical fragment (Pl. 16, fig. 11), RGM 541 438/1 apical fragment (Pl. 16, fig. 10), RGM 541 439/2 apical fragments, all leg. A.W. Janssen, 1984-1990; SMB unnumbered/14 fragments, leg. S. Mermuys, July 2006; **Saint-Etienne d’Orthe (Lestelle)**: RGM 541 454/1, RGM 541 455/8 fragments, leg. A.W. Janssen, 24 September 1990. Chattian.

Diagnosis – *Clio* species of flabelliform shape, apical angle of teleoconch almost 90°. Both sides with a radial ornament of 5 ribs, the middle one of these uncommonly subdivided in three. Larval shell with a slightly pointed protoconch-1 and a well-separated protoconch-2. Protoconch not deviating from the shell’s long axis.

Description – All available more or less complete specimens are preserved on small slabs of matrix and have suffered compression. Therefore, it is impossible to distinguish between ventral and dorsal sides. It seems likely that both sides have a similar ornamentation. The protoconch, retained in several specimens, apparently does not deviate from the shell’s long axis. Protoconch-1 is ovoid, very slightly pointed and somewhat higher than wide. Protoconch-2 is a rather distinctly separated swelling, twice as high as protoconch-1 (Pl. 16, figs. 10, 11). Right from the start of the teleoconch the shell becomes dorso-ventrally compressed and a squarish carina develops on both sides. From here on the sidelines are initially concave, but soon become straight, enclosing an apical angle of hardly less than 90°. Apparently both sides of the teleoconch are just slightly convex; differences in convexity between dorsal and ventral side could not be observed. At a short distance from the protoconch, a radial ornament develops, consisting of five rather flat ribs, separated by equally wide intervals. Together they occupy *c.* three fifths of the shell’s surface, leaving elongately triangular, smooth lateral areas. In at least two specimens (Pl. 21, fig. 8), the central rib is subdivided by two grooves and appears as a wider rib, flanked by a narrow secondary rib on both sides.

Discussion – This species resembles the Italian Miocene *Clio multicostata* (Bellardi, 1873) by the ornament of the teleoconch. However, that species reaches far larger dimensions, has a considerably smaller apical angle, its lateral areas are narrower and its protoconch-2 is not clearly separated (compare Janssen, 1995, pl. 6, fig. 5). *Clio sulcosa* (Bellardi, 1873) also has a smaller apical angle and a different configuration of the radial ribs (compare Janssen, 1995, pl. 7, figs. 7, 8).

It is curious that, although entirely different in shape of the full-grown shells, the species *Clio lozoueti* and *C. vasconiensis* have very similar protoconchs. They are the only known *Clio* species in which protoconchs-1 and -2 are separated. As far as available, all other species in this genus just have a simple larval shell bulb.

Distribution – Exclusively known from and common in the outcrops in Saint-Etienne-d’Orthe.

***Clio* sp. nov.?**

Pl. 20, figs. 4, 5; Pl. 22, figs. 1, 2.

Description – The single more or less adult specimen (Pl. 22, fig. 1a-d) lacks its larval shell and apertural parts. The teleoconch has a triangular outline with its apical part slightly curved dorsally (lateral view) and apical angle of *c.* 40° (frontal view), the sides are slightly concave, but straight adaperturally. The lateral carinae have a squarish transverse section. The shell width at the apertural side is approximately one and a half times the dorso-ventral diameter. Ventral and dorsal sides are both convex, the dorsal one slightly more so. Along the carinae flat, elongate lateral areas are vaguely separated. Apart from a faint central riblet in the apical part of the dorsal side, the shell surface is without ornament and growth lines are invisible.

A number of larval shells most probably belong to the same species, some of which retain the initial part of the teleoconch. Their protoconch is globular (Pl. 20, figs. 4, 5; Pl. 22, fig. 2a-c), with a short, distinct apical spine, higher than wide ($H = 0.35$, $W = 0.23$ mm), separated by a distinct constriction ($W = 0.18$ - 0.20 mm) from the teleoconch. The apical angle of the early teleoconch varies between 25 and 32°. At a very short distance from the protoconch, two squarish lateral carinae develop and the transverse section changes from circular to more or less triangular, with a flatter ventral and a more convex dorsal side. Incremental lines are more strongly curved in apertural direction on the dorsal than on the ventral side. A further teleoconch ornament is not present in these specimens.

Material examined – **Saint-Jean-de-Marsacq (Lahitet-1):** MNHN A32123/1 (Pl. 22, fig. 1a-d). **St Jean-de-Marsacq (Pinot):** RGM 541 389/3 protoconchs, RGM 569 467/1 protoconch (Pl. 22, fig. 2a-c), RGM 569 468/1 protoconch (Pl. 20, fig. 4a, b), RGM 569 469/1 protoconch (Pl. 20, fig. 5a, b), all leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Discussion – In general shape the most complete specimen resembles the Langhian species *Clio saccoi* Checchia-Rispoli, 1921. That species, however, has a distinctly wider apical angle, is far more strongly curved in its apical part and the lateral areas on the ventral side are wider. The larval shell of *C. saccoi* is still unknown.

***Clio* sp. 1**

Pl. 20, fig. 3; Pl. 22, fig. 3.

Description – Exclusively apical shell parts are available. The protoconch is oval, with a slightly pointed apex ($H = 0.30$, $W = 0.20$ mm), separated from the teleoconch by

a weak constriction ($W = 0.16$ mm). In the largest available specimen (height only 1.7 mm), the teleoconch hardly demonstrates a curvature and its transverse section is elliptical, with the dorso-ventral diameter slightly smaller than the shell width. A teleoconch ornament is not yet developed and no lateral carinae are present. The apical angle of this shell part is *c.* 22-25°.

Material examined – **Saint-Etienne-d’Orthe (Lartigaou)**: RGM 541 441/1 apical fragment (Pl. 20, fig. 3a, b), RGM 541 442/1 apical fragment (Pl. 22, fig. 3a, b); RGM 541 443/2 apical fragments, all leg. A.W. Janssen, 1984-1990. Chattian.

Discussion – No more adult specimen has been recognised. The present material is different from *C. vasconiensis*, occurring at the same locality, which species has a distinctly separated protoconch-1 and -2, and in which the early teleoconch is bicarinated.

Clio sp. 2

Pl. 22, fig. 4-6.

Description – Available are some apical fragments retaining the protoconch and some very small teleoconch fragments that might belong to the same species. The protoconch is oval ($H = 0.34$, $W = 0.23$ mm) and has a distinct apical spine. It is separated from the teleoconch by a clear constriction ($W = 0.18$ mm). In the largest available specimen (height only 1.68 mm), the teleoconch is almost straight; initially, its transverse section is circular, soon changing to triangular, with a flat ventral and a convex dorsal side. Three weak radial folds are just developed in the best preserved specimen. Squarish lateral carinae start at some distance from the boundary with the protoconch.

Material examined – **Saint-Martin-de-Hinx (Secat)**: MNHN A32124/1 protoconch (Pl. 22, fig. 5a-c); RGM 395.404/1 fragment (Pl. 22, fig. 6a, b) leg. A.W. Janssen, 30 July 1984, RGM 541 054/2 protoconchs, RGM 541 056/2 fragments, leg. A.W. Janssen, 1 August 1985; **Saubrigues (Tauziets)**: AWB/1 fragment, leg. A.W. Burger, 11 May 1992; RGM 541 606/1 protoconch (Pl. 22, fig. 4a-c), leg. A.W. Burger, 11 May 1992, don. November 2007; RGM 569 476/2 protoconchs, 2 fragments, leg. H.J. Mulder, 2007, don. October 2008. Langhian.

Discussion – Even though some of the present immature specimens agree in age with the single adult specimen from Saint-Jean-de-Marsacq (Lahitet-1), described above as *Clio* sp. nov.?, they apparently do not belong to the same species because of their triangular transverse section. The shells are too juvenile or incomplete to be identified. It cannot be excluded that they belong to *Clio ortheziana* (see above).

Family Cavoliniidae Gray, 1850

Genus *Cavolinia* Abildgaard, 1791

(emend. Philippi, 1853; *nom. cons.* International Commission on Zoological Nomenclature, 1969)

Type species – *Cavolinia tridentata* (Niebuhr, 1775) (Recent).

***Cavolinia zamboninii* Checchia-Rispoli, 1921**

Pl. 22, fig. 7.

- * 1921 *Cavolinia Zamboninii* Checchia-Rispoli, p. 26, fig. 12a, b.
- . 1968 *Cavolina zamboninii* Checchia-Rispoli, 1921; Sirna, p. 428, fig. 20.
- v. 1971 *Cavolina (Cavolina) zamboninii* (Checchia Rispoli, 1921); Robba, p. 103, pl. 5, figs. 9, 10.
1971 *Cavolinia zamboninii* Checchia-Rispoli; Jung, p. 220.
- non 1979 *Cavolinia zamboninii* Checchia Rispoli, 1921; D'Alessandro *et al.*, p. 91, pl. 15, fig. 14a-c (= *Cavolinia cookei* Simonelli, 1895).
- v. 1980 *Cavolinia zamboninii* Checchia Rispoli, 1921; D'Alessandro & Robba, p. 658.
- v. in press *Cavolinia zamboninii* Checchia-Rispoli, 1921; Janssen & Little, pl. 6, fig. 13.

Type locality – San Nicola Varano (Gargano, Italy); Lago di Varano Formation (Miocene). See also 'type locality' of *Cuvierina paronai*, above.

Type material – The whereabouts of Checchia-Rispoli's type material is unknown.

Description – Just two fragments are available from Aquitaine, both representing partially preserved dorsal shell parts. These both show the typical radial ornament, consisting of a distinct central riblet, flanked on both sides by a wider, but less clearly separated rib.

Material examined – **Saint-Martin-de-Hinx (Secat)**: RGM 395 406/1 fragment, leg. A.W. Janssen, 30 July 1984; RGM 541 058/1 fragment (Pl. 22, fig. 7), leg. A.W. Janssen, 1 August 1985. Langhian.

Discussion – These two fragments are the first extra-Mediterranean records of this species and also the first specimens found in shell preservation. All other occurrences are internal moulds.

Distribution – The species occurred exclusively during the Langhian and is known, apart from the type locality, from the Cessole Formation in northern Italy (Bric della Croce; Robba, 1971), the Ragusa Formation in Sicily, the Upper Globigerina Limestone Formation of Malta (RGM collections) and the Pakhna Formation of Cyprus (RGM collection; Janssen & Little, in press).

Genus *Diacrolinia* A.W. Janssen, 1995

Type species – *Diacrolinia aurita* (Bellardi, 1873) (Miocene, Langhian).

Discussion – In the Burdigalian sedimentary rocks of Aquitaine are found two species that are currently assigned to the genus *Diacrolinia*. There has been quite a lot of confusion about them, as the following historical overview may show.

Rang (1827, p. 383) described *Hyalea Orbignii* ('Hyale de d'Orbigny') from 'les sables fossiles de Saint-Paul-de-Dax' (most probably from the well-known locality at Moulin de Cabanes, Saint-Paul-lès-Dax, France). The species was not illustrated, but the concise description allows recognition of the species by the phrase '... la lame

dorsale ... sillonnée ...', indicating that radial ornament is present on the dorsal shell part.

In the same year, but shortly after Rang's paper was published, *Hyalaea Aquensis* Grateloup, 1827 ('Hyale de Dax') was introduced from an outcrop at Mandillot, another locality at Saint-Paul-lès-Dax. That species likewise was not illustrated, but the description contains the sentence 'On remarque quelquefois sur le dos une petite côte transversale,', referring to a single radial riblet on the base of the dorsal shell part. One year later, Grateloup (1828, p. 75) referred to this species with the same name.

Rang (1829, p. 493) referred to Grateloup's 1827 paper, considering *H. aquensis* a junior synonym of his '*H. Orbignii*'. Also (p. 496, pl. 19, fig. 3a-c) he repeated the description and added a primitive illustration in which a dorsal radial ornament is clearly indicated indeed.

Grateloup (1836, pp. 265, 295, pl. 1, figs. 1, 2) referred to Rang (1827), but maintained the name *Hyalaea aquensis*, considering *H. orbignii* a synonym, adding a not very successful illustration showing no radial ornament on the dorsal shell part. The same is true for the illustrations in Grateloup (1840, pl. 1, figs. 1, 2; explanation of pl. 1), where he only referred to Rang (1829). He still considered '*Hyalaea Orbignii*' a synonym of *H. aquensis*.

D'Orbigny (1834, p. 99, footnote 2) emended the name *Hyalaea Orbignii* to *H. Orbignyi*, but at the same time unwillingly introduced an incorrect spelling for *H. aquensis*, as *H. aguensis*. The same emendation of *H. orbignii* to *H. orbignyi* was made in Deshayes & Milne Edwards (1836, p. 417).

Souleyet (1852, p. 40, pl. 3, figs 16-18) repeated Rang's description, using the name *Hyalaea Orbignyi*, Rang. The illustration clearly shows the radial ornament of the dorsal shell part. The name *H. aquensis* Grateloup is considered a synonym by this author.

Benoist (1889, p. 24, pl. 1, fig. 4a-b) included Grateloup's species in his paper as *Cavolinia aquensis*, describing the ornamentation of the dorsal shell part correctly as "Valva dorsalis ..., in regionem mediana longitudinaliter costulata; costa inferne parvula, ante marginem oris evanescens ...". Benoist's illustration shows a specimen from Saucats (Moulin de l'Église), but the drawing does not show the central longitudinal riblet mentioned in the description. By the absence of any further radial ornament, this specimen indeed is identical with Grateloup's species. Benoist followed Rang (1829) in considering both taxa synonymous, but he used Grateloup's (younger) name, evidently not aware of Rang's earlier (1827) paper.

In 1932, Peyrot revised the known pteropods from the Aquitaine Basin and discussed one of these species, indicated by him also as *Cavolinia aquensis*. He adequately described the dorsal shell part as (p. 469) "l'ornementation de la valve dorsale comporte une costule médiane obsolète et des plissements transverses rapprochés, passant sur la costule médiane" Although he only had material of that species before him, he was the first to deny the identity of Grateloup's and Rang's species, because of the obvious presence of 'five or six' longitudinal dorsal folds in '*H. Orbignii*', so clearly indicated in Rang's illustration. Therefore, he concluded on the existence of two separate species, only one of which was before him and thus he correctly applied the name *Cavolinia aquensis*. Thus, Peyrot was the first to acknowledge the existence of two closely related species.

Van der Spoel (1973, p. 21) corrected an erroneous interpretation of the name

orbignii in several of his earlier papers, because of originally misunderstanding Souleyet (1852). In his papers he applied the name '*orbignii* (ms Rang) (Souleyet, 1852)' for a form of the Recent *Diacria quadridentata* (Blainville, 1821). He gives an excellent illustration of the holotype of '*Cavolinia orbignyi*', at the time housed in MNHN. His drawing clearly shows the presence of radial ornament on the dorsal shell part. Unfortunately, however, the holotype has since disappeared from the Paris collections (P. Lozouet, pers. comm.).

In the RGM collections at Leiden, a comparatively rich material of these rare species is available, on the basis of which Peyrot's (1932) conclusion can be substantiated. The various differences between the two species are given below. Both taxa unequivocally are species of the genus *Diacrolinia*. This genus is characterised (Janssen, 1995, p. 110) by the possession of a globular protoconch instead of a curved conical one as seen in *Cavolinia*. In virtually all available specimens, however, the larval shell is not preserved; in such cases the presence of a usually weak longitudinal riblet in the adapical half of the dorsal shell part, or dorsally oriented lateral slits, are good indications.

Diacrolinia orbignyi (Rang, 1827) (emend. d'Orbigny, 1834) is only known from the Moulin de Cabanes outcrop at Saint-Paul-lès-Dax, whereas *D. aquensis*, apart from its type locality Mandillot, is known from a number of localities more to the north in the Aquitaine Basin, such as Saucats and Léognan (see below). Because of the existing confusion between the two species, and in the absence of type specimens, it is considered of importance to designate neotypes for both (see below).

A further *Diacrolinia* species, of Late Aquitanian age, is described below as *D. cluzaudi* sp. nov. from Meilhan (Vives). The North Sea Basin taxon *Hyalea perovalis* von Koenen, 1882, for a long time an enigmatic cavoliniid from reworked boulders of Early Miocene age in northern Germany, of which recently a few new specimens surfaced, was synonymized with *Diacrolinia aquensis* by Janssen & Gürs (2002).

Several further species were described from the Miocene of northern Italy. The type species of *Diacrolinia* is *D. aurita* (Bellardi, 1873) (compare Janssen, 1995, p. 111, pl. 9, figs. 6-8, with lectotype designation), a Langhian species with a very wide geographical distribution for which several other names were introduced in the course of time. Few (juvenile) specimens of this species were also found in Langhian deposits of the Aquitaine Basin (see below). Both the type and its Tortonian successor *D. elioi* Janssen, 1995, differ from the above mentioned species by the presence of a distinctly three-lobed ventral shell part and their lateral slits are not turned into dorsal direction.

Two further species, however, are more closely related, both to *Diacrolinia orbignyi* and *D. aquensis*, viz. *D. interrupta* (Bellardi, 1873) and *D. revoluta* (Bellardi, 1873) (lectotypes for both taxa were also designated in Janssen, 1995). Like the two French species, they have an undivided ventral shell part and their lateral slits are directed in a dorsal direction. The stratigraphical range of both Italian species is imperfectly known, but is roughly estimated as Burdigalian/Langhian.

The dorsal shell part has the usual central radial rib in *D. interrupta*, which is quite strongly developed and reaches the apertural margin. The central rib is flanked on both sides by a slightly weaker rib and still weaker ones coincide with the lateral margins. This makes *D. interrupta* strongly resemble *D. orbignyi*, from which it differs merely by a relatively higher, narrower shell shape and only three radial dorsal ribs. *Diacrolinia*

revoluta has only one well-developed, vaguely delimited central radial rib and shows coarse concentric folds covering the dorsal shell part, rib and folds being much stronger than in *D. aquensis*.

***Diacrolinia aquensis* (Grateloup, 1827)**

Pl. 23, fig. 1.

- * 1827 *Hyalaea Aquensis*, Grateloup, p. 4.
- . 1828 *Hyalaea aquensis*; Grateloup, p. 75.
- . 1836 *Hyalaea aquensis*. Nob.; Grateloup, p. 265, 295, pl. 1, figs. 1, 2.
- . 1840 *Hyalea Aquensis*. Grat.; Grateloup, pl. 1, figs. 1, 2 (exclusive synonymy).
- . 1850 *Hyalaea aquensis*, Gratel.; Gray, p. 6.
- . 1852 *Hyalaea Aquensis*. Gratteloup [sic], 1825 [sic]; d'Orbigny, p. 96 (exclusive synonymy).
- . 1855 *Hyalaea aquensis* Grat.; Pictet, p. 318, pl. 70, fig. 15 (*mala*, exclusive synonymy).
- . 1874a *Hyalea Aquensis*. Grat.; Benoist, pp. 265, 422.
- . 1882 *Hyalea perovalis* v. Koenen, p. 354, pl. 7, fig. 15a-c.
- . 1884 *Hyalea Aquensis*, Grat.; du Boucher, p. 166.
- . 1885 *Hyalea aquensis* (Rang) [sic]; Quenstedt, p. 610.
- . 1886 *Hyalaea perovalis* v. Koenen; Kittl, p. 65.
- . 1887 *Hyalaea perovalis* v. Koenen; Gottsche, pp. 9, 13.
- . 1889 *Cavolinia Aquensis* (Grat.); Benoist, p. 24, pl. 1, fig. 4a-c.
- . 1915 *Hyalaea perovalis* v. K.; Gripp, pp. 29, 35.
- . 1932 *Cavolinia aquensis* Grateloup; Peyrot, p. 469, pl. 18 (not 'pl. 17'), figs. 45-47.
- . 1933 *Cavolinia aquensis* Grateloup; Peyrot, p. 19, pl. 18 (not 'pl. 17'), figs. 45-47.
- v. 1986 *Cavolinia perovalis*; Janssen, p. 149, fig. 10.
- v. 2002 *Hyalea perovalis* von Koenen, 1882; Janssen & Gürs, p. 144, figs. 1, 2.
- v. 2002 *Diacrolinia aquensis* (Grateloup, 1827); Janssen & Gürs, p. 146, figs. 3, 4

Type locality – '....le riche dépôt de Mandillot, à Saint-Paul, à une demi-lieue de Dax, le long d'un ruisseau ...' (= Saint-Paul-lès-Dax, Mandillot). Burdigalian.

Type material – In the FSUB collection at Bordeaux, just the label of the holotype remains, stating 'la coquille a été brisée' (the shell is broken). No fragments are present.

Neotype designation – RGM 541 320 (Pl. 23, fig. 1a-c), leg./don. W. Groeneveld, 1984-1986 (H = 6.66, W = 5.83, D-V = 4.33 mm, protoconch missing).

Neotype locality – Saucats (France, Gironde), outcrop La Coquillière, coordinates x = 367.500, y = 265.300, map-sheet XV-37 Pessac. Miocene, Burdigalian, Falun de Pont-Pourquey, level A 1 (Janssen, 1985a).

Description – Cavoliniform shell, slightly higher than wide, with a swollen ventral and a somewhat less convex dorsal shell part. Anteriorly the shell is broadly rounded, the posterior side is straight and the transition into the lateral margins is abrupt, forming an angle of c. 90° or slightly more. The ventral shell remains considerably lower than the dorsal part and is therefore wider than high, with the anterior part of the dorsal shell part overhanging the aperture. The ventral apertural margin is bent backwards as a reinforcement. Ornament of this shell part consists of weak and irregular

concentric folds, and two weak radial lines are visible running from the apex to the corners of the aperture. The dorsal side of the shell has stronger concentric ornament and a usually weak radial riblet runs in the centre of the shell from the apex to about half shell height. The dorsal apertural margin is provided with a distinct fold parallel to the margin, but not thickened as in *Diacria*. From the corners of the aperture, where dorsal and ventral shell parts are loosely connected by a kind of push-button construction, lateral slits are present until the base of the shell, where dorsal and ventral shell parts are connected. These slits are only visible in dorsal view.

Material examined – **Cestas (Cazeaux)**: FSUB/1, A. Magne collection (H = 5.33, W = 4.33, D-V = 3.42 mm, protoconch and apertural margin missing); **Saucats**: MBB/1, Duvergier collection; **Saucats (Coquillière)**: RGM 541 323/2 fragments, leg./don. F.A.D. van Nieulande, 1981; **Saucats (Coquillière-A 1)**: RGM 541 321/2 fragments, leg./don. W. Groeneveld, 1984-1986; RGM 541 322/1 fragment, leg. J. Gunst, 1982, don. F.A.D. van Nieulande; RGM 541 324/7 fragments, leg./don. F.A.D. van Nieulande, 1986; **Saucats (Coquillière-B 2)**: RGM 541 319/6 fragments, leg./don. W. Groeneveld, 1984-1986; **Saucats (Église)**: MBB/1, Benoist collection (illustrated by Peyrot, 1932, pl. 18, figs. 45-47) (H = 4.83, W = 4.17, D-V = 3.0 mm, protoconch missing); MBB/1, Degrange-Touzin collection (H = 5.0, W = 4.17, D-V = 3.17 mm, protoconch missing); **Saucats (Péloua)**: MBB/2, Degrange-Touzin collection (H = 5.17, W = 4.08, D-V = 3.17 mm, protoconch missing) (H = 4.83, W = 3.83, D-V = 3.0 mm, protoconch missing); **Saucats (Pont-Pourquey)**: MBB/1 fragment, Degrange-Touzin collection; MBB/1, Duvergier collection (H = 4.67, W = 5.0, D-V = 3.83 mm, protoconch and part of dorsal shell part missing). Burdigalian.

Discussion – *Diacrolinia aquensis* strongly resembles *D. orbigny* at first glance, which in part explains the confusion referred to above. There are, however, clear and constant differences. *Diacrolinia aquensis* is relatively more thickset, its dorsal side has only a short, central riblet in the apical part, its apertural margin is reinforced by a fold, but not thickened, and the lateral slits are not so strongly turned dorsally, whereas the ventral side has two weak radial lines, virtually absent in *D. orbigny*.

Distribution – Apart from the type locality Saint-Paul-lès-Dax (Mandillot) and the other localities referred to herein, this species was also recorded from Saucats (Giraudau) and Léognan by Peyrot (1932).

Diacrolinia aurita (Bellardi, 1873)

Pl. 22, fig. 8.

*v 1873 *Hyalaea aurita*, Bon.; Bellardi, p. 26, pl. 3, fig. 6 (mala).

v. 1995 *Diacrolinia aurita* (Bellardi, 1873); Janssen, p. 111, pl. 9, figs. 6-8.

Type locality – Rio della Batteria, Turin Hills, Italy (Miocene, Langhian, zone NN5).

Type material – Holotype, Museo Regionale die Scienze Naturali, Torino (BS 007.01.003/1)

Description – See Janssen (1995). Only two juvenile shells in pre-metamorphosis stage and two isolated protoconchs are available. In the juveniles, ventral and dorsal shell parts are not yet swollen (Pl. 22, fig. 8b) which makes the dorso-ventral diameter of the specimen very small. On the dorsal side, three radial ribs are visible. The protoconch has a width of 0.24 mm; its dorso-ventral diameter is slightly less. It is connected with the teleoconch by a neck-like constriction and a bit tilted in dorsal direction.

Material examined – **Saint-Martin-de-Hinx (Secat)**: MNHN A32125/1 juvenile (Pl. 22, fig. 8a-c); RGM 541 057/1 juvenile, 1 protoconch, leg. A.W. Janssen, 1 August 1985; **Saubrigues (Tauziets)**: SMF 332809/1 fragment?, leg. R. Janssen, 8 June 1981. Langhian.

Discussion – The immature specimens agree with similar material from the North Sea Basin and Malta in the RGM. Their presence at Saint-Martin-de-Hinx, and probably at Saubrigues (Tauziets), confirms a Langhian age.

Distribution – Langhian of the central Paratethys, Mediterranean, North Sea Basin, Caribbean and Japan.

***Diacrolinia cluzaudi* sp. nov.**

Pl. 22, figs. 9, 10.

Holotype – Pl. 22, fig. 9a-d, FSUB typotheque 52-4-8, leg./don. A. Cluzaud.

Type locality – Meilhan (Carrière Vives), coordinates 43° 54' 20" N, 0° 39' 45" W (Lambert: x = 359.100, y = 3182.800).

Stratum typicum – Calcareous shelly sands, dark grey to yellowish-pink upwards, with scleractinian corals and coarse-grained detritus (reefal facies; level 5 in Lozouet *et al.*, 2001) (Miocene, Late Aquitanian).

Derivatio nominis – The new species is named after the collector of the holotype, Mr Alain Cluzaud of Pessac, France, who made several further important specimens available for this paper.

Paratypes – **Meilhan (Vives)**: FSUB typotheque 52-4-9 (Pl. 22, fig. 10a-c), leg. A. Cluzaud; MNHN/A32126/1 specimen and 1 fragment of a very juvenile shell in premetamorphosis stage. Late Aquitanian.

Diagnosis – *Diacrolinia* resembling *D. orbigny*, but shell considerably smaller and dorsal side with three radial riblets instead of five, of which the lateral ones are very weak.

Description – Two specimens are available in FSUB (Cluzaud collection) that I erroneously identified as *Diacrolinia aquensis* in 2000. A further specimen and a small fragment are in MNHN. They resemble *D. orbigny* even more by their apertural margins reinforced by solid riblets instead of by a margin-parallel fold, by their lateral slits

strongly turned in a dorsal direction, by the absence of radial elements on the ventral shell and by the presence of radial ornament on the dorsal part. However, there are clear differences. The shell remains distinctly smaller (measured without the larval shell: holotype H = 4.75, paratypes H = 5.17 and H = 4.76 mm; neotype of *D. orbigny* H = 7.3 mm). The ornament on the dorsal shell part consists of the usual central riblet in the apical half, but it is accompanied on each side by just one, considerably weaker, lateral riblet, running from the apical shell part into the direction of the closing mechanism. The holotype is clearly more elongate than the illustrated paratype. It still possessed its protoconch, which unfortunately was disconnected from the teleoconch, but could be adequately replaced. It deviates from the teleoconch's axis with an angle of *c.* 45°. It is spherical and has a very slightly pointed tip. The paratype in MNHN agrees very well with the holotype, but does not show the flattening of the dorsal shell part (as seen in Pl. 22, fig. 9b).

Discussion – The holotype and one of the paratypes differ substantially in proportions, but their further characteristics indicate them as belonging to one species. They also originate from the same locality and stratigraphic level. The other *Diacrolinia* species known from Aquitaine are all from younger assemblages which makes me suggest that *D. cluzaudi* is the forerunner species of *D. orbigny*.

Distribution – Only known from the Late Aquitanian of Meilhan (Vives).

***Diacrolinia orbigny* (Rang, 1827) emend. d'Orbigny, 1834**
Pl. 23, figs. 2-4; Pl. 24, figs. 1, 2.

- * 1827 *Hyalea Orbignii* Rang, p. 383.
- . 1829 'Hyale' *Orbignii*, Rang; Rang, p. 496, pl. 19, fig. 3a-c.
- . 1834 *Hyalæa Orbigny* Rang; d'Orbigny, p. 99.
- . 1836 *Hyalea Orbigny*. Rang; Deshayes & Milne Edwards, p. 417.
- . 1852 *Hyalæa Orbigny*, Rang; Souleyet, p. 29, 40, pl. 3, figs. 16-18 (exclusive synonymy).
- . 1854 *Hyalæa Orbigny* Rang; Troschel, p. 198.
- . 1859 *Cavolina Orbigny*, Rang; Adams, p. 45 (exclusive synonymy).
- . 1932 *H. Orbignii*; Peyrot, p. 470.
- . 1933 *H. Orbignii*; Peyrot, p. 20.
- . 1962 *Cavolina orbigny* Rang; Zbyszewski & da Veiga Ferreira, p. 285.
- . 1973 *Cavolina orbigny* (Rang, 1827); van der Spoel, p. 23, figs. 1-3.

Type material – The holotype of this species (originating from the Miocene of Saint-Paul-lès-Dax) was last seen by van der Spoel (1973) and has since disappeared from the MNHN-collections (P. Lozouet, in litt.). Also, it was not found in the collections of the Zoologisch Museum, Amsterdam, where van der Spoel's material is housed.

Neotype designation – Because of the historical confusion, outlined above, between *Diacrolina aquensis* and the present species, caused by the resemblance between these two and by the insufficient illustrations in the classic literature, as well as by the fact that type material of both taxa has disappeared, it is considered essential to designate neotypes. For *D. orbigny* I herewith select a specimen in the Paris collection, where the holotype used to be housed, MNHN-A28097 (Pl. 23, fig. 2a-c).

Neotype locality – Saint-Paul-lès-Dax, outcrop near Moulin de Cabanes (France, Landes), coordinates X=328.335 Y=3164.600. Falun de Cabanes; Miocene, Early Burdigalian, N5 zone; reefal and shelly coarse sands, coastal facies.

Description – The shell is cavoliniform, approximately 1.2 times higher than wide, dorso-ventral diameter is *c.* 0.6 times the shell height (neotype H = 7.3, W = 6.1, D-V = 4.6 mm). Both the dorsal and the ventral shell parts are convex, the ventral more so than the dorsal. The ventral shell part is considerably lower than the dorsal and therefore wider than high. Both parts are connected at the squarish apical side of the shell. Conspicuous lateral slits, upturned in dorsal direction, are present from the adapical connection to the corners of the aperture, where dorsal and ventral shell parts are loosely connected with a closure mechanism. The ventral apertural margin is slightly curved, bending outwards as a reinforcement. Its ornament consists merely of somewhat irregular concentric folds, which are slightly recurved adapically in their centre, following the growth lines. The dorsal shell part has a strongly curved apertural margin overhanging the ventral shell part and thus covering the aperture in an adapical view. The dorsal apertural margin is firmly reinforced by a thickened rim as found in *Diacria*, which is connected with the edges of the lateral slits. The dorsal surface ornament shows a central radial rib starting at a short distance from the apex, accompanied on both sides by two weaker ribs, separated by wider interspaces. In a few specimens, the two outer ribs are only hardly visible. Concentric growth-lines may form some foldlike structures, especially in the apical part of the shell.

Apart from full-grown specimens, just a single, isolated protoconch was found at the Cabanes outcrop at Saint-Paul-lès-Dax (RGM 541 361, H = 0.26, W = 0.20, D-V = 0.17 mm; Pl. 24, fig. 2a, b), of spherical to slightly elliptical shape, with a gradually rounded tip and a clear constriction at the transition to the teleoconch (W = 0.18 mm). As *Diacrolinia orbigny* is the only species of this genus found at Cabanes, it may be safely assumed that it belongs to that species.

Material examined – **Saint-Paul-lès-Dax (Cabanes)**: ACP/1 (H = 6.17, W = 5.75, D-V = 4.17 mm, protoconch and dorsal margin missing), 3 fragments; MBB/1 fragment, De-grange-Touzain collection; MNHN unnumbered/4, 2 fragments, P. Lozouet collection; RGM 541 360/2 fragments, RGM 541 361/1 protoconch (Pl. 24, fig. 2a, b), leg. S. Mer-muys, 2003-2004, don. November 2006); RGM 541 374/1 (Pl. 23, fig. 4a-c; Pl. 24, fig. 1a, b), RGM 541 375/1 (Pl. 23, fig. 3a-c), RGM 541 376/7 fragments, all leg. A.W. Janssen, 1979-1987; RGM 541 378/7 fragments, leg./don. W. Groeneveld; SMF 332809/1 and 6 fragments, K. Jung collection, 1883-1885; SMF 332810/1 dorsal shell part, K. Jung collection, 1883-1885; SMF 332811/1, O. Boettger collection, ex K. Jung, 1883-1884. Earliest Burdigalian.

Discussion – *Diacrolinia orbigny* apparently is the successor species of *D. cluzaudi*, described above. For differences see that description. *Diacrolinia aquensis* (see above) has for a long time been synonymised with the present species, but there are clear differences. The most important of these are the presence of radial ribs on the dorsal shell part and a completely different development of the dorsal apertural margin reinforcements, as a margin parallel fold in *D. aquensis*, and as a thickened rim (as seen in *Diacria* species)

in *D. orbignyi*. Also, the lateral slits are much more strongly directed in dorsal direction than they are in *D. aquensis*. The two species do not co-occur.

Distribution – This species is known exclusively from Saint-Paul-lès-Dax (Cabanes).

Genus *Edithinella* A.W. Janssen, 1995

Type species – *Edithinella undulata* (Gabb, 1873) (Miocene, Santo Domingo; see Janssen, 1995, pl. 10, fig. 5a-d).

Edithinella caribbeana (Collins, 1934)

Pl. 24, fig. 3.

- *v 1934 *Vaginella caribbeana* Collins n. sp., p. 220, pl. 14, figs. 16, 17.
- 1970 *Vaginella caribbeana* Collins; Woodring, p. 427.
- 1977 *Vaginella caribbeana* Collins; Robba, p. 592.
- v. 1979 *Vaginella caribbeana* Collins, 1934; Pavia & Robba, p. 557, pl. 53, figs. 1-5.
- 1982 *Vaginella caribbeana* Collins; Bernasconi & Robba, pp. 217, 218.
- v. 1995 *Edithinella caribbeana* (Collins, 1934); Janssen, p. 125, text-fig. 3, pl. 10, figs. 6-9.
- v. 1999c *Edithinella caribbeana* (Collins, 1934); Janssen, p. 115, fig. 12a-c.
- v. in press *Edithinella caribbeana* (Collins, 1934); Janssen & Little, pl. 3, figs. 6, 7.

Type locality – Gatun, Panama Canal Zone (Middle Miocene, Gatun Formation).

Type material – USNM 645196 (illustrated type no. 24173).

Description – Just one fragmentary specimen is known from Aquitaine. It is the apertural half of a shell which is otherwise well-preserved and retains its apertural structures. The shell is vaginelliform with an apical angle close to the aperture of *c.* 7°, dorso-ventrally flattened and slightly curved, with the ventral side convex and the dorsal one slightly concave (lateral view). The ventral side has no ornament, even incremental lines are hardly visible and it is gradually curved transversely. Dorsally the surface bears undulations, three of which are visible in the available fragment, the spaces in between are wider than the undulations themselves. The lateral margins of the shell are shaped as a shallow groove.

The present specimen is the only one known in which the apertural features are well-preserved. The apertural margin is recurved over a short distance and laterally widened. The dorsal apertural margin is higher than the ventral one and gradually curved. The ventral margin is also curved, but remains lower.

Material examined – **Salles (Moulin Ruiné)**: RGM 393 122/1 (illustrated Janssen, 1995, p. 129, pl. 10, fig. 9a-c) (Pl. 24, fig. 3a-c herein), leg. F.A.D. van Nieulande, 8/10 August 1988, don. 1994. Serravallian.

Discussion – The single specimen from Salles resembles the type specimen from Panama better than the Tortonian material from northern Italy (Tetti Borelli) (Pavia & Robba, 1979); the undulations are more remote and the radial ornament seen in the Italian specimens is lacking in the shell from Salles.

Distribution – ‘Middle Miocene’ of Panama (Gatun; Collins, 1934), Serravallian of Aquitaine (Salles; Janssen, 1995; herein), Tortonian of northern Italy (Tetti Borelli; Pavia & Robba, 1979; Janssen, 1995) and Sicily (Poggio Musenna; Janssen, 1999c), (reworked?) Tortonian of Malta (Greensand Formation; RGM collection), Tortonian of Cyprus (Janssen & Little; in press).

***Edithinella varanica* (Sirna, 1968)**

Pl. 24, fig. 4.

- * 1968 *Vaginella varanica* Sirna n. sp., p. 426, fig. 16.
- v. 1977 *Vaginella varanica* Sirna, 1968; Robba, p. 591, pl. 18, figs. 5, 6, pl. 19, figs. 1-3.
- v. 1979 *Vaginella* cf. *varanica* Sirna, 1968; D’Alessandro *et al.*, p. 89.
- v. 1980 *Vaginella varanica* Sirna, 1968; D’Alessandro & Robba, p. 633, pl. 68, figs. 1-9.
- 1982 *Vaginella varanica* Sirna; Bernasconi & Robba, p. 217.
- 1995 *Vaginella varanica* Sirna; Janssen, p. 125.

Type locality – ‘Dei calcari del Serravalliano di S. Nicola Varano (Gargano)’ (Sirna, 1968).

Type material – Sirna (1968, p. 426) stated that the holotype and one paratype are in the Museo dell’Istituto di Geologia e Paleontologia dell’Università di Roma. However, something quite curious has happened with part of Sirna’s type specimens. When visiting the Geology and Palaeontology Department of the Università degli Studi at Milano, Italy, in 1992, Professor Elio Robba entrusted me, among other things, with a number of slides, containing specimens from the Gargano Miocene. These slides appeared to contain pteropods, partly type and/or illustrated specimens, published by Sirna (1968). After study of these specimens, I repeatedly tried to contact the institute in Rome, but never received any reply. Over the years, I tried several times to contact other institutes, as apparently the institute at the Rome university was no longer in existence, but with no results at all. Quite recently, early 2008, I found out that all collections of the former institute are nowadays in APAT (Rome), which is the National Agency for the Environmental Protection and Technical Services. Contacting that institute, however, did not lead to a useful contact and Sirna’s specimens are still in coll. RGM, where I registered them for safety. Holotype and paratype of the present species are in RGM 569 479 and 569 480. Type and/or illustrated specimens of other taxa described by Sirna are also in coll. RGM, but the material is not complete.

Description – The shell is vaginelliform with its apical part slightly bent ventrally. The adult shell part is dorso-ventrally compressed, with an elliptical transverse section, but initially the dorso-ventral diameter exceeds the width. Both sides of the shell are convex, flattening slightly towards the aperture. The ventral shell part, however, is narrower than the dorsal one, resulting in clear lateral grooves visible from the ventral side only, accompanying more or less distinct lateral carinae. In many adult specimens (but not in the one discussed here) the flattened dorsal shell part has transverse undulations. The aperture is laterally widened when fully grown. The protoconch is still unknown.

Material examined – **Orthez (Paren)**: SMF 332812/1 fragment (Pl. 24, fig. 4), leg. R. Janssen, 20 June 1981.

Discussion – The single fragmentary specimen represents the curved initial part of the shell, but the larval shell is missing. No undulations are present (yet) on its dorsal side. *Edithinella varanica* is a common species in late Langhian and Serravallian deposits of the Mediterranean, where all specimens are preserved as internal moulds. The present fragment is the first extra-Mediterranean specimen and the only specimen known in shell preservation.

Genus *Gamopleura* Bellardi, 1873

Type species – *Gamopleura taurinensis* (Michelotti, 1847) (Miocene, northern Italy).

Gamopleura taurinensis (Michelotti, 1847)

Pl. 24, fig. 5.

1842 *Hyalaea Taurinensis* E. Sism.; Sismonda, p. 26 (*nomen nudum*).

* 1847 *Hyalaea Taurinensis* Sism.; Michelotti, p. 148, pl. 5, figs. 13, 14, 141.

v. 1873 *Gamopleura taurinensis* (E. Sism.); Bellardi, p. 28, pl. 3, fig. 9a-c.

v. 1995 *Gamopleura taurinensis* (Michelotti, 1847); Janssen, p. 130, pl. 11, figs. 1, 2 (not fig. 12).

Type locality – ‘Colli Torinesi’ (Bellardi, 1873). Miocene (Burdigalian?).

Type material – Neotype (Janssen, 1995, p. 131, pl. 11, fig. 1a-c), Dipartimento di Scienze della Terra, Torino, Italy (Bellardi & Sacco collection), BS 007.03.001.

Description – See Janssen (1995). The single available specimen from Aquitaine lacks the greater part of its apertural shell parts, with only a small part of the ventral apertural margin remaining. Dorsal and ventral shell parts are convex, resulting in an almost globular shell of oval shape, with the greatest width above mid height. Both sides are covered with an ornament of numerous narrow concentric ridges, reaching the aperture. These ridges are stronger curved on the dorsal shell part than on the ventral. The lateral connection of both sides of the shell is formed as a ridge, running from the apex until the corners of the aperture. There are no lateral slits. Just a small part of the ventral apertural margin is retained, showing a distinct backwards curvature.

Material examined – **Meilhan (Vives)**: FSUB typothèque 52-4-10/1 (Pl. 24, fig. 5a, b), A. Cluzaud collection.

Discussion – The only available specimen differs from the northern Italian material solely by the almost complete absence of the weak radial ornament of the dorsal side. The stratigraphical origin of all northern Italian samples is a bit doubtful and was indicated as Burdigalian? (Janssen, 1995, pp. 203-204). The Meilhan specimen, of Late Aquitanian age, may suggest that also the Italian occurrences are somewhat older.

Distribution – Hitherto recorded from several localities in northern Italy. The Meilhan specimen is the first extra-Mediterranean occurrence.

Genus *Vaginella* Daudin, 1800

Type species – *Vaginella depressa* Daudin, 1800 (Miocene, Burdigalian, France).

Discussion – Species of *Vaginella* are known from a relatively short time interval, *viz.* Rupelian to Tortonian. Quite a number of species have been described from this time span, but several taxa, once included in *Vaginella*, are nowadays considered to belong in other genera, such as *Creseis*, *Cuvierina*, *Ireneia* or *Edithinella*. Still, it is clear that the genus underwent a rapid development in various parts of the world's oceans. This, and the lack of unequivocal distinguishing criteria between several of the c. 15 species recognised, has led to the introduction of superfluous names and a very confusing literature (Janssen, 1995, pp. 133-134). However, some species have very specific characteristics, such as the Chattian *V. tricuspidata* or the Burdigalian *V. victoriae* (see below), allowing certain identification.

All species in this genus have a similar construction plan, more or less resembling a miniature dagger sheath (hence, of course, also the latin name). Shells consist of a usually straight, more or less elongately triangular shell, with dorsal and ventral sides distinctly separated by lateral carinae that as a rule extend from just above the larval shell until somewhat more than half the shell height. The sidelines in a frontal view may be curved or straight, or somewhat flexuous in their lower part. Just below the generally widened aperture there may be a constriction, the diameter of which may be smaller than that of the lower part of the shell, as in *V. depressa*.

The larval shell consists of clearly separated protoconchs-1 and -2, the tip of which may be rounded or slightly pointed. The axis of the larval shell in some species deviates from the long axis of the teleoconch. The larval shell is shed by the living animal during or shortly after metamorphosis in just three known species, after which a septum is formed to close the opening, *viz.* *Vaginella floridana* Collins, 1934 (p. 216, pl. 13, figs. 22, 23), from the Miocene of the U.S.A., *V. venezuelana* Collins, 1934 (p. 219, pl. 14, figs. 18-20) from the Early Miocene of Venezuela and *V. basitruncata* Janssen, 2005b (p. 74, figs. 1, 2) from the Late Oligocene of the North Sea Basin.

Near the aperture of the adult shell, both ventrally and dorsally, more or less clearly developed vertical folds may be present that lay closer on the ventral side. These folds are most clearly observed in an adapical view. It is assumed (Janssen, 1995, p. 135) that the apertural margin is higher on the dorsal side, indicated also by growth-lines on the dorsal side being a bit more strongly curved adaperturally. This means that in species with a deviating protoconch, such as *V. austriaca*, the larval shell is curved ventrally. Further, the apertural margin sometimes (*V. tricuspidata*, see below) has specific structures. The surface ornament of the teleoconch consists of incremental lines only; there is no microornament. A comparatively coarse radial (but not micro-) ornament has been described for '*Vaginella rzehaki* Kittl, 1886' in its original description, acknowledged by D'Alessandro & Robba (1981, p. 632) and Janssen (1984b, p. 77, pl. 3, figs. 3, 4), a taxon nowadays synonymised with *V. austriaca*. Such radial lines are interpreted as a senile characteristic. In the descriptions below it is only indicated in how far a species deviates from this general pattern.

In the evolution of *Vaginella* during the Miocene there is a distinct trend of pro-

gressively developing more elongate shells. The closely related species *V. depressa*, *V. austriaca*, *V. acutissima* and *V. lapugyensis*, spanning the Aquitanian-Serravallian interval, apparently form a gradually changing evolutionary lineage and it is commonly difficult to assign certain specimens to one or another of these taxa. In such cases, rather subjective criteria have to be applied, such as the apical angle of the teleoconch basis. Subjectivity of this measurement is caused by the sidelines of the shell hardly ever being straight, which makes this parameter only applicable with much caution. With this restriction in mind, *V. depressa* is the species with the widest apical angle (40° or more), *V. austriaca* (c. 20° or more) and *V. acutissima* (c. 15-18°) are intermediate, and *V. lapugyensis* (c. 8-13°) is the most slender, the latter with completely straight sidelines. Only *V. acutissima* of these (occurring abundantly during the Mediterranean Langhian) has not yet been found in the Aquitaine material.

Vaginella depressa was the first fossil pteropod (although not recognised as such) ever described in literature and it is not surprising that this was from the rich fossiliferous deposits of the northern Aquitaine Basin, where this species is very common in the Aquitanian/Early Burdigalian assemblages. As such assemblages are commonly of shallow water facies, it is remarkable to find a pteropod species in such abundance. Obviously, *V. depressa* was an epipelagic species, easily transported into shallow water from oceanic water bodies.

Also, the earliest occurring *Vaginella* species originates from the Aquitaine Basin. It is represented by just a single specimen from the Rupelian of Gaas (Espibos), here introduced as *V. gaasensis* sp. nov.

Vaginella specimens are hardly ever found in perfect condition. Practically always the apical part with protoconch is missing and usually also the apertural parts are imperfect. Well-preserved juvenile specimens (extracted from the sediment contents of larger benthic gastropods) of *Vaginella austriaca* from the North Sea Basin (Winterswijk-Miste) and *V. depressa* from Aquitaine (Martillac) (Janssen, 1985b, figs. 8-13) allowed a reconstruction of shell metamorphosis during ontogeny. Immediately after the larval shell (protoconchs-1 and -2), the veliger develops widely triangular, very flat and flexible dorsal and ventral shell parts (Pl. 24, fig. 10a-c; Pl. 20, fig. 9a). During metamorphosis this flat shell changes into a less triangular, more elongate shell with a much more circular transverse section, most probably partly or even completely by dissolution of the aragonitic shell, after which the wall is solidified in its permanent shape by renewed internal precipitation of aragonite. In practically all specimens, this deformation of the shell (or, if decalcification was complete, of the organic tissue covering the animal) leaves characteristic wrinkles at the sides of the early teleoconch (Pl. 24, fig. 11a, b), as also clearly seen in species of the genus *Cavolinia*. The few *Vaginella*-specimens found in pre-metamorphosis state suggest a very similar protocol as found in other cavolinioid pteropods (Bandel & Hemleben, 1995; Janssen, 2007a).

There have been suggestions in literature to include the genus *Vaginella* in the family Cuvierinidae (see above in the discussion of *Ireneia*). However, individuals of this genus undergo shell metamorphosis during ontogeny, a convincing reason to maintain *Vaginella* in the Cavoliniidae.

***Vaginella austriaca* Kittl, 1886**
Pl. 20, figs. 6-8; Pl. 24, figs. 6, 7.

- *v 1886 *Vaginella austriaca* Kittl n. f., p. 54, pl. 2, figs. 8-12.
v. 1984b *Vaginella austriaca* Kittl, 1886; Janssen, p. 73, pl. 4, figs. 1-8.
v. 1995 *Vaginella austriaca* Kittl, 1886; Janssen, p. 139, pl. 11, figs. 7-10.

Type locality – Baden, Lower Austria; ‘Badener Tegel’, Upper Lagenidae Zone, Miocene, Badenian (= Langhian).

Type material – Lectotype in NMV (1990/1297/1), designated Janssen (1984b, pl. 4, fig. 1a-c; also nicely illustrated in Zorn, 1990, pl. 14, fig. 1a, b; 1991a, pl. 4, fig. 1a-c).

Description – The available Aquitaine material of this species is predominantly fragmentary. *Vaginella austriaca* is characterised by an apical angle of the early teleoconch of *c.* 20° or more. Its sidelines in frontal view are slightly curved or, usually, somewhat flexuous. In most specimens, the middle part of the shell is slightly widened, but the width of that shell part does not exceed the width of the aperture. A sub-apertural constriction is hardly indicated and its width is not smaller than the lower parts of the teleoconch. The larval shell in this species deviates clearly (15-25°) from the long axis of the adult shell, in a ventral direction (Pl. 24, fig. 6b). Its apex is rounded or slightly pointed. Apertural folds are barely indicated.

Material examined – **Saint-Martin-de-Hinx (Secat)**: RGM 541 060/1 fragment, leg. A.W. Janssen, 1 August 1985. Langhian.

Saint-Jean-de-Marsacq (Lahitet-1): MNHN PL 3665/30, 34 fragments, MNHN A32127 and A32128/2 retaining protoconch (Pl. 24, figs. 6a, b, 7a, b); **Saint-Jean-de-Marsacq (Lahitet-2)**: MNHN PL 10445/1, 5 fragments (2 of which retaining protoconch); **Saint-Jean-de-Marsacq (Pinot)**: RGM 429 266/1 protoconch, RGM 429 267/14 fragments (3 of which retaining protoconch), both leg. F.A.D. van Nieulande, July 1996, don. October 1996; RGM 516 561/2 fragments, leg./don. J. van der Voort, 22 June 1997; RGM 541 390/many fragments, RGM 541 391a/many protoconchs, RGM 541 391b-d/3 protoconchs (Pl. 20, figs. 6-8), leg./don. G. Garding, 3 July 1996. Late Burdigalian.

Discussion – My (1984b) designation of a lectotype from Kittl’s (1886) syntype material has been a bit unfortunate. A much better knowledge of the various *Vaginella* species after all these years has demonstrated that the lectotype, with an apical angle of *c.* 20-22°, is relatively slender, considerably more so than the bulk of the *V. austriaca* specimens known from all over Europe and, in fact, approaches the lectotype of *V. acutissima* (compare Janssen, 1995, pl. 11, fig. 3a-c), which has an apical angle of *c.* 18°. This once more demonstrates the close affinity of these species.

Vaginella austriaca is the obvious successor species developing from *V. depressa*. It differs from the latter by a smaller apical angle of the teleoconch, flexuous sidelines instead of convex ones, a less swollen central shell part and a sub-apertural constriction (if present at all) that is not narrower than the widest shell part at approximately

mid-height. Further, its larval shell deviates from the teleoconch axis, which it usually does not in *V. depressa*.

Transitional populations between these two taxa are not known from the Aquitaine Basin, although among the abundant *Vaginella depressa* from the Early Burdigalian specimens may be found, extremes in the range of variability that already strongly resemble *V. austriaca* (Pl. 20, fig. 5a, b). However, in the Mediterranean, and also in the North Sea Basin, the vertical distribution of both species is obvious, indicating that the transition must have taken place during the Late Burdigalian. In the North Sea Basin, these pteropod distributions led to a revised age interpretation of the local stage 'Hemmoorian', which, on the base of its rich benthic mollusc assemblages was correlated with the Aquitaine (Early!) Burdigalian for a long time, but is now considered to be Late Burdigalian/Langhian (Janssen, 2001).

The single fragment from Saint-Martin-de-Hinx was isolated from similar (and larger) fragments of *Vaginella lapugyensis* (see below) because of its wider apical angle. A co-occurrence of these species is well-known from the Mediterranean Langhian, for example.

Distribution – *Vaginella austriaca* is widely distributed in the central Paratethys, the North Sea Basin and the Mediterranean. Its developmental optimum was during the Langhian. From Aquitaine (Saint-Jean-de-Marsacq), *V. austriaca* was already recorded by du Boucher (1887, p. 147, fig. 1). The species *V. floridana* was earlier (Janssen, 1995, p. 140) incorrectly interpreted as a synonym of *V. austriaca*, but in the former species the larval shell is shed and a closing septum is found instead.

Vaginella chattica R. Janssen, 1979

Pl. 24, fig. 8.

- . 1846 *Belemnites lanceolatus* Boll nov. sp., p. 176, pl. 2, fig. 16a-c (*non* Schlotheim, 1813, *nec* Sowerby, 1829).
- v. 1886 *Vaginella lanceolata* v. Koenen; Kittl, p. 60, pl. 2, fig. 34.
- v 1932 *Vaginella Calandrelli* Michelotti; Peyrot, p. 474 (*partim, non* Michelotti).
- v 1933 *Vaginella Calandrelli* Michelotti; Peyrot, p. 23 (*partim, non* Michelotti).
- *v. 1979 *Vaginella chattica* R. Janssen *nom. nov.* [pro *Belemnites lanceolatus* Boll, 1846 (*non* Schlotheim, 1813)], p. 351.
- v. 1984b *Vaginella lanceolata*, *Vaginella chattica*; A.W. Janssen, p. 75, pl. 3, fig. 5a-d.
- v. 1986 *Vaginella chattica*; A.W. Janssen, p. 149, fig. 6.
- v. 1993 *Vaginella chattica* R. Janssen; Zorn & Janssen, p. 64, pl. 2, fig. 6a, b.

Type locality – Boll (1846) did not mention a locality for his specimen. It originated from the 'Sternb. Kuchen', meaning that it was collected from reworked boulders of so-called 'Sternberger Gestein' of Chattian age, most probably from a northern Germany locality.

Type material – The whereabouts of Boll's specimen is unknown.

Description – *Vaginella chattica* resembles *V. depressa* closely, but is distinguished by gradually convex sidelines with a hardly or not indicated preapertural constriction. The

apical angle of the early teleoconch can hardly be measured, but seems to be even wider than in *V. depressa*. Aperturally, the shell is slightly more flattened dorso-ventrally than in *V. depressa*. The presence of two relatively strong vertical furrows running on both sides from the apertural margin downwards, lying more closely on the ventral side, is very characteristic. The single more or less completely preserved specimen from Aquitaine has damaged apertural shell parts, but the two folds of the ventral shell part are clearly visible.

Material examined – **Peyrehorade (Peyrère)**: FSUB typotheque 23-4-18/1, A. Peyrot collection (Pl. 24, fig. 8a-c; specimen referred to in Peyrot, 1932, as *Vaginella calandrelli*); RGM 541 408/1 fragment, leg. A.W. Janssen, 10 June 1981.

Discussion – Considering its distribution during the Chattian, as well as its morphological features, it seems likely that *Vaginella chattica* is the forerunner species of *V. depressa*. Of the other specimens referred to as '*Vaginella calandrelli*' by Peyrot (1932), from Saucats (Péloua and Moulin de l'Église) and Léognan (Thibaudeau and Coquillat), only those from Péloua and Église are present in MBB, but both were found to belong to *V. depressa*.

Distribution – The species is not rare in part of the Late Oligocene deposits of the North Sea Basin. Janssen (2005b) found it restricted to the later part of the Eochattian (Chattian B) where its first occurrence datum indicates the base of pteropod zone 16b. The few specimens from Peyrehorade (Peyrère) referred to above are the first certain records of this species from outside the North Sea Basin.

Vaginella depressa Daudin, 1800

Pl. 20, fig. 9a-c; Pl. 24, figs. 9-11; Pl. 25; Pl. 26, figs. 1-5.

* 1800 *Vaginella depressa*, Daudin, p. 145, pl. 11, fig. 1.

v 1933 *Vaginella calandrelli* [sic] Mich.; Peyrot, pl. 18, figs. 31, 32 (*non* Michelotti).

v. 1995 *Vaginella depressa* Daudin, 1800; Janssen, p. 145, pl. 11, figs. 11-13.

Type locality – 'Environs de Bordeaux'.

Type material – Daudin's specimen has not been found in the various Bordeaux and Paris collections, and must be considered lost.

Neotype designation – Considering the long-time confusion, existing especially between this species and *Vaginella austriaca*, it is considered essential to designate a neotype. The neotype locality of Léognan is chosen (which is within the 'environs de Bordeaux', the type locality), as most probably that was the most popular collecting area in older times. A specimen from old collections (leg. unknown) in the Leiden museum, registered as RGM 396 088, is here designated neotype and transferred to the MNHN collection, where one would expect to find the type of this species. Its registration number is MNHN A28096 (Pl. 24, fig. 9a-d). Its age is Burdigalian.

Description – Measurements of the neotype are H = 5.17, W = 2.25, D-V = 1.75, W at aperture 2.20 mm, larval shell missing. The shell has convex sidelines along the base of the teleoconch that gradually change to concave in the adapertural half, leading to a laterally widened aperture. The constriction has a width of 2.0 mm. The apical angle of the teleoconch base, although difficult to measure, can be estimated at approximately 45°. In lateral view the shell shows gradually convex sidelines. Close to the apex the dorso-ventral diameter exceeds the shell width, but in the apertural direction the shell becomes gradually flattened. Distinct lateral carinae are present on both sides, reaching to almost half the shell height. Close to the apertural margin the ventral shell part has two weak folds, bordering a swelling in the middle (apertural view; Pl. 24, fig. 9a). Of the usual two more distant folds on the dorsal apertural margin, just one is (barely) visible in this specimen. There is no further reinforcement on the margins. The apertural margins are both gently curved (ventral view), the dorsal one slightly higher than the ventral. The shell surface is without ornament. Growth-lines are curved adaperturally, on the dorsal side somewhat stronger than on the ventral one and meet on the lateral carinae in a v-shape.

The numerous available specimens of *V. depressa* demonstrate a considerable variability. One of the samples in the Degrange-Touzin collection (in MBB) from Léognan (Coquillat) was found to contain no less than 6,022 specimens. This very large sample gives an excellent idea of the extreme variability of this species. Thirty selected adult individuals from this sample are represented in outline drawings (Pl. 25). Especially striking is the difference in size. Of all these specimens height and width were measured, and the drawings are arranged according to increasing H/W-ratio. As all specimens lack their larval shell and most of them have (more or less strongly) damaged apertural parts, the impression given by this series of specimens is rather irregular, which is caused by the greatest width of the shell occurring at mid-height in some shells, and at the aperture in others.

Specimens of *Vaginella depressa* still retaining their larval shells are rare (Janssen, 1985b). The axis of the larval shell does hardly or not deviate from the long axis of the adult shell. Protoconchs-1 and -2 are distinctly separated by constrictions. The height of the larval shell reaches c. 0.5 mm, protoconch-2 is higher and more swollen than protoconch-1. The apex is pointed (Pl. 20, fig. 9b). Shell metamorphosis is described above in the introduction to the genus. Two specimens in pre-metamorphosis stage are illustrated herein (Pl. 20, fig. 9a; Pl. 24, fig. 10a-c).

Material examined – **Bordeaux**: MNHN/72, old collection, leg. unknown, sample with two 19th century labels, viz. Bordeaux and Léognan, 5 specimens had been glued to this latter label originally; SMF 332813/1, leg. unknown; SMF 332814/2, leg. unknown (as '*Vaginella acuminata*'); **Canéjan (Bouscaut)**: MBB/1, Duvergier collection; **Cestas (Fourcq)**: FSUB/5, Peyrot collection; **Cestas (Cazeaux)**: FSUB/14; FSUB typothèque 33-4-9/1 (Pl. 26, fig. 1a-c), both A. Magne collection; **Dax**: MHB/1, leg. unknown, label partly unreadable; **La Brède (Moras)**: SMF 332814-6, 14, 7, and 45 + some fragments, all K. Jung collection, 1883-1885; **Léognan**: BMNH PITG25519/1, D. Curry collection; JRP/27, L. Gougerot collection; MHB/11, leg. unknown; NMV unnumbered/4, leg. unknown (illustrated Kittl, 1886, pl. 2, figs. 12, 17-19 and Janssen, 1984a, pl. 4, figs. 20, 21, 9, 12, 10, respectively); NMV/69, leg. unknown; RGM 396 082/7, RGM 396 088/4, both leg. un-

known (old collection); RGM 396 111/7, Erb collection, don. Instituut voor Mijnbouwkunde van de Technische Hogeschool, Delft, 1984/1985; SMF 332817/123, leg. unknown; SMF 332818/5, Peyrot collection, don. H. Schlesch; SMF 332819/9, leg. unknown; **Léognan (Bougès)**: SMF 332820/297, leg. R. Janssen, 19 July 1978; **Léognan (Coquillat)**: BMNH PITG25523/1 and 1 fragment (both juveniles in pre-metamorphosis stage); BMNH PITG25524/10 apical shell parts and protoconchs; BMNH PITG25525/88 and 5 fragments, all D. Curry collection; FSUB/930, FSUB/1 resembling *V. austriaca*, all from Croizier, Magne and Peyrot collections; SMF 332821/211 (from *Turritella* level), K. Jung collection, 1883-1885; MBB/6.022 (30 of which illustrated Pl. 25), MBB/63, both Degrange-Touzin collection; **Léognan (Thibaudeau)**: MBB/1, Degrange-Touzin collection; MBB/46, Duvergier collection; RGM 396 101/2, leg. unknown, don. Instituut voor Mijnbouwkunde van de Technische Hogeschool, Delft, 1984/1985; SMF 332822/1, K. Jung collection, 1883-1885; **Martillac (Barreau)**: ABH 8602/63, leg. A.W. Burger, leg. 4 August 1985; MBB/47, MBB/246, both Degrange-Touzin collection; RGM 227 565-568/4 juveniles (illustrated Janssen, 1985b, p. 203, fig. 10-13) (Pl. 24, fig. 10a-c; Pl. 26, fig. 2a-c herein); RGM 396 112/many, leg. A.W. Janssen, 5-6 August 1985 and 10/11 July 1986; RGM 396 113/20; RGM 396 488/many; RGM 396 489/12 with preserved protoconchs, all leg. A.W. Janssen, 6/7 August 1984; **Mérignac**: NHB unnumbered/18, leg. unknown; RGM 396 083/12, RGM 396 102/28 protoconchs, RGM 396 103/16 protoconchs, all leg./don. F.A.D. van Nieulande, 20 July 1980; **Mérignac (couche 6)**: MBB/10, Degrange-Touzin collection; **Mérignac (Pontic)**: FSUB/22, Peyrot collection; MBB/71, Duvergier collection; MNHN J09567/6, M. Cossmann's collection; **Pessac**: RGM 396 087/14, leg./don. P. Hessel, 25 April 1989; **Pessac (Lorient)**: MBB/2, Duvergier collection; **Saint-Médard (Gajac)**: MBB/5, Duvergier collection; **Saint-Paul-lès-Dax**: FSUB/24, Grateloup collection (this sample probably includes the illustrated specimen of Grateloup, 1836, pl. 1, figs. 3-4 and 1840, pl. 1, figs. 3-4 *sub nomine* '*Cleodora strangulata* Desh. '); MBB/6, Degrange-Touzin collection; **Saint-Paul-lès-Dax (Cabanes)**: ABH 8Sp1/3, 8Sp2/10, 3 fragments, leg. A.W. Burger, 15-16 June 2002; AJB/61; MBB/103, Degrange-Touzin collection; MNHN PL 1966/125; RGM 396 093/many, RGM 396 094-099/6 (Pl. 26, fig. 3a-b), RGM 396 100/2, 2 fragments retaining protoconch, all leg. A.W. Janssen, 1979-1987; RGM 541 362/many (hundreds), RGM 541 363/1 monstrosity, RGM 541 364/1 juvenile (Pl. 20, fig. 9a-c), RGM 541 365/14 protoconchs, all leg. S. Mermuys, 2003-2004, don. November 2006; SMF 158693/150, SMF 158693a/1, both O. Boettger collection, 1884; SMF 332823-4/80 and 1 apical fragment retaining protoconch, K. Jung collection, 1883-1885; SMF 332825/20, O. Boettger collection, ex K. Jung, 1883-1885; SMF 332826-7/96 and 2 apical fragments retaining protoconch, leg. R. Janssen, 9 June 1981; WGS/30; **Saint-Paul-lès-Dax (Mainot)**: MNHN J09568/4, M. Cossmann's collection; **Saucats**: RGM unnumbered/22; RGM unnumbered/1, leg. unknown, both ex collection Rijks Geologische Dienst, Haarlem; **Saucats (Coquillière)**: BRS/93, 3 juveniles, leg. B.G. Roest, 8 May 1985; RGM 396 084/30, leg./don. P. Hessel, 25 April 1989; RGM 396 085/many, RGM 396 090/1 and 10 fragments, RGM 396 091/7, all leg./don. F.A.D. van Nieulande, July 1982; RGM 396 092/many, leg. J. Gunst, July 1982, don. F.A.D. van Nieulande; RGM 396 104/1, RGM 396 105/2 juveniles, 3 fragments, both leg./don. H.P.J. Keukelaar; RGM 396 107/c. 20 juveniles, leg./don. F.A.D. van Nieulande, July 1981; RGM 396 108/28 protoconchs, leg./don. F.A.D. van Nieulande, July 1981; RGM 396 110/c. 15, leg. J. Gunst, July 1982, don. F.A.D. van Nieulande; RGM 429 725/14 fragments, 2 protoconchs, leg. A.W. Janssen, 21 and 24 July

1984; **Saucats (Gieux)**: MBB/7, Degrange-Touzin collection; **Saucats (La Cassagne)**: FSUB/14, leg. unknown; **Saucats (Église)**: MBB/1, Degrange-Touzin collection, as *Vaginella calandrellii*; **Saucats (Lagus)**: AJB/3; AJB/125; FSUB/156, leg. unknown; FSUB/279, L. Reyt collection; MNHN PL 2240/101, 81 and 71; MNHN J09569/119, M. Cossmann's collection; RGM 396 086/5, leg./don. A.C. Janse; SMF 332828/232, K. Jung collection, 1883-1885; SMF 332829/22, leg. J. Görge; **Saucats (Péloua)**: FSUB/5, Reyt collection; FSUB/14, leg. unknown; JRP/1 juvenile, L. Gougerot collection; MBB/14, MBB/204, MBB/1 fragment (as *Vaginella calandrellii*), all Degrange-Touzin collection; MBB/19, Duvergier collection; RGM 227 556/2, leg./don. D. Gourgues, 1984; RGM 396 081/30, leg. A.W. Janssen, 17 June 1979; RGM 396 114/9, leg./don. F.A.D. van Nieulande, July 1980; Réserve Géologique de Saucats/1; **Saucats (Pont-Pourquey)**: FSUB/3, Croizier & Magne collection; MBB/3, Degrange-Touzin collection; MBB/6, Degrange-Touzin collection; MNHN A32129/2 (one of which transitional to *V. austriaca*; Pl. 26, fig. 5a, b); SMF 332830/1, K. Jung collection, 1883-1885; SMF 332831-2/1 and 2, K. Jung collection, 1883-1885; SMF 332833/1 apical fragment retaining most of protoconch, leg. R. Janssen, 19 July 1978; RGM 396 109/many, leg./don. F.A.D. van Nieulande, July 1980; **Uzeste (Gamachot)**: BRS 124.1-1 16447M/5 fragments, leg. B.G. Roest, 18 July 1989; MBB/1, Degrange-Touzin collection; FSUB/1, Peyrot collection; RGM 396 115/1 protoconch (Pl. 24, fig. 11a, b), RGM 396 116/1 protoconch (Pl. 26, fig. 4a, b), leg. A.W. Janssen, 1986; SMF 332834/1 fragment, leg. R. Janssen, 22 June 1981; **Villandraut (Berdigots)**: RGM 396 080/1 fragment, 23 protoconchs, leg./don. F.A.D. van Nieulande. Burdigalian.

La Brède: RGM 396 089/2 fragments, 10 protoconchs, leg. J. Gunst, July 1982, don. F.A.D. van Nieulande; **Meilhan (Vives)**: HMM unnumbered/23; RGM 396 106/1, leg. F.A.D. van Nieulande, 17 July 1996, don. September 1996; RGM 516 560/12, leg./don. J. van der Voort; RGM 569 421/43, RGM 569 422/2, RGM 569 423/many protoconchs, all leg. S. Mermuys, 2006, don. 2007. Aquitanian.

Discussion – *Vaginella depressa*, the first fossil pteropod ever described in the literature, is by far the most common of the Aquitaine Basin. Its stratigraphical range includes the Aquitanian and the Early Burdigalian. Late Burdigalian sedimentary rocks do not outcrop in the northern part of the Aquitaine Basin, but during this interval *Vaginella austriaca* developed from *V. depressa* stock, which can easily be demonstrated in the Mediterranean, and which agrees with observations in the central Paratethys and the North Sea Basin. Curiously, however, this development does not take place in the Pacific realm (Japan, Australia, New Zealand), where *V. depressa* continued until the Langhian/Serravallian (Janssen, 2006, p. 80).

The relationship of *Vaginella depressa* with the Mediterranean *V. sannicola* Janssen, 1990a, remains unclear. The latter is a small species with likewise a wide apical angle of the basal teleoconch, but with a practically absent constriction below the aperture and an apertural width that is always smaller than the overall shell width. This species so far is exclusively known from the Mediterranean.

Distribution – Apart from the Aquitaine Basin, *Vaginella depressa* is known from the central Paratethys (Zorn, 1990, 1991a), the North Sea Basin (Janssen & King, 1988), the Caribbean (Jung, 1971) and the Pacific realm (Japan, Australia, New Zealand; many references).

Vaginella gaasensis sp. nov.

Pl. 26, fig. 6.

v. 1982 *Vaginella* sp.; Lozouet & Maestrati, p. 183, fig. 9.

Holotype – RGM 541 402, illustrated in Lozouet & Maestrati (1982, fig. 9) (Pl. 26, fig. 6a-d herein), leg. A.C. Janse, don. May 2007.

Type locality – Gaas (Espibos).

Stratum typicum – Oligocene, Rupelian, Marnes de Gaas, level 6 with *Oostrombus* (as described in Janssen, 1985a).

Derivatio nominis – Named after the type locality.

Diagnosis – *Vaginella* species with straight or somewhat irregular sidelines, with an apical angle of c. 13°. Ventral shell more convex than dorsal part. Aperture rhomboidal with a weak swelling dorsally and ventrally. Both apertural margins curved, the ventral one remaining lower than the dorsal. Lateral carinae present, almost reaching the aperture. Apical shell parts unknown.

Description – The only available specimen, H = 5.33, W (at aperture) = 1.71, D-V (at mid-height) = 1.10 mm, is a somewhat simply constructed *Vaginella* with a conical shell, the sidelines of which are straight (but a bit irregular at one side). The apical shell parts are missing and the apical angle in the lower part of the shell is approximately 13°. Both sides are gradually curved and convex, but the ventral side clearly more so. Towards the aperture the shell is flattened dorso-ventrally. Lateral carinae are distinct and continue almost to the aperture. Both apertural margins are curved, but the ventral one remains a bit lower than the dorsal (ventral or lateral view). In the centre of both sides, the shell wall is weakly produced near the aperture, resulting in a rounded rhomboidal shape (adapical view). There is no surface ornament, growth lines are clearly visible where light reflects on the shiny surface of the shell. They are curved adapically on both side, but less strongly so on the ventral one.

Discussion – It is, admittedly, highly unusual to introduce a new species based on just a single specimen. Still, in this case, I consider it a necessary action, as it is the oldest known representative of the genus and therefore at the inception of the almost explosive development of the genus *Vaginella* during the Oligocene and the Miocene, for which it would be very inconvenient not to be able to indicate it with a name. Furthermore, it deviates considerably from all known species in this genus. The morphologically most closely related species is *V. basitruncata* Janssen, 2005b, from the early Late Oligocene of the North Sea Basin, which differs from *V. gaasensis* by its less slender shell, its gradually convex sidelines (frontal view), its far greater convexity and by a differently shaped aperture, in which the ventral margin is straight instead of curved. In *V. basitruncata* the larval shell is shed and the opening is closed with a septum. In the holotype of the new species, however, the apical part of the shell is missing.

Distribution – Only known from the Gaas (Espibos) locality.

***Vaginella lapugyensis* Kittl, 1886**

Pl. 26, figs. 7, 8.

*v 1886 *Vaginella lapugyensis* Kittl n. f., p. 52, pl. 2, figs. 4, 5.

v. 1984b *Vaginella lapugyensis* Kittl, 1886; Janssen, p. 76, pl. 3, figs. 6-10, pl. 4, fig. 7a-c.

v. 1995 *Vaginella lapugyensis* Kittl, 1886; Janssen, p. 154, pl. 12, figs. 3, 4.

Type locality – Lapugy (= Lăpugiu de Sus), Romania (Miocene, 'Badenian' = Langhian).

Type material – Lectotype (Janssen, 1984b, pl. 4, fig. 7a-c), NMV not registered.

Description – *Vaginella lapugyensis* has a very slender, elongately triangular shell with straight or practically straight sidelines. Its larval shell has clearly separated protoconchs-1 and -2 (Pl. 26, fig. 7b, c) not deviating from the shell's long axis. The apex of protoconch-1 is pointed. The width is approximately 0.10 mm and its height c. 0.15 mm. Protoconch-2 is swollen, width 0.15 mm, height 0.20 mm. The constriction between protoconch-2 and teleoconch is at c. 0.35 mm from the apex. Initially the dorso-ventral diameter of the teleoconch is somewhat more than the shell width, but it changes soon to circular, becoming dorso-ventrally flattened adaperturally. Lateral carinae develop shortly above the larval shell and continue to just over half the shell height. The aperture in all available specimens from Aquitaine is damaged, but will be slightly widened in full-grown, complete specimens. Its transverse section is elliptical.

Material examined – **Saint-Martin-de-Hinx (Secat)**: MNHN PL 3351/7 fragments, A32130/1 fragment (Pl. 26, fig. 7a-c); MNHN A32131/1 (Pl. 26, fig. 8a-c); RGM 395 964/3, 3 fragments, leg. A.W. Janssen, 30 July 1984; RGM 541 059/1 protoconch, 16 fragments, leg. A.W. Janssen, 1 August 1985; **Saubrigues (Jean Tic)**: SMF 332834/1 apical fragment, leg. R. Janssen, 22 June 1981; **Saubrigues (Tauziets)**: RGM 541 349/1 fragment, leg. A.W. Janssen, 1979/1981; RGM 569 477/9 fragments, leg. H.J. Mulder, 2007, don. October 2008. Langhian.

Discussion – The apical angle (c. 13-14°) of the only well-preserved specimen from the Aquitaine Basin (Pl. 26, fig. 8b) is larger than in the lectotype specimen (c. 10°), but the straight sidelines are quite typical for this species. In the slightly less slender *Vaginella acutissima* Audenino, 1899 (lectotype, see Janssen, 1995, p. 135, pl. 11, fig. 3), the sidelines are somewhat curved to flexuous in the apical half of the shell. Initially, the fragmentary material from Saint-Martin-de-Hinx was identified as *V. acutissima*, but careful comparison with the one complete specimen indicates that it all belongs to *V. lapugyensis*, apart from one fragment with a distinctly wider apical angle, which was identified as *V. austriaca* (see above).

Distribution – *Vaginella lapugyensis* was recorded from the central Paratethys (Kittl, 1886 and many later records), from the North Sea Basin (Janssen, 1984a) and from vari-

ous localities in the Mediterranean, all of Langhian age. It is furthermore known from the Serravallian Blue Clay Formation of Malta (RGM collection).

Vaginella bicarinata Tate, 1887 (Miocene of S. Australia) and *V. bicostata* (Gabb, 1881) (Miocene of Costa Rica) could represent further occurrences of *V. lapugyensis*, but are based on insufficient material to be certain of that identification.

***Vaginella tricuspidata* Zorn & Janssen, 1993**

Pl. 20, figs. 10, 11; Pl. 26, figs. 9-14.

*v 1993 *Vaginella tricuspidata* Zorn & Janssen sp. nov., p. 63, pl. 1, pl. 2, figs 1-5, pl. 3, pl. 4, figs 1-5.

?v 2002 *Vaginella* aff. *tricuspidata*; Gürs & Janssen, p. 124, table 1.

?v 2004a *Vaginella* ?*tricuspidata* Zorn & Janssen, 1993; Janssen, p. 19, pl. 4, figs. 12, 13.

. 2004 *Vaginella tricuspidata* Zorn & Janssen, 1993; Bohn-Havas *et al.*, p. 41, pl. 1, fig. 5.

v. 2006 *Vaginella tricuspidata* Zorn & Janssen, 1993; Piehl, p. 15.

Type locality – Saint-Etienne-d’Orthe (Casenave). Oligocene, Chattian, Marnes de Saint-Etienne d’Orthe.

Type material – Holotype, RGM 229 954, leg. A.W. Janssen, 1984-1990, illustrated Zorn & Janssen, 1993, pl. 2, fig. 3; paratypes from Saint-Etienne-d’Orthe (Casenave, Hondelatte, Lartigaou and Verdun) and from Hungary, as specified in Zorn & Janssen (1993). The original illustrations of the holotype and three paratypes are, somewhat refurbished, copied herein (Pl. 26, figs. 9-13).

Description – Slender and elongate *Vaginella*, adults are approximately six times as high as wide and reach a shell height of c. 7 mm. The few more or less complete specimens are all crushed and preserved on small pieces of marl. The sidelines in frontal view appear to be very slightly convex to almost straight, not flexuous in their apical part. Both ventral and dorsal shell parts are gradually convex, and towards the aperture the shell is dorso-ventrally flattened. The apertural morphology of this species is very characteristic. The ventral margin is straight, whereas the dorsal one is higher and provided with three significant denticles. The shell wall just below these denticles is weakly folded.

The larval shell is not preserved on any of the adult specimens, but was recognised in sieving residues. It closely resembles the larval shell of *Spoelia torquayensis* and only specimens in which the lateral carinae are retained can be identified with certainty.

Material examined – **Orthevielle (Tauzia)**: MNHN PL 5480/1 fragment; **Saint-Etienne-d’Orthe**: BRS 124.1-7 16337S/14 fragments, leg. B.G. Roest, 16 June 1987; **Saint-Etienne d’Orthe (Église-C)**: MNHN unnumbered/11 and 44 fragments, leg. P. Lozouet; MNHN, PL 6581/2; MNHN PL 6584/2 and 3 fragments; **Saint-Etienne-d’Orthe (Hondelatte)**: RGM 541 460/12 fragments, leg. A.W. Janssen, 24 September 1990; **Saint-Etienne-d’Orthe (Lartigaou)**: RGM 541 440/2, RGM 541 448a-b/many apical fragments, RGM 541 448c-d/2 apical fragments (Pl. 26, figs. 10a, b, 11a, b), leg. A.W. Janssen, 1984-1990; RGM 541 451/3 apical fragments, leg./don. A.C. Janse; SMB unnumbered/36 fragments, leg. S. Mermuys, July 2006; **Saint-Etienne d’Orthe (Lestelle)**: RGM 541 456/5 fragments, leg. A.W. Janssen, 24 September 1990; **Saint-Paul-lès-Dax (Estoti)**: FSUB ty-

pothèque 32-4-37/1 fragment (cf., illustrated Pl. 26, fig. 14a-c), A. Cluzaud collection; MNHN unnumbered/6 fragments, P. Lozouet collection (cf., differing from *V. tricuspidata* by slightly wider apical angle and somewhat more irregular shell). In the absence of typical specimens this sample was identified in open nomenclature; MNHN PL 390/6 fragments; MNHN PL 377/1 juvenile (paratype of *Spoelia torquayensis*), registered as RGM 229 509, but returned to Paris (misunderstanding). Chattian.

Discussion – The three denticles on the dorsal apertural margin distinguish this species from all other vaginellids. A comparable structure is found in *Vaginella victoriae* (see below), but in that species just two of these denticles are present. *Vaginella tricuspidata*, however, is not easily recognised if the apertural features are absent.

Distribution – Apart from the occurrences in Aquitaine and Hungary, referred to above and Bohn-Havas *et al.*, (2004), this species is recorded with certainty from the North Sea Basin (Late Oligocene boulders of so-called ‘Sternberger Gestein’, locality Kobrow, northern Germany; RGM 396 480, leg./don. H. Moths). Some Early Miocene specimens from the Brodersdorf borehole (northern Germany; RGM-collection, don. Landesamt für Natur und Umwelt Schleswig-Holstein, Flintbek, Germany) have the slender shape, but lack the final proof of the apertural denticles. The same is true for several specimens from localities in Malta (Janssen, 2004a, p. 20, pl. 4, figs. 12, 13).

***Vaginella victoriae* A.W. Janssen, 1990a**

Pl. 27, figs. 1-3.

*v 1990a *Vaginella victoriae* Janssen sp. nov., p. 57, pl. 9, figs. 1-6.

v. 1999c *Vaginella* aff. *victoriae* A.W. Janssen, 1995 [sic]: Janssen, p. 115, fig. 7.

Type locality – Muddy Creek, Hamilton, Otway Basin, Tyrenderra Embayment, Victoria, Australia (Miocene, Balcombian-Bairnsdalian = Langhian/Serravallian).

Type material – Holotype in MVM (P123409); paratypes, AMS C124.717, RGM 229 478-481 and SAM T 235.

Description – In its typical form, a very slender and elongate *Vaginella* species, but in its type area (South Australia) quite variable in H/W-ratio (varying between 5.5 and 3.6 times higher than wide). The few available Aquitaine specimens all lack their basal parts, but are certainly between 4.5 and 5.0 times higher than wide. The apical half of the shell has convex sidelines, in apertural direction gently curving to concave, which gives the shell a very elegant shape. The aperture is laterally widened and may even slightly exceed the width of the basal shell part. Both sides of the shell have indistinct incremental lines, curved adaperturally, that meet on weak lateral carinae in a V-shape. These carinae disappear at about half shell height. At mid-height the transverse section of the shell is approximately circular, flattening towards the aperture. Two strong radial folds develop close to the aperture on both sides of the shell, lying closer on the dorsal side. In apertural view this results in a very peculiar shape of the aperture (Pl. 27, figs. 1a, 2a, 3c). In one specimen the dorsal apertural margin bears two weak denticles,

reminiscent of the three denticles present in *Vaginella tricuspidata*. These protuberances are not incidental damage of the apertural margin, as is clear from the shape of the growth lines (Pl. 27, fig. 1e).

Material examined – **Saint-Paul-lès-Dax (Cabanes)**: FSUB typotheque 25-4-10/1 (Pl. 27, fig. 2a-d), A. Cluzaud collection; MNHN A32132/1 (Pl. 27, fig. 3a-d); RGM 541 366/1 (Pl. 27, fig. 1a-e), leg. S. Mermuys, 2003-2004, don. November 2006. Early Burdigalian.

Discussion – *Vaginella victoriae* might be another descendant from the *V. chattica*-*V. depressa* lineage. The least slender specimens described from Australia (Janssen, 1990a, pl. 9, fig. 4) resemble slender *V. depressa*, but do have the strong apertural folds. Apertural folds are present in *V. depressa* as well, but remain considerably weaker.

Distribution – At the time of introduction of the present species, only the Australian occurrences were known. The presence of unmistakably the same species in the considerably older (Early Burdigalian) Aquitaine locality is surprising. The stratigraphical distribution is further complicated by an, admittedly, doubtful specimen from the Tortonian clays of Poggio Musenna (Sicily, Janssen, 1999c; RGM 397 501a).

Family Sphaerocinidae Janssen & Maxwell in Janssen, 1995
Genus *Hameconia* Janssen, 2008b

Type species – *Hameconia edmundi* Janssen, 2008b (Oligocene, Chattian, France).

***Hameconia edmundi* A.W. Janssen, 2008b**
Pl. 27, fig. 4.

*v 2008b *Hameconia edmundi* Janssen spec. nov., p. 160, figs. 2-5.

Type locality – Saint-Etienne-d’Orthe, outcrop in Ruisseau de l’Église, east of Lartigaou, coordinates X = 316.400, Y = 149.800 (France, Landes). Marnes de Saint-Etienne-d’Orthe, Chattian.

Type material – Holotype RGM 541 444 (Pl. 27, fig. 4a, b).

Description and discussion – See Janssen (2008b).

Material examined (all paratypes) – **Bélus (Marcon)**: MNHN A32133/1 fragment; **Saint-Etienne-d’Orthe (Église-B)**: MNHN A32134/3, 2 fragments; **Saint-Etienne-d’Orthe (Église-C)**: MNHN A32135/25, leg. P. Lozouet; **Saint-Etienne-d’Orthe (Lartigaou)**: RGM 541 445/1, RGM 541 446/1, RGM 541 447/32, all leg. A.W. Janssen, 1984-1990; SMB unnumbered/2, leg. S. Mermuys, July 2006. Chattian.

Distribution – Only known from Bélus and the Saint-Etienne-d’Orthe area (Chattian).

Superfamily Cymbulioidea Gray, 1840
Family Peraclididae Tesch, 1913
Genus *Peracle* Forbes, 1844

Type species – *Peracle physoides* Forbes, 1844 = *Peracle reticulata* (d'Orbigny, 1834) (Recent).

Notes – Pelseneer (1888, p. 32) emended the name *Peracle*, introduced by Forbes (1844, p. 186), to *Peraclis*, which has subsequently been applied by numerous authors. Pelseneer explained his emendation in a footnote, stating '*Per*, meaning exaggeration, and *aclis*, a small javelin, in allusion to the long rostrum of the shell'. Pelseneer was right that the '*aclis*'-part of the name is a noun and should not be changed. But art. 32.5.1 of International Commission on Zoological Nomenclature (1999) clearly states 'Incorrect transliteration or latinization, or use of an inappropriate connecting vowel, are not to be considered inadvertent errors', and thus the name *Peracle* is available.

Peracle sp.
Pl. 27, fig. 5.

Description – A single specimen (H = c. 0.9, W = c. 0.8 mm) belonging to this genus was collected from the Late Oligocene at Saint-Etienne-d'Orthe. It is apparently a juvenile shell consisting of 2½ convex whorls, of which the first one and a half are planispiral, resulting in a blunt apex. The aperture occupies 3/5th of the shell height and is widest in its upper third part, tapering downward to the angular transition into the columellar side. The base of the shell has a relatively narrow umbilicus, bordered by an obtuse carina. Some vague subsutural crests are visible on the last whorl, changing to widely prosocline growth lines lower on the whorl.

Material examined – **Saint-Etienne-d'Orthe (Église C)**, MNHN A32136, 1 specimen, P. Lozouet collection (Pl. 27, fig. 5a-c). Chattian.

Discussion – This specimen resembles the Langhian species *Peracle lata* (Krach, 1979) from Poland, which, however, has a clearly more circular aperture without the angular transition into the columellar side (Janssen & Zorn, 1993, pl. 5, fig. 4a, b) and reaches double the size of the present shell. An Aquitanian, maybe Chattian, specimen from the Lower *Globigerina* Limestone Member of Malta (*Peraclis* sp. in Janssen, 2004a, pl. 4, fig. 15) also has its aperture rounded and is considerably more slender.

Clade Gymnosomata Blainville, 1824
Superfamily Clionoidea? Rafinesque, 1815
Family Clionidae? Rafinesque, 1815
Genus *incertae sedis*
Gymnosomata sp.
 Pl. 27, fig. 6

Description – Just a single specimen is available, consisting of protoconchs-1 and -2, and an early teleoconch. Shell height is 1.0 mm, width at aperture approximately 0.35

mm. Protoconch-1 is ovoid, H = 0.20 mm, W = 1.8 mm, separated from protoconch-2 by a clear constriction, in which short vertical ridges are visible. Protoconch-2 is no more than a slightly swollen annulation, separated from the early teleoconch by a clear constriction. Total height of the protoconch is 0.26 mm. The teleoconch is conical with an apical angle of *c.* 14° and a circular transverse section. Weak and slightly oblique incremental lines are visible where light reflects on the shell's surface.

Material examined – **Saint-Paul-lès-Dax (Cabanes)**: RGM 541 367/1 (Pl. 27, fig. 6), leg. S. Mermuys, 2003-2004, don. November 2006. Early Burdigalian.

Discussion – The shape of this specimen resembles gymnosomatous larval shells described from the Red Sea by Kunz (1996, pl. 32, figs. 3, 4; copied in Janssen, 2007a, text-figs. 6, 7). The short vertical ridges between protoconchs-1 and -2 are reminiscent of other gymnosomatous larval shells, such as those illustrated in Janssen (2007a, pl. 23, figs. 3-7). Hitherto, Miocene gymnosomatous larval shells have only been recorded from Malta (Janssen, 2004a), distinctly belonging to other species than the present one from Aquitaine.

As so little is known about the larval shells of the many Recent Gymnosomata species it is difficult to assign these protoconchs to one of the two superfamilies (Clionoidea Rafinesque, 1815 or Hydromyloidea Pruvot-Fol, 1942). Considering the number of living species recognised in these groups (48 in Clionoidea and only two in Hydromyloidea; van der Spoel, 1967), most probably all of the fossils species belong to the Clionoidea, but there is no objective criterion to decide this on the larval shells. Several of the larval shell forms resemble one of the few described protoconchs of a Recent species, namely *Paedoclione doliiformis* Danforth, 1907 (Lalli & Conover, 1973), belonging to the Clionidae. Although supposingly (most of?) the fossil protoconchs belong to the Clionidae I prefer to indicate them herein as 'Gymnosomata sp.'.

Distribution – Saint-Paul-lès-Dax (Cabanes) only.

Unidentifiable fragmentary Chattian specimens (possibly belonging to either *Spoelia* or *Vaginella*)

Material examined – **Bélus (Marcon)**: MNHN ex PL 6582/17 fragments; MNHN unnumbered/3 fragments, P. Lozouet collection; MNHN unnumbered/47 fragments, P. Lozouet collection; **Peyrehorade (Tauziède)**: MNHN PL 5896/14 fragments; **Saint-Etienne-d'Orthe (Église-B)**: MNHN unnumbered/4 fragments, P. Lozouet collection.; **Saint-Etienne-d'Orthe (Église-C)**: MNHN unnumbered/9 and 17 fragments, P. Lozouet collection; **Saint-Etienne-d'Orthe (Hondelatte)**: MNHN PL 6585/8 fragments; **Saint-Etienne-d'Orthe (Verdun)**: MNHN, PL 6581/10 fragments; MNHN, ex PL 6584/1 fragment; **Saint-Paul-lès-Dax (Abesse)**: MNHN unnumbered/7 fragments, P. Lozouet collection; **Saint-Paul-lès-Dax (Bezoye)**: MNHN PL 1368/16 fragments; **Saint-Paul-lès-Dax (Estoti)**: MNHN unnumbered/2 juveniles, P. Lozouet collection (incorrectly identified 1991 as *Spoelia torquayensis*, no paratypes); MNHN unnumbered/7 and 1 fragment, P. Lozouet collection (identified 'indet.' in 1992, re-identified *Spoelia torquayensis*, by Lozouet?) (label states 12 + 1 specimens, but only 7 + 1 were found).

Stratigraphy and pteropod zonation

A biostratigraphical zonation, based on holoplanktonic molluscs, has only been realised so far for the North Sea Basin (NSB). Within the framework of I.G.C.P. project 124 (The NW European Tertiary Basin), the results of which were published in Vinken (1988), Janssen & King (1988, pp. 356-368, fig. 188) presented a tentative pteropod zonation covering the latest Paleocene up to and including the Pliocene of that basin. They described for that interval 17 zones, numbered 6 to 22 (leaving numbers 1-5 for possible future discoveries from older levels). Most of the zones are taxon ranges zones, but some are qualified as interval zone, concurrent range zone or partial range zone.

Although there is a significant dissimilarity in the species compositions of the pteropod assemblages occurring in the North Sea and Aquitaine basins, as a result of their different geographical positions, it is attempted here to establish a correlation and to apply the North Sea Basin zone numbers also for the southwest of France. For the Aquitaine Oligo-Miocene, the Sr estimated ages indicated below have been adjusted to the 'Global Time Scale 2004' (Gradstein *et al.*, 2004).

Eocene – In the southern Aquitaine, we find two different pteropod assemblages of Eocene age, *viz.* those from the two Gan localities (Tuilerie and Bosdarros), dated as Ypresian, and those from Biarritz and Peyrehorade (Arribaouts), both dated as Priabonian. Furthermore, a single occurrence of a Lutetian species is recorded in literature.

The pteropod fauna from Gan is rich in species and can be compared with the NSB zonation by the abundant occurrence of *Camptoceratops priscus*, which is the characteristic species of NSB pteropod zone 9, supposed to be on the Early-Middle Eocene transition (nannoplankton zones NP13-14; Müller & Köthe, 1988, fig. 129). In the NSB, this zone 9 yielded just a few further pteropod species which, however, do not occur at Gan. A correlation of the two Gan localities with zone 9 of NSB seems to be warranted, however, by the joint common presence of *Camptoceratops*. The 'Middle to Late Ypresian, NP 13-14' age of zone 9 agrees fairly well with the 'Middle to Late Ypresian age' for the Gan localities, as determined on the basis of calcareous nannoplankton, NP12-13 zones (Nolf *et al.*, 2002).

Hodgkinson *et al.* (1992) published a range chart of pteropods for North America. Two species, *Skaptotium? reklawensis* Garvie in Hodgkinson *et al.*, 1992 (= *Currylimacina cossmanni* in the present paper), and *Camptoceratops americanus* (= *C. priscus* herein), also occur at Gan and in North America, are recorded from the NP 13-14 interval. They mention, apart from several species not known from Europe, also the species *Limacina taylori* Curry, 1965, which in the NSB ranges from pteropod zones 7 to 9. These occurrences, therefore, can be correlated with pteropod zone 9, too. *Altaspiratella bearnensis*, a common species in both Gan localities, was recorded by Hodgkinson *et al.* only from the Lutetian NP15 zone. In the systematic part, above, it is suggested, considering the morphological differences between the European and American occurrences, that this taxon might be in need of a new name.

From sedimentary rocks of Lutetian age in Aquitaine, just a single species is known, *viz.* *Praeuvierina lura*, from Peyrehorade (Trompe) (see above; Lozouet & Le Renard, 2007). This deposit was correlated with nannoplankton zone NP15 (Steurbaut *in* Lo-

zouet & Le Renard, 2007, p. 3), which is more or less in the middle of pteropod zone 10.

The Biarritz occurrence, as well as the Peyrehorade (Arribaouts) locality, are both dated as Priabonian, zones NP19-20, from which interval in the NSB (= supposed pteropod zone 12) no pteropods are known. Just one species is common to the NSB and Aquitaine occurrences, namely *Heliconoides nemoris*, which species Janssen & King (1988) only recorded from the base of pteropod zone 11, of Bartonian age. Two other species from Biarritz, *Creseis corpulenta* and *C. simplex*, are also known from North America, the former recorded from the interval NP17-23 and the latter from NP15-17 (Hodgkinson *et al.*, 1992). It must be concluded that the real ranges for these species are far from completely known. By means of the Biarritz/Peyrehorade (Arribaouts) pteropods, we can only conclude on a correlation with NSB pteropod zones 11-12, whereas the nannoplankton zones NP19-20 rather suggest a correlation with zone 12.

Oligocene – We describe six pteropod species above from just two localities dated as Rupelian and 16 species from ten Chattian sites. In the NSB pteropod zone 13 was considered to be of ‘Early Oligocene’ age, but is nowadays dated as ‘presumably Priabonian’, since the base of the Rupelian also became the start of the Oligocene. This zone yielded three pteropod species which are unknown from Aquitaine.

Two further pteropod zones, 14 and 15, are recognised during the NSB Rupelian, zone 14 with only one, maybe two species. Zone 15, on the contrary, subdivided into subzones 15a and 15b by Gürs & Janssen (2004), is far richer with some 15 species recorded from the NSB. There is no indication of pteropod zone 14 in Aquitaine. Of all the species in zone 15, just one, *Praehyalocylis maxima*, restricted to subzone 15a, correlated with NP 23, is also present in the Gaas (Lagouarde) locality. This zone includes, both in the NSB as well as in Aquitaine, several species that are insufficiently identified and recorded in open nomenclature. Therefore, further similarities in the pteropod assemblages of both areas might be found, but now there is no indication for the presence of subzone 15b. Gaas localities are dated as the middle part of the Rupelian, SBZ21, on the basis of larger foraminifera (Cahuzac & Poignant, 1997), P19 zone in correlation and 31.6 Ma as Sr estimated age, which is in agreement with pteropod zone 15.

All Chattian rocks in the NSB belong to pteropod zone 16 (Janssen & King, 1988), including (Müller & Köthe, 1988) the upper half of nannoplankton zone NP24 and zone NP25. The Aquitaine Chattian occurrences with pteropods are, without exception, correlated with nannoplankton zone NP25 (latest Chattian; Steurbaut *in* Zorn & Janssen, 1993; Cahuzac *et al.*, 1995), as well as foraminiferal zones P22 (Müller & Pujol, 1979; Cahuzac *et al.*, 1995) and SBZ23 (larger foraminifera; Cahuzac & Poignant, 1997); the Sr estimated ages range of these outcrops is *c.* 25.3 (Saint-Etienne-d’Orthe) to 23.4 Ma (Saint-Paul-lès-Dax, Abesse). One outcrop only was allocated to NP24 zone, at Pontonx (Haillets, Landes department, Cahuzac *et al.*, 1995), but has yielded no pteropods.

From NSB zone 16, six pteropod species are known (Janssen & King, 1988). However, Janssen (2005b, p. 79), recorded nine species from the same interval on the basis of new material, no less than five of which also occur in the Aquitaine Chattian faunas. These species are *Heliconoides hospes*, *Styliola subula*, *Spoelia torquayensis*, *Vaginella chattica* and *V. tricuspidata*. Janssen (2005b) subdivided pteropod zone 16 into three subzones (16a-c), characterized by the FOD of, respectively, *Vaginella basitruncata* Janssen, 2005b, *Ireneia tenuistriata* (Semper, 1861) and *Vaginella chattica*. Four of the five mutual NSB/

Aquitaine Chattian pteropod species occur in the NSB both in zones 16b and 16c, but *Vaginella tricuspidata* is only known there from zone 16b. On the basis of the existing knowledge, it seems logical to assign the Aquitaine assemblages to pteropod zone 16b, but its most common species, *Ireneia tenuistriata*, is absent in the Aquitaine area.

Miocene – Pteropod zones 17 to 21 are recognised by Janssen & King (1988) in the NSB Miocene, the last one already partly of Pliocene age. The distribution of one important, but at the time insufficiently known species, '*Cavolinia perovalis*' von Koenen, 1882, was indicated by Janssen & King (1988) as occurring in pteropod zone 18. This was corrected by Janssen & Gürs (2002), who recorded new material of that species and its accompanying pteropod fauna from a reworked boulder of so-called 'Holsteiner Gestein'. They also considered *C. perovalis* to be a junior subjective synonym of *Diacrolinia aquensis*, which was exclusively known from the Aquitaine Basin. The co-occurrence in that boulder of *D. aquensis* and *Vaginella depressa* clearly indicated pteropod zone 17 of Early Miocene age. Other specimens found as juvenile individuals in younger Miocene sedimentary rocks, also recorded by Janssen & King as *C. perovalis*, were later identified as *Diacrolinia aurita*.

Pteropod zone 17 can easily be recognized in the Aquitaine Basin as well, as it is a taxon range zone defined by the range of *Vaginella depressa*. Herein we record that species from 23 localities in Aquitaine, all of Aquitanian to Early-Middle Burdigalian age. The second species known from pteropod zone 17 in the NSB, *Diacrolinia aquensis*, was found to be present at six Aquitaine localities, five of which are among the 21 assemblages yielding *V. depressa*. The sixth is Saint-Paul-lès-Dax (Mandillot), the type locality of *S. aquensis*, from where we did not see any further pteropod material. The upper boundary of zone 17 is marked by the LOD of *V. depressa* and the FOD of *V. austriaca*.

Contrary to the NSB, there is good reason to subdivide pteropod zone 17 in the Aquitaine Basin into three parts, which we indicate as subzones 17a-c. *Vaginella depressa* occurs in all three subzones, but in zone 17a (of Aquitanian age), in which we also note the FODs of what presumably is *Heliconoides inflata* (only known as yet by juvenile specimens), *Limacina bulimoides*, *Limacina valvatina* and *Creseis roesti*, and two further species are restricted to this subzone, viz. *Diacrolinia cluzaudi* and *Gamopleura taurinensis*. Only a few occurrences of deposits dated as Aquitanian can be assigned to the pteropod zonation, many further localities yield faunas from too shallow, euryhaline or even freshwater environments, in which no pteropods can be expected. The localities assigned to pteropod subzone 17a correspond to the N4 and SBZ24 zones (larger foraminifera; Cahuzac & Poignant, 1997).

Zone 17b, represented in the Saint-Paul-lès-Dax (Cabanes) assemblage, yielded 13 pteropod species, of which *Heliconoides mermuyisi*, *Creseis tugurii*, Cuvierinidae sp. 2, *Diacrolinia orbigny*, *Vaginella victoriae* and Gymnosomata sp. are restricted to this subzone. Further, in subzone 17b is the FOD of *Heliconoides tertiaria*, *Ireneia nieulandei* and *Cuvierina paronai*? Several localities of early Burdigalian age, such as Léognan (Thibaudeau) or Corbleu (Carro), yielded only few pteropods, but might also belong to zone 17b.

Most of the localities yielding *Vaginella depressa*, however, are considered herein to belong to pteropod subzone 17c, with *Diacrolinia aquensis* as characteristic species, albeit recorded here only from six localities. A number of further localities where *D. aquensis* was not found, but where *V. depressa* is present without one of the other charac-

teristic species of subzone 17b present, is also assigned to subzone 17c. In just two localities, Léognan (Château de France) and Martillac (Vigne), considered to be of Early Burdigalian age, both *D. aquensis* and *V. depressa* were not found, most probably because of undersampling. They are assigned to zone 17c with a query. The 21 Aquitaine localities assigned to pteropod subzone 17c correspond to the N5 and NN2 zones, to the lower SBZ25 zone (larger foraminifera; Cahuzac & Poignant, 1997) and to an interval of Sr ages from 20 to 18.4 Ma (Cahuzac *et al.*, 1997; Cahuzac & Turpin, 1999) (Early–Middle Burdigalian).

It was tempting to consider also the common occurrence of *Johnjagtia moulinsii* at Cabanes as characteristic for pteropod zone 17b. Just one specimen, however, which is its holotype, originates from Saucats (Église), from which locality also *Diacrolinia aquensis* is known, typical for zone 17c. Could it be possible that at the said locality both subzones are present? The level from which Benoist (1874a) recorded the *J. moulinsii* type specimen is not known, which is also true for the specimens of *D. aquensis*, collected there long ago as well.

In the NSB, pteropod zones 18 and 19 (Janssen & King, 1988) cover the later part of the Early and the complete Middle Miocene, respectively. Ten NSB pteropod species are known from zone 18, including *Clio irenae* Janssen, 1989 (later recognised as a junior synonym of *Clio bellardii* Audenino, 1899), *Diacrolinia aurita* (as *Cavolinia perovalis, pro parte*), *Vaginella austriaca* and *V. lapugyensis*. The deposits from which these species originated, the so-called ‘Hemmoorian’, were hitherto considered to be Burdigalian, based on the similarity of benthic mollusc faunas in the NSB compared to the rich Burdigalian assemblages in the northern Aquitaine Basin. The boundary between the ‘Hemmoorian’ and the subsequent ‘Reinbekian’ was correlated with the Burdigalian/Langhian boundary. Therefore, Janssen & King (1988) included pteropod zone 18 completely in the Early Miocene.

This concept, however, was revised on the basis of NSB pteropod occurrences by Janssen (2001) and Gürs & Janssen (2002). It was concluded that all assemblages including the species *Vaginella austriaca* must be younger than c. 19 Ma (middle to upper part of the Burdigalian) and that the later part of pteropod zone 18 is already of Langhian age, younger than 16.4 Ma (nowadays re-dated as 15.97 Ma; Gradstein *et al.*, 2004). This later part of zone 18 is characterized by the sudden occurrence of several pteropod species, most of which are known from Langhian deposits in the Mediterranean. Gürs & Janssen (2002) subdivided pteropod zone 18 into two subzones, indicated 18 and 18a.

On the basis of these data, a subdivision of zone 18 seems realistic and it is supported by the Aquitaine pteropod distribution. At two localities, *Vaginella austriaca* is relatively common, both at Saint-Jean-de-Marsacq (Lahitet and Pinot). These two localities are dated as Late Burdigalian on the basis of plankton assemblages (NN4 and N6-7 zones; Cahuzac *et al.*, 1995; Cahuzac & Poignant, 2004) and Sr data (17.3 to 17.4 Ma; Cahuzac *et al.*, 1997; Cahuzac & Turpin, 1999), and indicated here as representing pteropod zone 18.

Some of the species marking the Langhian in the NSB (pteropod zone 18a), namely *Diacrolinia aurita* and *Vaginella lapugyensis*, are in Aquitaine recorded from Saint-Martin-de-Hinx (Secat), together with the species *Cavolinia zamboninii*, which is unknown from the NSB, but is known to be a common occurrence in central Mediterranean Langhian deposits (Malta, Italy, Cyprus; RGM collections). Two further localities at Saubrigues

(Jean Tic and Tauziets) also yielded *V. lapugyensis* and are here included in pteropod zone 18a. Both were allocated to N8-N9 *pars* and NN5 zones, with estimated Sr age of 15.6 Ma for a neighbouring level from the same Langhian 'Marnes de Saubrigues' Formation (Cahuzac *et al.*, 1997; Cahuzac & Poignant, 2000).

Janssen (2001) restricted the NSB pteropod zone 19, initially covering the complete Middle Miocene, to the Serravallian, albeit that its lower boundary was difficult to define, as little pteropod material was available from there. Three localities in the Aquitaine area, dated as Serravallian (on the basis of plankton, NN6-7 and *c.* N11-13 zones; Müller & Pujol, 1979; Folliot *et al.*, 1993; Cahuzac *et al.*, 1995; Cahuzac & Poignant, 1996) yielded two pteropod species that give an indication of the age. *Edithinella varanica*, known from a single specimen from Orthez (Paren), hitherto was exclusively known from the Mediterranean, occurring in Late Langhian and Serravallian sedimentary rocks. *Edithinella caribbeana*, known in a single specimen from Salles and originally described from unspecified 'Middle Miocene' of Panama, is known from several deposits in the Mediterranean Basin (northern Italy, Sicily, Malta, Cyprus), all of them Tortonian. We here assign these three Serravallian occurrences to pteropod zone 19, realising that the presence of *E. caribbeana* might indicate a relatively somewhat later Serravallian age for the Salles (Moulin Ruiné) fauna than for Orthez. It cannot be excluded that the range of *E. caribbeana* has started a little earlier than so far known and includes the later Serravallian. Concerning Sr data, the Serravallian Sr isotopic curve seems non-linear, with a large scattering of the points in several relevant DSDP wells, so the Sr ages are not very accurate in this interval. However, the localities from the Orthez gulf seem to be a little older (12.0-12.8 Ma) than those from the Salles area (*c.* 11.0-12.4 Ma; *cf.* Cahuzac & Turpin, 1999).

Conclusions

1. From the Cenozoic of the Aquitaine Basin (Early Eocene to Middle Miocene), 75 species of holoplanktonic molluscs are recorded herein.
2. Five of these species are supposed to be Heteropoda, four of which are represented by juvenile specimens that could only be identified in open nomenclature.
3. Seventy species of Pteropoda are recorded from *c.* 60 localities.
4. Twelve nominal species of pteropods are described herein as new to science, *viz.* *Heliconoides daguini*, *H. merlei*, *H. pyrenaica*, *Limacina? vegrandis*, from the Ypresian; *Creseis antoni* and *Vaginella gaasensis* from the Rupelian, *Clio lozoueti* and *Clio vasconiensis* from the Chattian; *Diacrolinia cluzaudi* from the Aquitanian; *Creseis roesti* from the Aquitanian/Burdigalian; and *Heliconoides mermuysi* and *Creseis tugurii* from the Early Burdigalian.
5. A correlation with the existing North Sea Basin pteropod zonation (Janssen & King, 1988) led to a recognition of pteropod zones 9, 10, 11/12 (Eocene), 15a and 16b (Oligocene), and 17-19 (Miocene) in the Aquitaine Basin.
6. On the basis of data from the Aquitaine Basin, pteropod zone 17 could be subdivided into three subzones, 17a (Aquitanian), 17b (earliest Burdigalian) and 17c (Burdigalian).
7. The North Sea Basin subdivision of pteropod zone 18, into subzones 18 and 18a (Late Burdigalian and Langhian, respectively), could also be recognised in the Aquitaine Basin.

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gene), planktonic foraminifera; SBZ, Shallow Benthic Foraminifera Zones. Biozone numbers indicated in this table concern datings of studied samples from the Aquitaine Basin.

Early Miocene		Middle Miocene
Burdigalian		Langhian
Serravallian		
Saint-Paul-lès-Dax (Cabanes)		
Léognan (Thibaudeau)		
Corbleu (Carro)		
Saucats (Église)		
Uzeste (Gamachot)		
Villandraut (Berdigots)		
Saucats (Péloua)		
Léognan (Coquillat)		
Léognan (Château de France)		
Mérignac [(Pontic), (couche 6), "Mérignac"]		
Pessac (Lorient)		
Saint-Médard (Gajac)		
Saucats (La Cassagne)		
Saucats (Gieux); Saucats (Lagus)		
Léognan (Bougès)		
"Léognan"; "Bordeaux"		
La Brède (Moras)		
Martillac (Barreau, Vigne)		
Saucats (Coquillière)		
Saucats (Pont-Pourquey)		
Canéjan (Bouscaut)		
Cestas (Cazeaux)		
Cestas (Fourcq)		
Saint-Paul-lès-Dax (Mandillot)		
Saint-Jean-de-Marsac (Lahit 1 and 2)		
Saint-Jean-de-Marsac (Pinot)		
Saint-Martin-de-Hinx (Secat)		
Saubrigues (Jean Tic)		
Saubrigues (Tauziets)		
Orthez (Le Paren)		
"Salles"		
Salles (Moulin ruiné) (Larieux)		

Cont. next page

Early Miocene										Middle Miocene																							
Burdigalian																				Langhian					Serravallian								
Saint-Paul-lès-Dax (Cabanes)	Léognan (Thibaudeau)	Corbleu (Carro)	Saucats (Église)	Uzeste (Gamachot)	Villandraut (Berdigots)	Saucats (Péloua)	Léognan (Coquillat)	Léognan (Château de France)	Mérignac [(Pontic), couche 6], "Mérignac"	Pessac (Lorient)	Saint-Médard (Gajac)	Saucats (La Cassagne)	Saucats (Gieux), Saucats (Lagus)	Léognan (Bougès)	"Léognan"; "Bordeaux"	La Brède (Moras)	Martillac (Barreau, Vigne)	Saucats (Coquillière)	Saucats (Pont-Pourquey)	Canejan (Bouscaut)	Cestas (Cazeaux)	Cestas (Fourcq)	Saint-Paul-lès-Dax (Mandillot)	Saint-Jean-de-Marsacq (Lahit 1 and 2)	Saint-Jean-de-Marsacq (Pinot)	Saint-Martin-de-Hinx (Secat)	Saubrigues (Jean Tic)	Saubrigues (Tauziets)	Orthez (Le Paren)	"Salles"	Salles (Moulin ruiné) (Larieux)		
C	:	:	:	:	:	II	II	:	:	:	:	:	:	:	I	:	:	I	:	:	:	:	:	:	C	:	I	II	C				
:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	II	:	:	:	:	:	:	:	:	:	:	:	:	:	:	:	
CC	C	..	II	I	C	CC	CC	..	CC	C	I	C	CC	CC	CC	..	CC	CC	CC	II	C	I											
:	:	II	C	C	:	:	I	:	C	II	C	C	CC	..	:	:	:	I	..	CC	..	CC	C	I	CC		
II	II	
I																																	
..	C	I	C	..	I	

Stages	Eocene			Oligocene								Aquitanian									
	Ypresian	Lutetian	Priabonian	Rupelian	Chattian																
	Gan (tuilerie)	Gan (Bosdarros)	Peyrehorade (Trompe)	Biarritz (Les Bains)	Peyrehorade (Arribaouts)	Gaas (Espibos)	Gaas (Lagouarde)	Saint-Etienne-d'Orthe (Lartigaou)	Orthevielle (Tauzia)	Belus (Marcon, Sas)	Peyrehorade (Peyrère)	Peyrehorade (Tauziède)	Pontonx (Mineur)	Saint-Paul-lès-Dax (Lestrilles)	Saint-Paul-lès-Dax (Abesse, Abesse A, B)	Saint-Paul-lès-Dax (Bezoye)	Saint-Paul-lès-Dax (Estofi)	Saint-Paul-lès-Dax (Mainot)	La Brède	Meilhan (Vives)	Saucats (Larley)
<i>Praehyalocylis annulata</i>			rr																		
<i>Creseis</i> sp. nov. 1			r																		
<i>Creseis corpulenta</i>			r																		
<i>Creseis simplex</i>			r	rr																	
<i>Heliconoides nemoris</i>			c																		
<i>Praecuvierina lura</i>		c																			
Limacinidae sp. 2	rr																				
<i>Heliconoides daguini</i>	r																				
<i>Limacina pygmaea</i>	r	r																			
<i>Currylimacina cossmanni</i>	c																				
<i>Heliconoides auriformis</i>	c																				
<i>Heliconoides merlei</i>	c																				
<i>Heliconoides paula</i>	c																				
<i>Heliconoides pyrenaica</i>	c																				
? <i>Limacina vegrandis</i>	c																				
<i>Altaspiratella multispira</i>	c	c																			
<i>Camptoceratops priscus</i>	cc	c																			
<i>Euchilotheca ganensis</i>	cc	c																			
<i>Limacina gormani</i>	cc	c																			
<i>Altaspiratella bearnensis</i>	cc	c																			
Pteropod zones	9	10	11/12	15a	16b								17a								
Foraminifera/	NP	NP	NP	P18/19	NP25 / P22 / SBZ23								N4 / SBZ24								
Nannoflora zones	12/13	15	19/20																		

cc = very common (> 100); c = common (> 10); r = rare (2-10); rr = very rare (1).

		Early Miocene		Middle Miocene	
Burdigalian				Langhian	
				Serravallian	
		Saint-Paul-lès-Dax (Cabanes)			
		Léognan (Thibaudreau)			
		Corbleu (Carro)			
		Saucats (Église)			
		Uzeste (Gamachot)			
		Villandraut (Berdigots)			
		Saucats (Péloua)			
		Léognan (Coquillat)			
		Léognan (Château de France)			
		Mérignac [(Pontic), couche 6], "Mérignac"			
		Pessac (Lorient)			
		Saint-Médard (Gajac)			
		Saucats (La Cassagne)			
		Saucats (Gieux); Saucats (Lagus)			
		Léognan (Bougès)			
		"Léognan"; "Bordeaux"			
		La Brède (Moras)			
		Martillac (Barreau, Vigne)			
		Saucats (Coquillière)			
		Saucats (Pont-Pourquey)			
		Canejan (Bouscaut)			
		Cestas (Cazeaux)			
		Cestas (Fourcq)			
		Saint-Paul-lès-Dax (Mandillot)			
		Saint-Jean-de-Marsac (Lahit 1 and 2)			
		Saint-Jean-de-Marsac (Pinot)			
		Saint-Martin-de-Hinx (Secat)			
		Saubrigues (Jean Tic)			
		Saubrigues (Tauziets)			
		Orthez (Le Paren)			
		"Salles"			
		Salles (Moulin ruiné) (Larieux)			
17b			17c	18	18a
N5 / NN2		N5 / NN2 / SBZ25	N5 / N6	NN3/4 N6/7	NN5 N8/9
					N11/13

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Plate 1

Atlanta sp. 1

Fig. 1. Saint-Jean-de-Marsacq (Pinot), RGM 541 379a, juvenile specimen. a, frontal view. b, microornament of initial whorl.

Atlanta sp. 2.

Fig. 2. Saint-Jean-de-Marsacq (Pinot), RGM 541 380, juvenile specimen. a, frontal view. b, microornament of initial whorl.

Atlanta sp. 3.

Fig. 3. Meilhan (Vives), RGM 569 427, juvenile specimen. a, frontal view, b, microornament at base of initial whorl.

Carinariidae? sp.

Fig. 4. Saint-Jean-de-Marsacq (Pinot): RGM 541 381. a, frontal view. b, apical view.

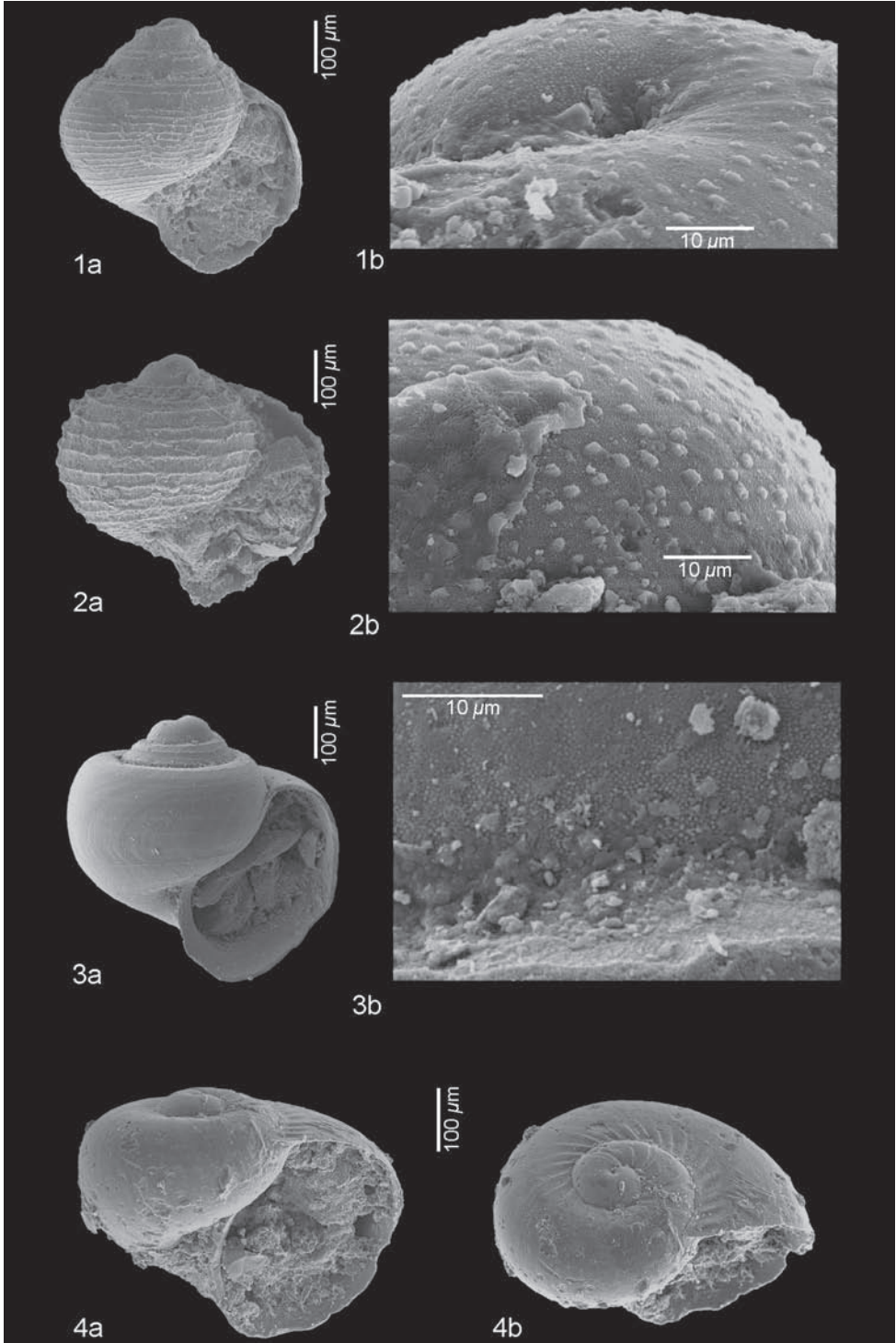


Plate 2*Altaspiratella bearnensis* (Curry, 1982)

Fig. 1. Gan (tuilerie), RGM 229 306. a, apertural. b, lateral. c, umbilical view.

Fig. 2. Gan (tuilerie), holotype, BMNH GG. 21255. a, apertural. b, lateral view.

Fig. 3. Gan (tuilerie), RGM 229 305. a, apertural. b, lateral. c, apical view.

Fig. 4. Gan (tuilerie), RGM 229 307. a, apertural. b, dorsal view.

Altaspiratella elongatoidea (Aldrich, 1887)

Fig. 5. Choctaw Corner, Alabama, U.S.A. (Early Eocene, Wilcox Group, Hatchetigbee Formation, Bashi Member), holotype USNM 638 862. a, apical. b, apertural. c, lateral, d, dorsal view.

Altaspiratella multispira (Curry, 1982)

Fig. 6. Gan (tuilerie), holotype BMNH GG. 21256. a dorsal. b, oblique lateral. c, apertural view.

Figs. 7-8. Gan (tuilerie), paratypes BMNH GG. 21257. 7, apertural view. 8, lateral view.

Fig. 9. Gan (tuilerie), J. Le Renard collection (Plaisir, France). a, apertural. b, lateral view.

Fig. 10. Reconstruction of complete, full-grown specimen.

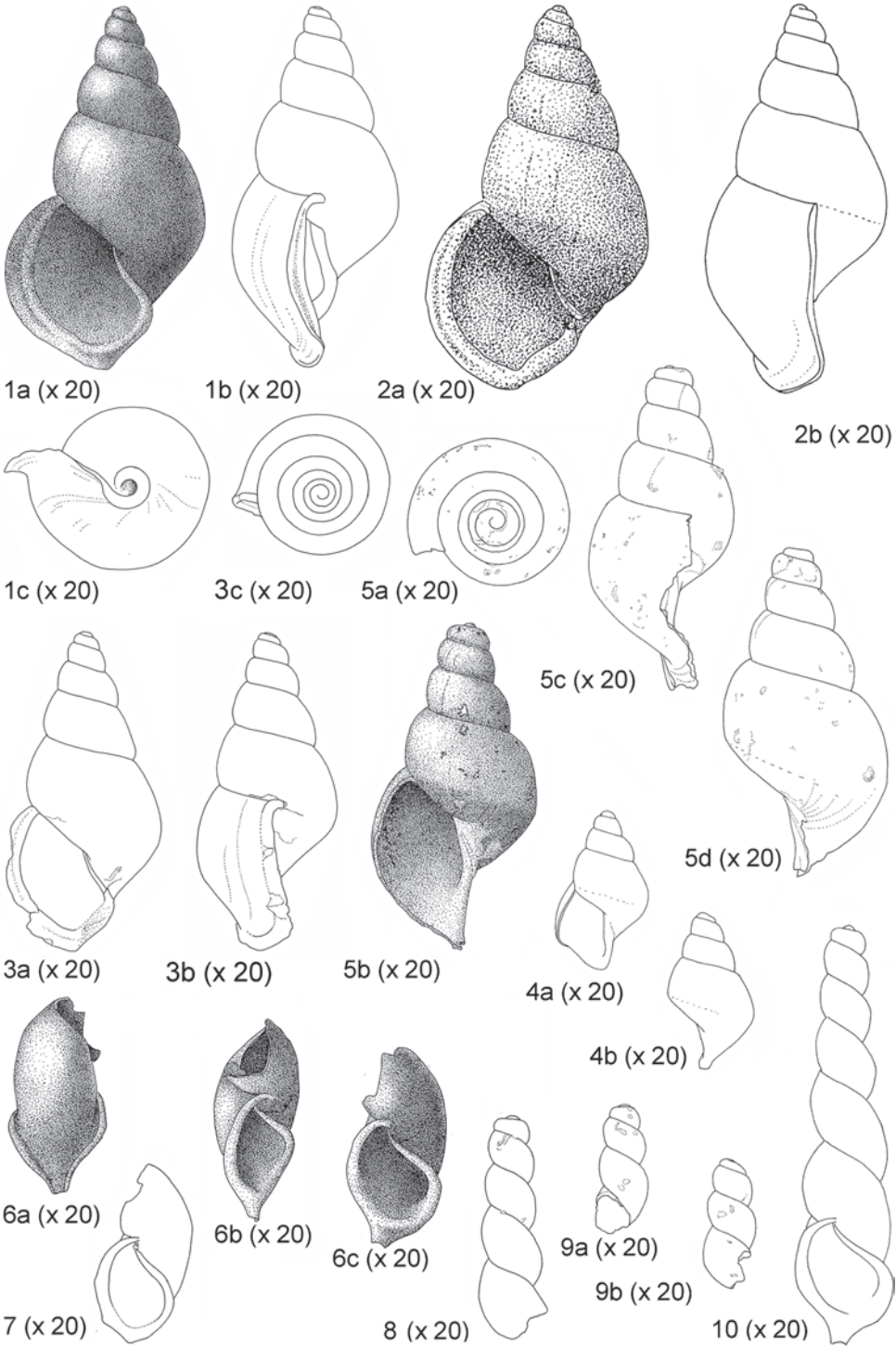


Plate 3

Altaspiratella bearnensis (Curry, 1982)

Fig. 1. Gan (tuilerie), RGM 569 449. a, apertural view. b, apical whorls enlarged.

Heliconoides paula (Curry, 1982)

Fig. 2. Gan (tuilerie), RGM 569 453. Apertural view.

Heliconoides merlei sp. nov.

Fig. 3. Gan (tuilerie), RGM 569 460, paratype, juvenile specimen. Apertural view.

Heliconoides pyrenaica sp. nov.

Fig. 4. Gan (tuilerie), RGM 569 456, paratype, juvenile specimen. Apertural view.

Limacina bulimoides (d'Orbigny, 1836)

Fig. 5. Saucats (Coquillière), RGM 541 548. a, apertural view. b, microornament on early whorls.

Limacina gormani (Curry, 1982)

Fig. 6. Gan (tuilerie), RGM 541 550, juvenile specimen. Apertural view.

Fig. 7. Gan (tuilerie), RGM 541 421, juvenile specimen. Umbilical view.

Fig. 8. Gan (tuilerie), RGM 541 316. a, apical view. b, early whorls enlarged showing subsutural crests.

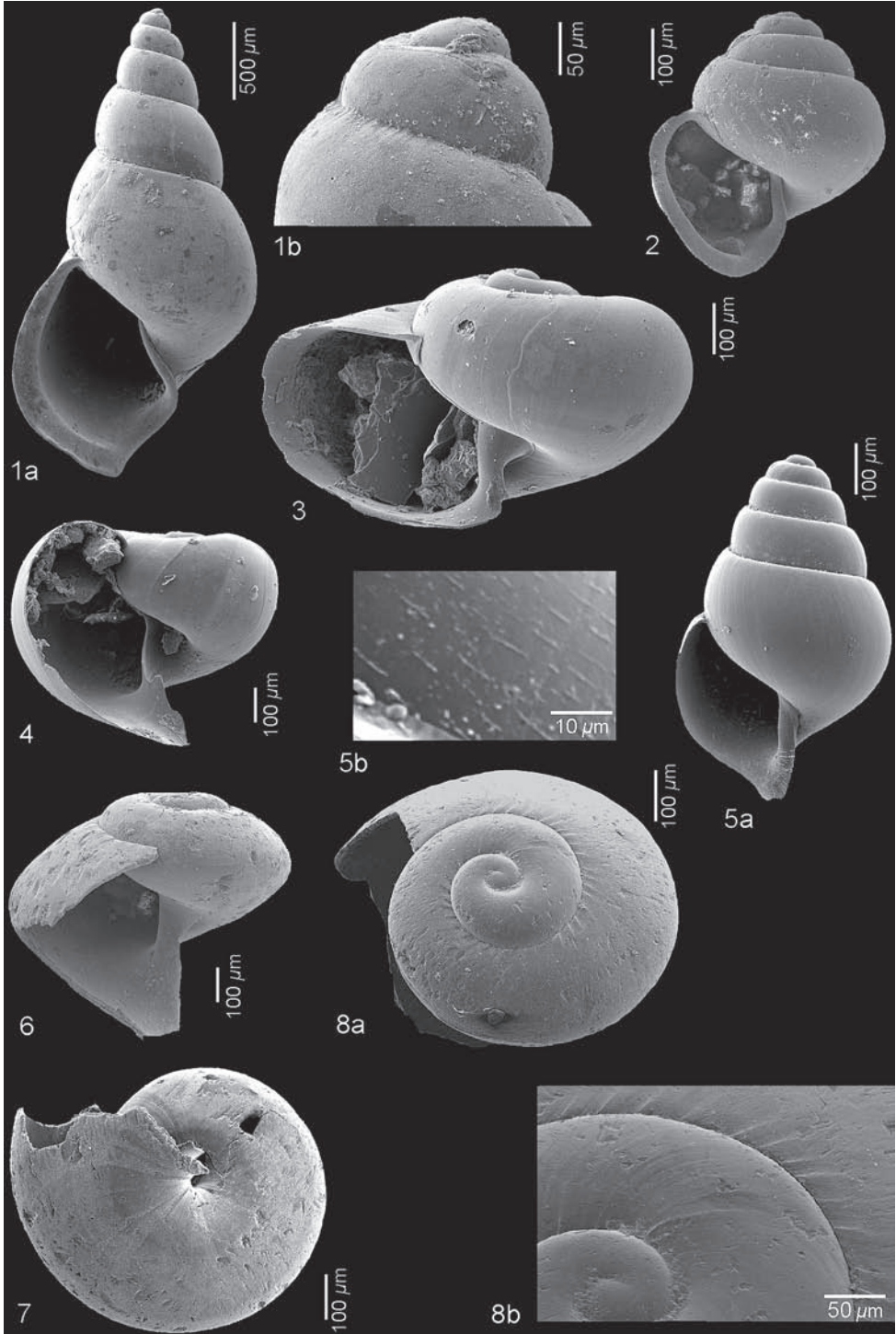


Plate 4

Currylimacina cosmmani (Curry, 1982)

Fig. 1. Gan (tuilerie), holotype, BMNH GG. 21253. a, apertural. b, lateral view.

Fig. 2. Gan (tuilerie), paratype, BMNH GG. 21254. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 3. Gan (tuilerie), RGM 396 596. a, apical. b, apertural. c, umbilical view.

Fig. 4. Gan (tuilerie), RGM 396 597. a, apertural. b, apical. c, umbilical. d, lateral view.

Fig. 5. Gan (tuilerie), RGM 396 594. Apertural view.

Fig. 6. Gan (tuilerie), RGM 396 595. Apertural view.

Fig. 7. IJsselmuiden-I borehole (Netherlands, Overijssel), depth 829-833.6 m-RT, Eocene, Ypresian, Ieper Clay Formation. RGM 397 062, leg./don. P.A.M. Gaemers, September 1987 (pyritic internal mould). a, apertural. b, apical view.

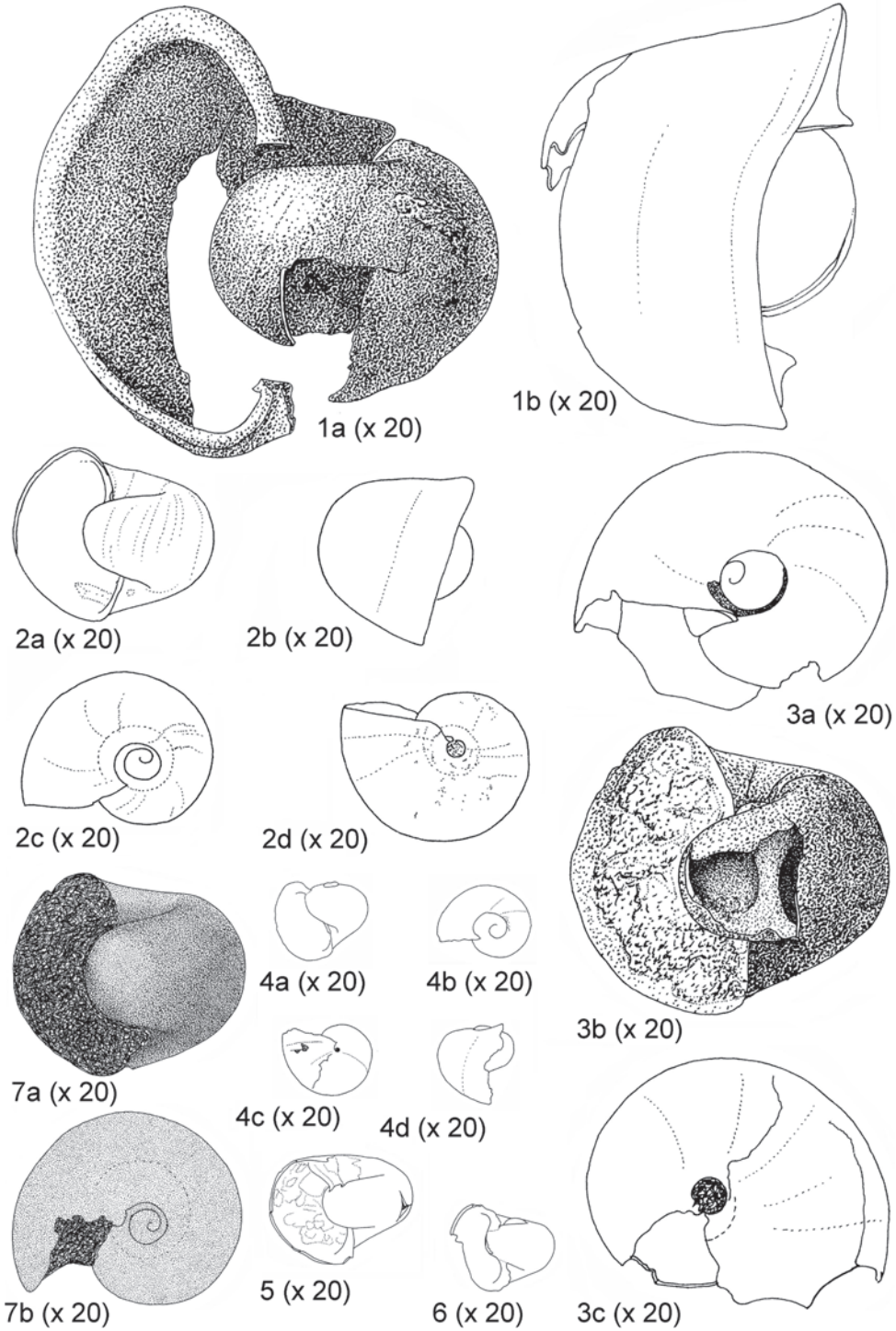


Plate 5

Currylimacina cosmanni (Curry, 1982)

Fig. 1. Gan (tuilerie), RGM 569 451, juvenile specimen. Apertural view.

Fig. 2. Gan (tuilerie), RGM 569 454, juvenile specimen. a, apical view. b, initial whorls enlarged.

Fig. 3. Taylor Branch (Texas, USA), RGM 429 742, Eocene, Reklaw Formation, Marquez Shale Member. Fragment demonstrating microornament.

Camptoceratops priscus (Godwin-Austen, 1882)

Fig. 4. Gan (tuilerie), RGM 569 459. Fragment retaining complete apertural margin.

Fig. 5. Gan (tuilerie), RGM 541 556. Apical fragment.

Fig. 6. Gan (tuilerie), RGM 541 557. a, apical fragment. b, protoconch enlarged.

Creseis antoni sp. nov.

Fig. 7. Gaas (Espibos, level 6), RGM 541 399, paratype. Frontal view.

Creseis roesti sp. nov.

Fig. 8-10. Meilhan (Vives), RGM 569 418-420, paratypes. a, frontal views. b, protoconchs enlarged.

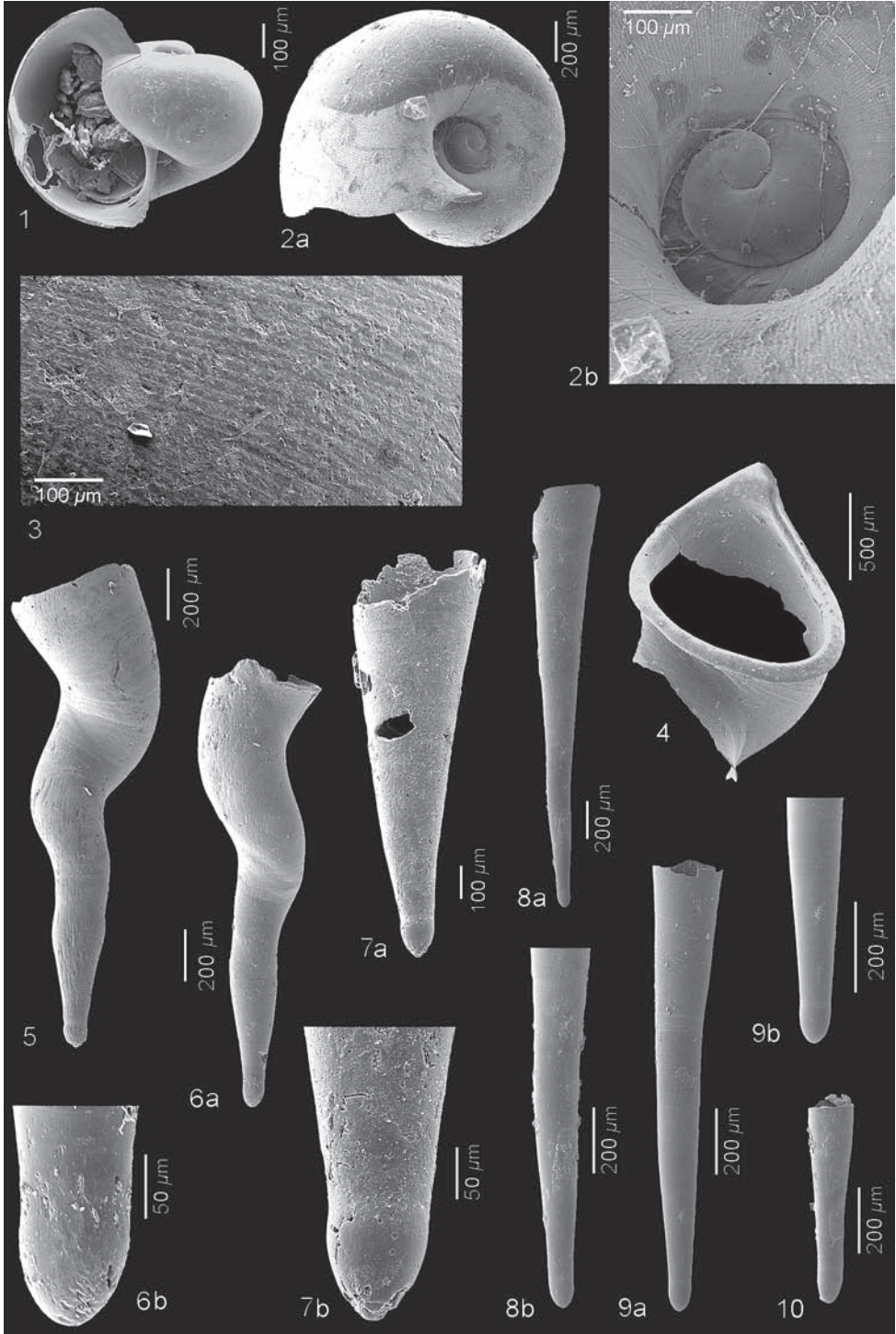


Plate 6*Heliconoides auriformis* (Curry, 1982)

Fig. 1. Gan (tuilerie), holotype, BMNH GG. 21252. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 2. Gan (tuilerie), RGM 396 585. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 3. Gan (tuilerie), RGM 396 604. a, apertural. b, lateral. c, dorsal view.

Fig. 4. Gan (tuilerie), RGM 396 586. a, apertural. b, apical. c, umbilical view.

Fig. 5. Gan (tuilerie), RGM (specimen lost). a, apertural. b, apical. c, umbilical view.

Heliconoides daguini sp. nov.

Fig. 6. Gan (tuilerie), holotype, RGM 396 587. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 7. Gan (tuilerie), paratype, RGM 396 588. a, apertural. b, apical. c, umbilical view.

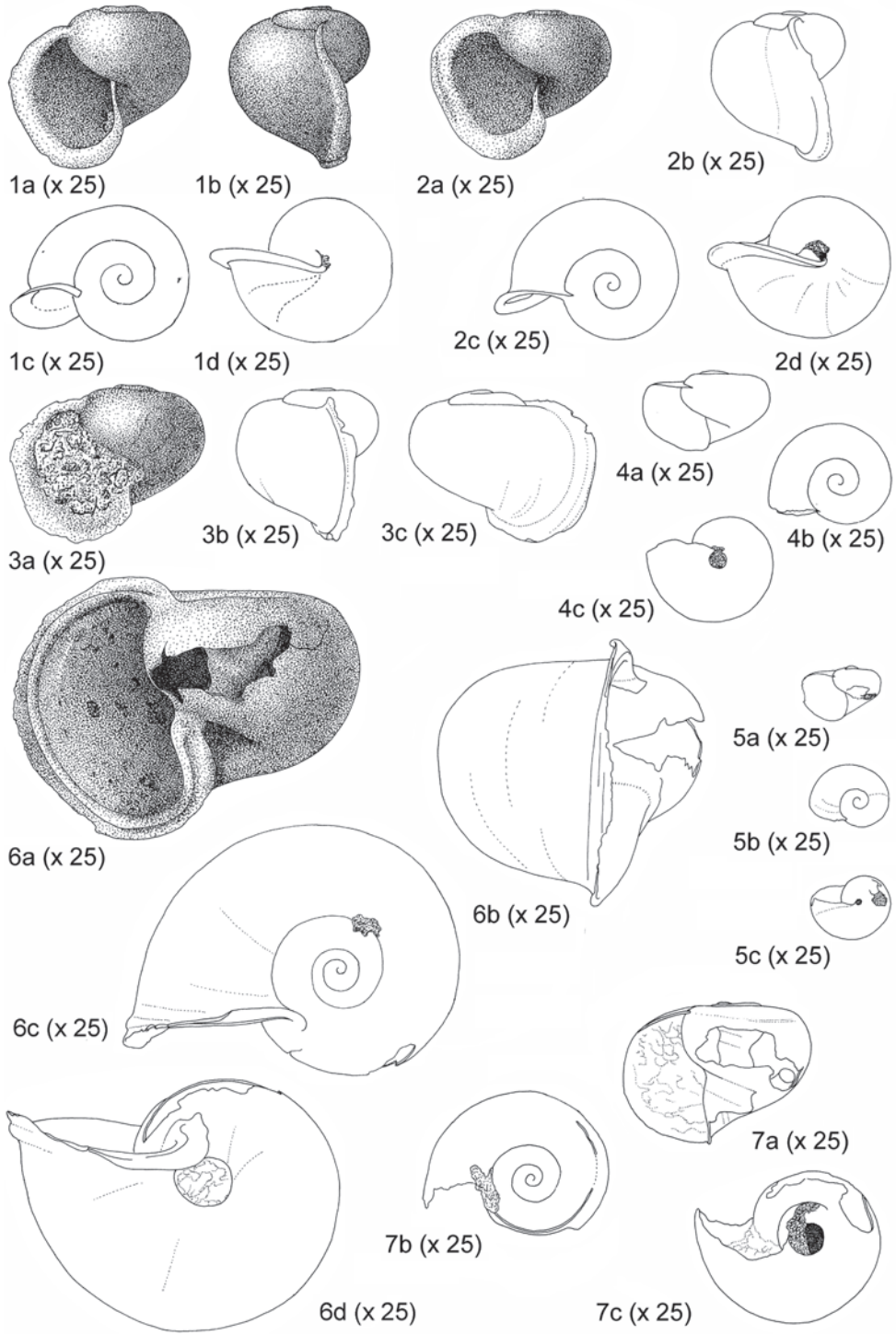


Plate 7*Heliconoides hospes* (Rolle, 1861)

Fig. 1. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 414. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 2. Bélus (Marcon), MNHN A32085. a, apertural. b, lateral. c, apical. d, umbilical view.

Figs. 3-4. Saint-Etienne-d'Orthe (Verdun), MNHN A32087. 3a, apertural. b, apical view; MNHN A32086. 4a, apertural. b, lateral view.

Fig. 5. Peyrehorade (Peyrère), MNHN A32092, P. Lozouet collection. a, apertural. b, lateral. c, oblique apertural. d, apical view.

Figs. 6-7. Saint-Paul-lès-Dax (Estoti), MNHN A32089. 6a, apertural. b, apical view. 7a, apertural. b, oblique apical. c, apical view.

Fig. 8. Peyrehorade (Peyrère), RGM 541 404. a, apertural. b, apical view.

Fig. 9. Saint-Paul-lès-Dax (Abesse), MNHN A32088. Apertural view.

Heliconoides inflata (d'Orbigny, 1834)

Fig. 10. Saucats (Coquillière), RGM 541 329. a, apertural. b, apical view.

Fig. 11. Saint-Martin-de-Hinx (Secat), MNHN A32091. a, apertural. b, lateral. c, apical view.

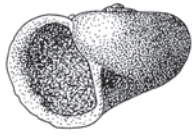
Heliconoides inflata? (d'Orbigny, 1834), juvenile specimens

Fig. 12. Orthez (Le Paren), MNHN A32090. Apertural view.

Fig. 14. Orthez (Le Paren), RGM 541 313. a, apertural. b, lateral. c, umbilical. d, apical view.

Heliconoides sp. (*inflata* or *tertiaria*)

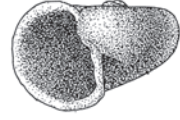
Fig. 13. Saint-Paul-lès-Dax (Cabanes), MNHN A32093. Apertural view.



1a (x 25)



1b (x 25)



2a (x 25)



2b (x 25)



1c (x 25)



1d (x 25)



2c (x 25)



2d (x 25)



3a (x 25)



4a (x 25)



5a (x 25)



5b (x 25)



6a (x 25)



3b (x 25)



4b (x 25)



5c (x 25)



5d (x 25)



6b (x 25)



7a (x 25)



7b (x 25)



7c (x 25)



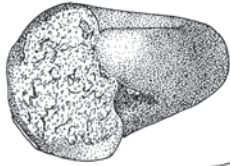
8a (x 25)



8b (x 25)



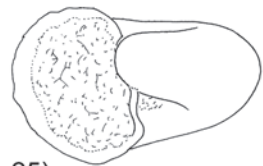
9 (x 25)



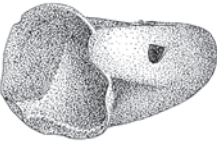
11 (x 25)



12 (x 25)



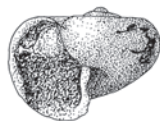
13 (x 25)



10a (x 25)



11b (x 25)



14a (x 25)



14b (x 25)



10b (x 25)



11c (x 25)



14c (x 25)



14d (x 25)

Plate 8

Heliconoides inflata (d'Orbigny, 1834) f. *microstralis* (Kautsky, 1925)

Fig. 1. Gram (Denmark, Jylland), borehole Enderupskov DGU 141,196, 54 m below surface (Arnum Formation (Miocene, 'Hemmoorian' = Late Burdigalian/Langhian), RGM 541 464, leg. Danmarks Geologiske Undersøgelse, 1989 (don. L.B. Rasmussen). a, apertural. b, lateral. c, apical view.

Heliconoides linneensis A.W. Janssen, 2008a

Fig. 2. Saint-Etienne-d'Orthe (Lartigaou), holotype, RGM 541 416. a, apical. b, apertural. c, lateral view.

Fig. 3. Béhus (Marcon), paratype MNHN A32071. a, apertural. b, lateral view.

Fig. 4. Peyrehorade (Peyrère), paratype, MNHN A32074. a, apical. b, apertural. c, lateral view.

Fig. 5. Saint-Paul-lès-Dax (Lestrilles), paratype, MNHN A32083. a, apertural. b, lateral view.

Fig. 6. Saint-Paul-lès-Dax (Estoti), paratype, MNHN A32082, P. Lozouet collection. a, apical. b, apertural. c, lateral view.

Heliconoides merlei sp. nov.

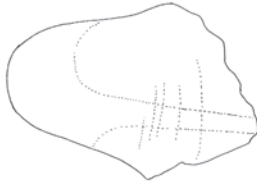
Fig. 7. Gan (tuilerie), holotype, BMNH GG. 21247a. a, apical. b, umbilical. c, apertural. d, lateral view.

Fig. 8. Gan (tuilerie), paratype, BMNH GG. 21247b. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 9. Gan (tuilerie), paratype, RGM 396 850. a, apertural. b, apical view.



1a (x 25)



1b (x 25)



1c (x 25)



2a (x 25)



2b (x 25)



3a (x 25)



3b (x 25)



2c (x 25)



4a (x 25)



4b (x 25)



4c (x 25)



5a (x 25)



5b (x 25)



6a (x 25)



6b (x 25)



6c (x 25)



7a (x 25)



7c (x 25)



8a (x 25)



8b (x 25)



7b (x 25)



7d (x 25)



8c (x 25)



8d (x 25)



9a (x 25)



9b (x 25)

Plate 9

Heliconoides mercinensis (Watelet & Lefèvre, 1885)

Fig. 1. Saint-Gobain (France, Aisne) (Sables de Cuise, Eocene, Ypresian), RGM 541 461. a, apertural. b, lateral view.

Heliconoides mermuysi sp. nov.

Fig. 2. Saint-Paul-lès-Dax (Cabanes), holotype, RGM 541 350. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 3. Saint-Paul-lès-Dax (Cabanes), paratype, MNHN A32084. a, apical. b, apertural. c, lateral view.

Heliconoides nemoris (Curry, 1965)

Fig. 4. Bramshaw (England, Hampshire), Upper Bracklesham Beds, Shepherd's Gutter Bed, Eocene, Late Lutetian), holotype, BMNH GG. 7100. a, apical., b, umbilical. c, apertural. d, lateral. e, oblique apertural (to show inner marginal ridge) view.

Fig. 5. Biarritz, BMNH GG. 21268. a, apertural. b, apical view.

Heliconoides paula (Curry, 1982)

Fig. 6. Gan (tuilerie), holotype, BMNH GG. 21251. a, apertural. b, umbilical. c, apical view.

Heliconoides pyrenaica sp. nov.

Fig. 7. Gan (tuilerie), holotype, BMNH GG. 21266. a, apertural. b, lateral view.

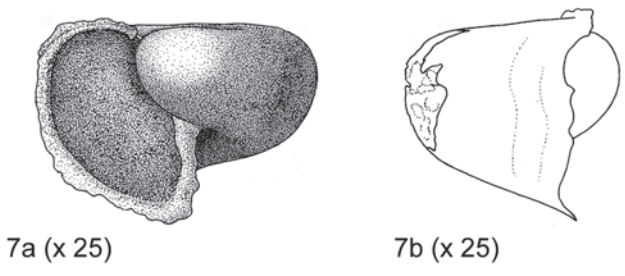
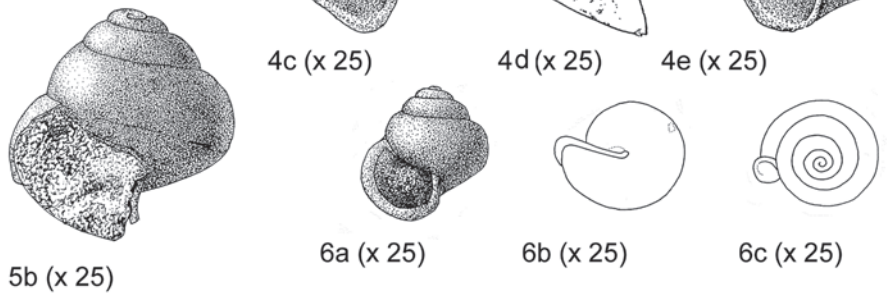
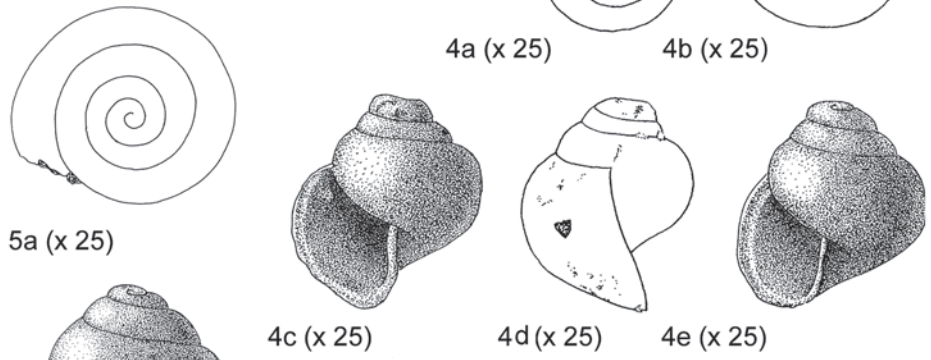
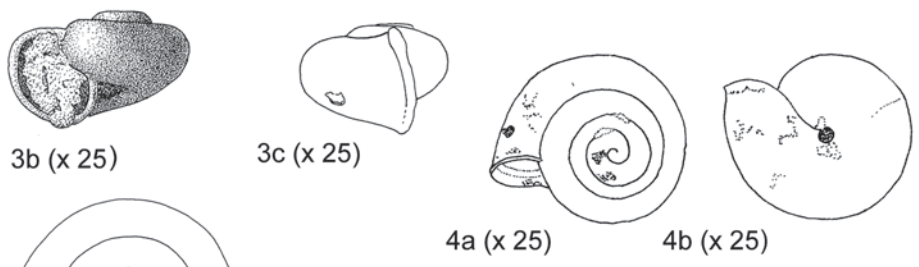
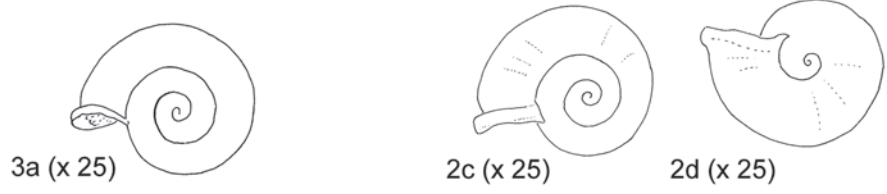
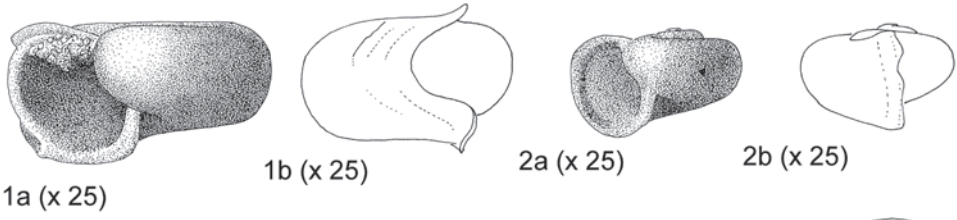


Plate 10

Heliconoides tertiaria (Tate, 1887)

Fig. 1. Saint-Paul-lès-Dax (Cabanes), RGM 541 352. a, apical. b, apertural view.

Figs. 2-3. Saint-Jean-de-Marsacq (Lahitet), MNHN A32094 and A32095. a, apical. b, apertural views.

Limacina bulimoides (d'Orbigny, 1836)

Fig. 4. Saucats (Coquillière), RGM 541 547. Apertural view.

Fig. 5. Red Sea (Suakin Deep), RGM 541 549, Recent, apertural view.

Limacina gormani (Curry, 1982)

Fig. 6. Gan (tuilerie), holotype, BMNH GG. 21249. a, apical. b, lateral. c, dorsal., d, apertural view.

Fig. 7. Gan (tuilerie), RGM 396 589. a, apical. b, apertural. c, lateral view.

Fig. 8. Gan (tuilerie), RGM 396 592. a, apical. b, lateral. c, apertural view.

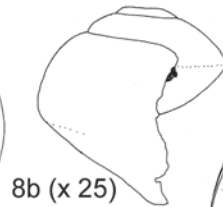
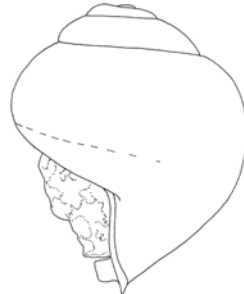
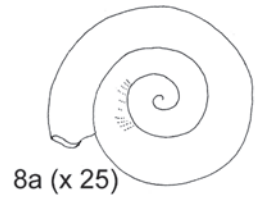
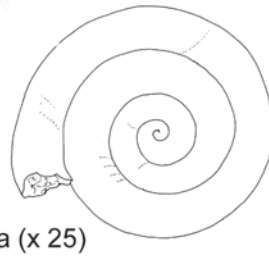
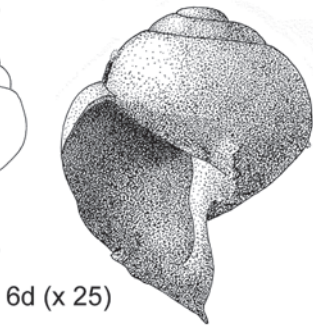
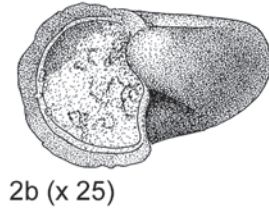
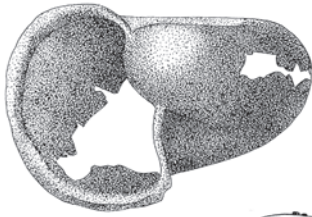
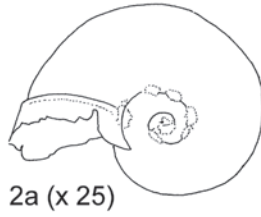
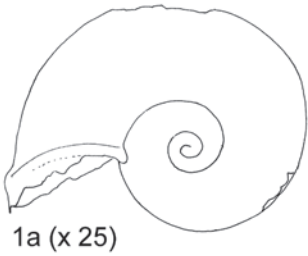


Plate 11

Limacina gormani (Curry, 1982)

Fig. 1. Gan (tuilerie), RGM 569 452, aberrant specimen showing spiral ridge on second and third whorl.
a, oblique apical view. b, apical whorls enlarged.

Limacina? vegrandis sp. nov., paratypes

Fig. 2. Gan (tuilerie), RGM 541 533, paratype. a, apertural view. b, umbilical region enlarged.

Fig. 3. Gan (tuilerie), RGM 541 534, paratype. Apical view.

Fig. 4. Gan (tuilerie), RGM 569 457, paratype. Apertural view.

Fig. 5. Gan (tuilerie), RGM 569 458, paratype. a, apertural view. b, first whorl enlarged.

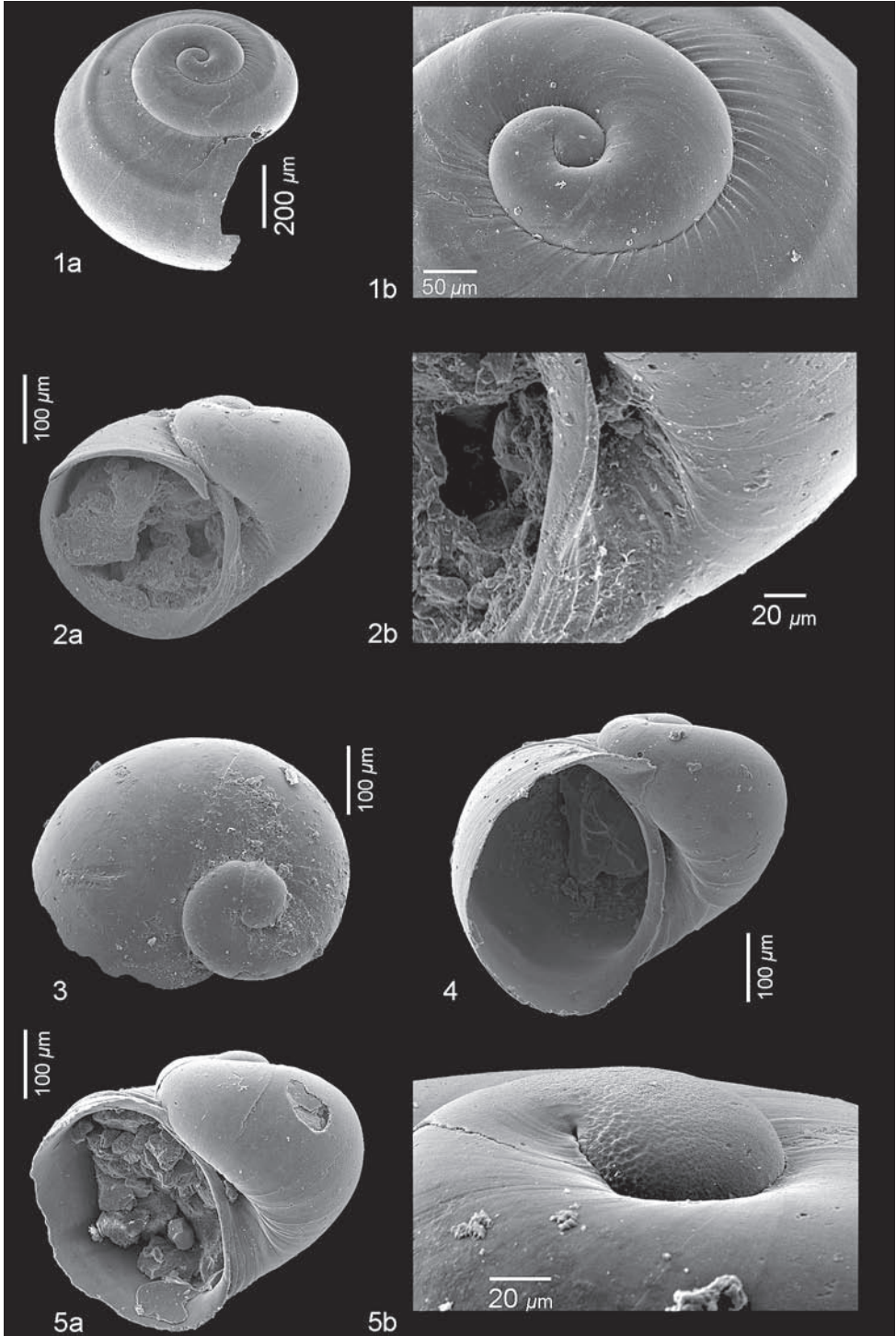


Plate 12*Limacina gormani* (Curry, 1982)

Fig. 1. Gan (tuilerie), RGM 396 591. a, apical. b, apertural. c, lateral view.

Fig. 2. Gan (tuilerie), RGM 396 590, a, apical. b, apertural. c, umbilical view.

Limacina pygmaea (Lamarck, 1805)

Fig. 3-4. Gan (tuilerie), BMNH GG. 21258. Apertural views.

Fig. 5. Gan (tuilerie), RGM 396 849. Apertural view.

Limacina valvatina (Reuss, 1867)

Fig. 6. Meilhan (Vives), MNHN A32096. Apertural view.

Fig. 7. Saint-Paul-lès-Dax (Cabanes), RGM 541 552. Apertural view.

Fig. 8. 'Saucats, Bordeaux', MHB unnumbered, as '*Spiratella* (*Spiratella* b) *praerangi praerangi* Tembrock MS'. Apertural view.

Fig. 9. Saucats (Coquillière), RGM 541 335. Apertural view.

Fig. 10. Saint-Jean-de-Marsacq (Pinot), RGM 541 551. Apertural view.

Fig. 11. Orthez (Le Paren), RGM 541 305. a, apertural. b, lateral. c, apical. d, umbilical view.

Fig. 12. Orthez (Le Paren), RGM 541 314. a, apertural. b, lateral. c, apical. d, umbilical view.

Limacina? vegrandis sp. nov.

Fig. 13. Gan (tuilerie), holotype, RGM 396 598. a, apical. b, apertural. c, lateral. d, umbilical view.

Limacina sp. 1

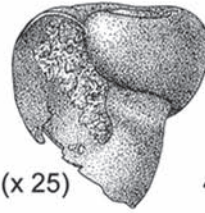
Fig. 14. Gaas (Lagouarde), MNHN A32097. a, apertural. b, lateral view.



1a (x 25)



2a (x 25)



3 (x 25)



4 (x 25)



1b (x 25)



2b (x 25)



5 (x 25)



6 (x 25)



1c (x 25)



2c (x 25)



7 (x 25)



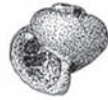
8 (x 25)



9 (x 25)



10 (x 25)



11a (x 25)



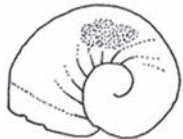
11b (x 25)



12a (x 25)



12b (x 25)



13a (x 50)



11c (x 25)



11d (x 25)



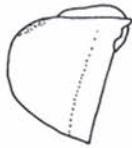
12c (x 25)



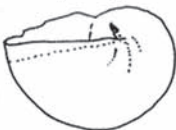
12d (x 25)



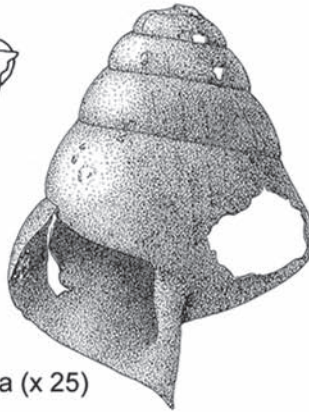
13b (x 50)



13c (x 50)



13d (x 50)



14a (x 25)



14b (x 25)

Plate 13*Limacina* sp. 2

Fig. 1. Pontonx (Mineur), MNHN A32098. Apertural view.

Fig. 2. Saint-Paul-lès-Dax (Estoti), MNHN A32099. Apertural view.

Limacinidae sp. 1

Figs. 3-4. Gaas (Lagouarde), MNHN A32101. 3a, apertural. b, oblique apical. c, apical view; 4a, apertural. b, apical view;

Fig. 5. Gaas (Lagouarde), MNHN A32100. a, apertural. b, oblique apical. c, apical view.

Limacinidae sp. 2

Fig. 6. Gan (tuilerie), RGM 396 609. a, apertural. b, apical view.

Camptoceratops priscus (Godwin-Austen, 1882)

Fig. 7. Isle of Sheppey (England, Kent), lectotype, BMNH G. 459. Dorsal view.

Fig. 8. Gan (tuilerie), RGM 396 582. a, apertural. b, lateral. c, dorsal view.

Figs. 9-10. Gan (tuilerie), RGM 396 583. Frontal views.

Fig. 11. Gan (tuilerie), BMNH GG. 7109. a, apertural. b, oblique apertural view.

Figs. 12-13. Gan (tuilerie), RGM 569 447 and RGM 569 448 (specimen lost). Frontal views.

Fig. 14. Gan (tuilerie), BMNH GG. 21248. a, apertural. b, oblique apertural. c, lateral view.

Fig. 15. Gan (tuilerie), RGM 541 555. Frontal view.

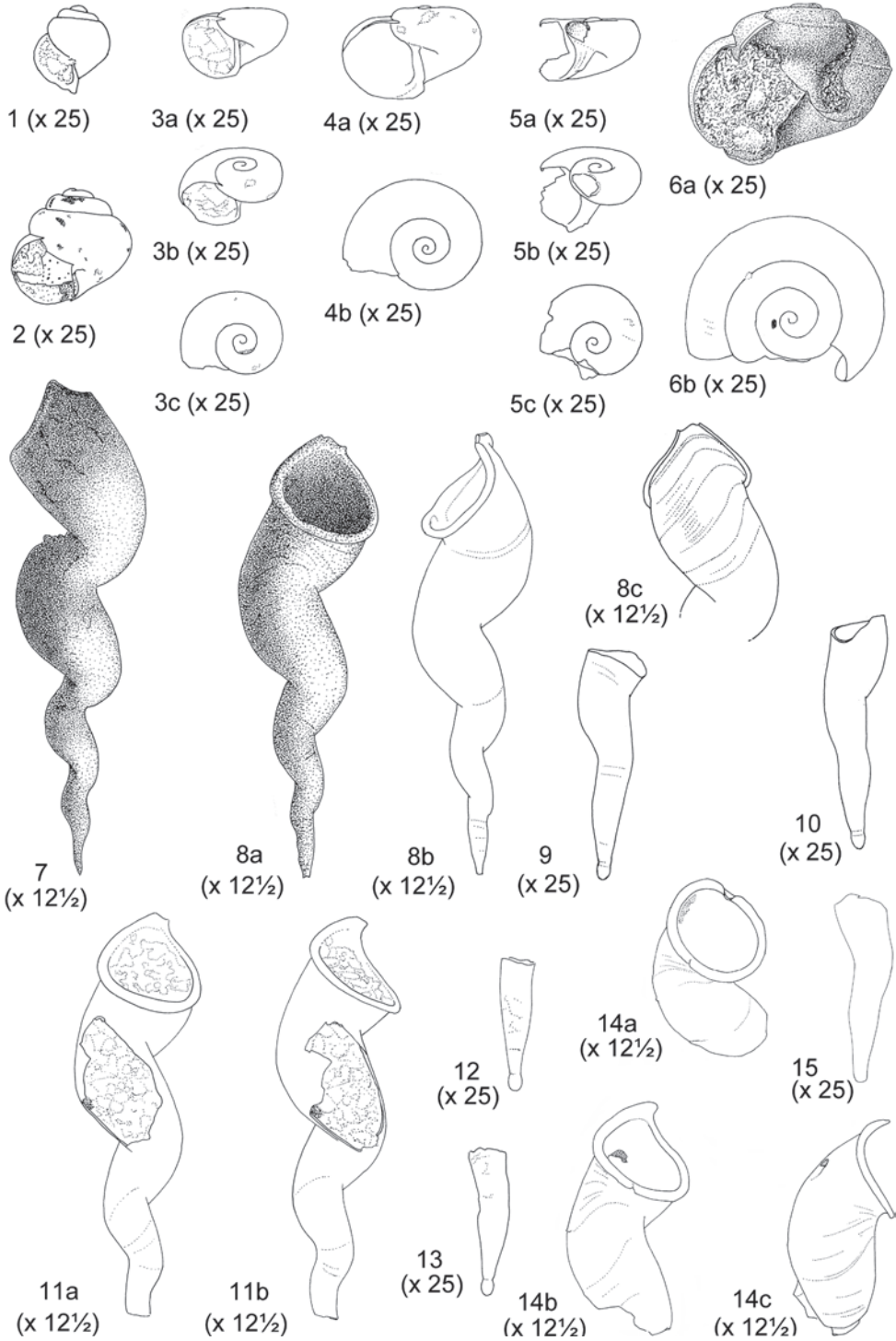


Plate 14

Clio antoni sp. nov.

Figs. 1-2. Gaas (Espibos). 1, holotype, RGM 541 400. 2, paratype, RGM 541 401. a, frontal. b, lateral views.

Creseis corpulenta (Mayer, 1887)

Fig. 3. Biarritz, BMNH GG. 21265. a, apertural. b, frontal. c, lateral view.

Creseis roesti sp. nov.

Fig. 4. Martillac (Barreau), holotype, RGM 569 470. a, frontal. b, apertural. c, lateral views. d-e, protoconch frontal and lateral views.

Fig. 5. Meilhan (Vives), paratype, RGM 569 417. a, frontal. b, lateral view.

Creseis simplex (Meyer, 1886)

Fig. 6. Jackson, Hinds Co. (USA, Mississippi) (Eocene, Bartonian, Moody Branch Formation), holotype, USNM 638841, apical shell part (reduced after Hodgkinson *et al.*, 1992, pl. 9, fig. 4).

Fig. 10. Peyrehorade (Arribaouts), RGM 541 411. a, frontal view of compressed specimen in matrix. b, apical shell part.

Fig. 12. Biarritz, BMNH PITG25515. a, frontal view of compressed specimen in matrix. b, apical shell part.

Creseis simplex? (Meyer, 1886)

Fig. 11. Biarritz, BMNH GG. 21262. Frontal view of compressed specimen in matrix.

Creseis spina (Reuss, 1867)

Fig. 7. Vicksburg, Warren Co. (USA, Mississippi) (Early Oligocene, Vicksburg Group), holotype of *Creseis hastata* (Meyer, 1886), USNM 644595. Apical shell part (reduced after Hodgkinson *et al.*, 1992, pl. 9, fig. 2).

Fig. 8-9. Wieliczka, Poland; Wieliczka Formation (Miocene salt rock, 'Badenian' = Langhian), NMV 1867. VII-41. 8, lectotype a, frontal. b, lateral view. 9, paralectotype, frontal view.

Fig. 13. Gaas (Espibos), MNHN PL 5503. a, apertural. b, frontal view. c, apical shell part.

Fig. 14. Gaas (Lagouarde), MNHN PL 6612. a, frontal. b, lateral view. c, apical shell part.

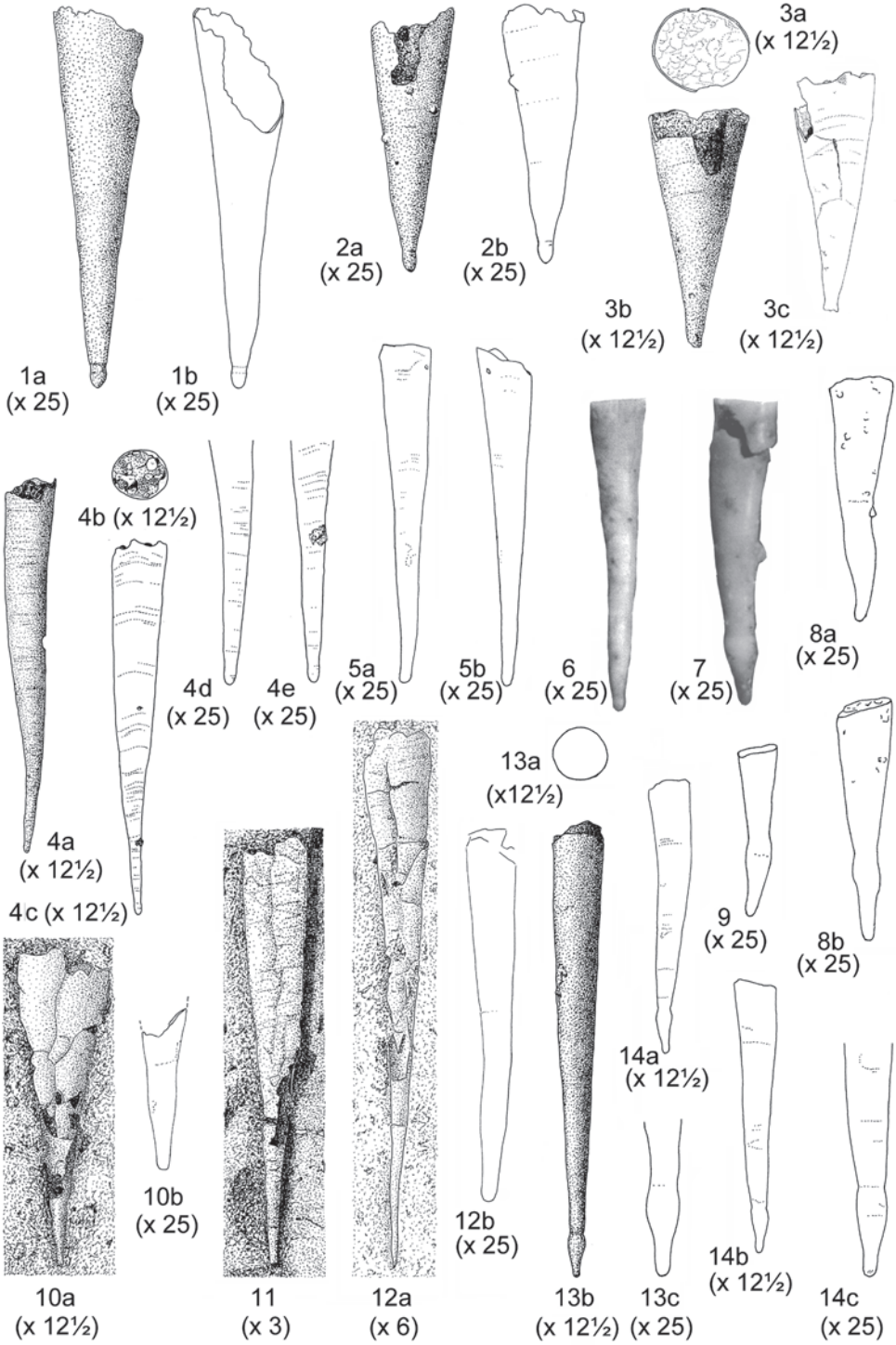


Plate 15*Creseis spina* (Reuss, 1867)

Figs. 1-5. Gaas (Espibos), RGM 541 393-397. Frontal views.

Fig. 6. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 420. Frontal view.

Fig. 7. Bélus (Marcon), MNHN A32102. Frontal view.

Figs. 8-11. Saint-Paul-lès-Dax (Estoti), MNHN A32104, P. Lozouet collection. a, frontal views. b, apical shell parts.

Fig. 12. Saint-Paul-lès-Dax (Abesse), MNHN A32103. a, frontal. b, lateral view.

Figs. 13-14. Saint-Jean-de-Marsacq (Pinot), RGM 569 409 and 569 428. Frontal views.

Figs. 15-16. Orthez (Le Paren), RGM 541 308-309. a, frontal. b, lateral views.

Creseis tugurii sp. nov.

Fig. 17. Saint-Paul-lès-Dax (Cabanes), holotype, RGM 569 410. a, frontal view. b, apical shell part.

Creseis sp. nov. 1

Figs. 18-19. Biarritz, BMNH PITG25518. Frontal views.

Creseis sp. nov. 2

Figs. 20-21. Bélus (Marcon), MNHN A32107. Frontal views.

Fig. 22. Peyrehorade (Peyrère), RGM 541 406. a, frontal. b, lateral view.

Fig. 23-24. Saint-Etienne-d'Orthe (Lartigaou), RGM 569.471a-b. Frontal views.

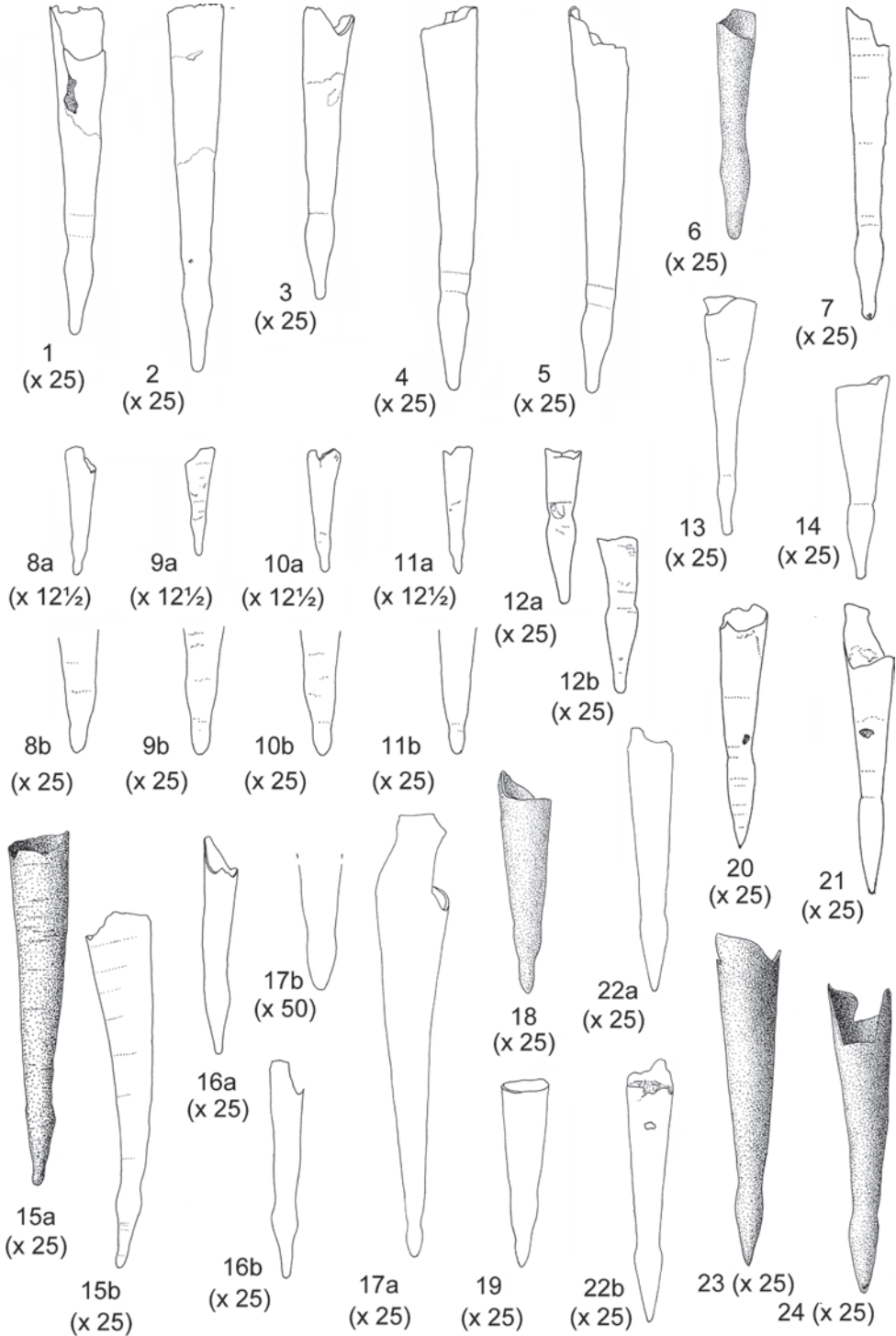


Plate 16

Creseis tugurii sp. nov.

Fig. 1. Saint-Paul-lès-Dax (Cabanes), RGM 569 411, paratype. a, frontal view. b, protoconch enlarged.

Fig. 2. Saint-Paul-lès-Dax (Cabanes), RGM 569 415, paratype. a, lateral view. b, protoconch enlarged.

Euchilotheca ganensis Curry, 1982

Fig. 3. Gan (tuilerie), RGM 569 450. Fragment retaining apertural reinforcements.

Styliola subula (Quoy & Gaimard, 1827)

Fig. 4. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 424, apical fragment. a, frontal view. b, protoconch-1 enlarged.

Cuvierina (Cuvierina) paronai? Checchia-Rispoli, 1921

Fig. 5. Saint-Martin-de-Hinx (Secat), RGM 395 405. Juvenile specimen retaining protoconch.

Johnjagtia moulinsii (Benoist, 1874a)

Fig. 6. Saint-Paul-lès-Dax (Cabanes), RGM 569 461, apical fragment. a, dorsal view. b, protoconch enlarged.

Fig. 7. Saint-Paul-lès-Dax (Cabanes), RGM 569 462, apical fragment. a, ventral view. b, protoconch enlarged.

Fig. 8. Saint-Paul-lès-Dax (Cabanes), RGM 569 463. Apical fragment, dorsal view.

Fig. 9. Saint-Paul-lès-Dax (Cabanes), RGM 569 464. Apertural fragment showing reinforcements.

Clio vasconiensis sp. nov.

Fig. 10. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 438, paratype. Apical fragment retaining protoconch, frontal view.

Fig. 11. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 437, paratype. Apical fragment retaining protoconch, lateral view.

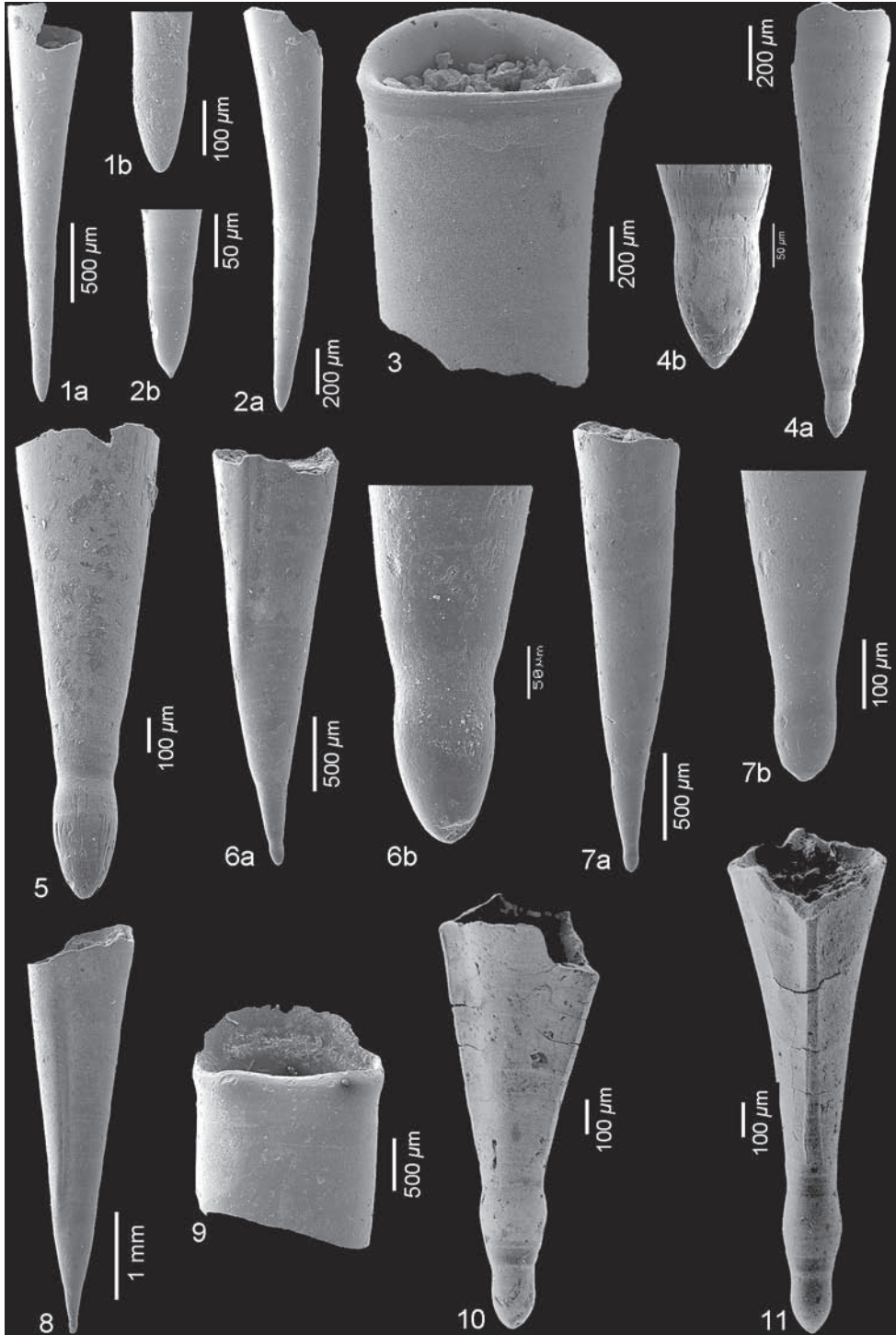


Plate 17

Euchilotheca ganensis (Curry, 1982)

Fig. 1. Gan (tuilerie), holotype, BMNH GG. 21259. a, apertural. b, ventral. c, left lateral view.

Fig. 2. Gan (tuilerie), paratype, BMNH GG. 21260. a, frontal view. b, apical shell part.

Figs. 3-4. Gan (tuilerie), BMNH GG. 21263 (as *Creseis* cf. *hastata*). Frontal views.

Fig. 5. Gan (tuilerie), BMNH GG. 21261 (as *Creseis* cf. *hastata*). Frontal view.

Figs. 6-7. Gan (tuilerie), RGM 396 578. 6a, ventral. b, left lateral view. c, apical shell parts, d-e, apertural shell part from ventral and left lateral. RGM 396 580. 7a, frontal view. b, apical shell part.

Praehyalocylis maxima (Ludwig, 1864)

Figs. 8-9. Gaas (Lagouarde), MNHN A32108. 8, 9a, frontal views. 9b, apical shell part.

Fig. 10. Gaas, SMF 332797/1. Frontal view.

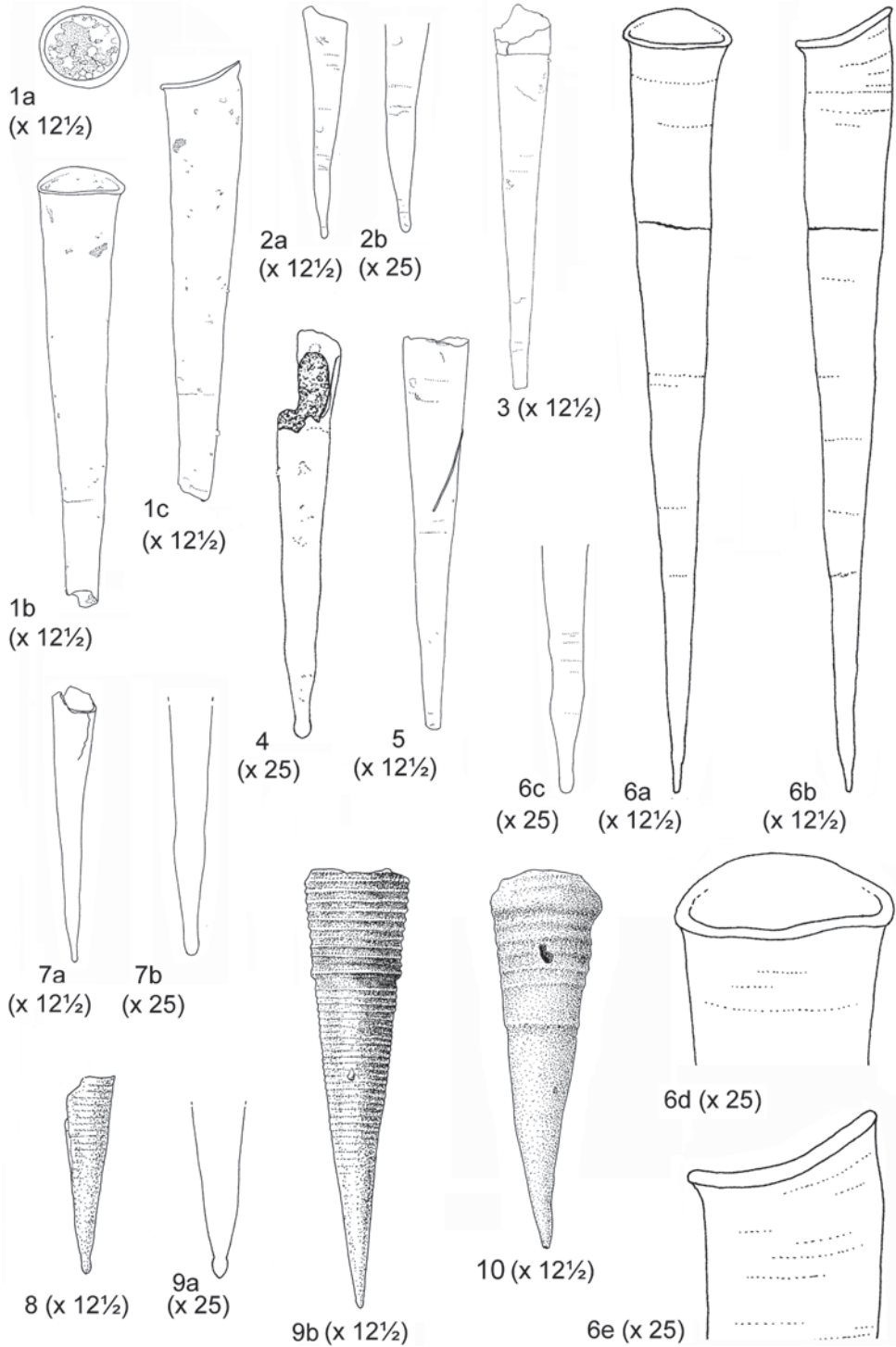


Plate 18

Styliola subula (Quoy & Gaimard, 1827)

Fig. 1. Saint-Paul-lès-Dax (Cabanes), RGM 541 373. Dorsal view.

Cuvierina (Cuvierina) paronai? Checchia-Rispoli, 1921

Fig. 2. Saint-Paul-lès-Dax (Cabanes), RGM 541 356. a, apertural. b, ventral. c, left lateral view.

Fig. 3. Saint-Jean-de-Marsacq (Pinot), RGM 541 388. a, frontal view. b, apical shell part.

Fig. 4. Saucats (Coquillière), RGM 541 337, frontal view.

Fig. 5. Saint-Martin-de-Hinx (Secat), RGM 541 055. a, frontal view. b, apical shell part.

Ireneia nieulandei A.W. Janssen, 1995

Fig. 6. Saint-Paul-lès-Dax (Cabanes), MNHN A32110. a, ventral. b, left lateral. c, dorsal view, d, apertural shell part from ventral. e, apertural view.

Johnjagtia moulinsii (Benoist, 1874a)

Fig. 7. Saucats (Église), holotype, MBB unnumbered, Benoist collection. Dorsal view.

Fig. 8. Saint-Paul-lès-Dax (Cabanes), FSUB (A. Cluzaud collection) typothèque 25-4-11. a, apertural. b, ventral. c, right lateral. d, dorsal view.

Fig. 9. Saint-Paul-lès-Dax (Cabanes), MNHN A32111. a, ventral. b, left lateral. c, dorsal view. d, apical shell part from ventral. e, identical, but from left lateral.

Fig. 10. Saint-Paul-lès-Dax (Cabanes), RGM 541 377. a, dorsal. b, left lateral. c, ventral. d, apertural view.

Spoelia torquayensis A.W. Janssen, 1990a

Fig. 11. Saint-Paul-lès-Dax (Estoti), paratype, MNHN unnumbered. a, adapical. b, frontal. c, lateral. d, apertural view.

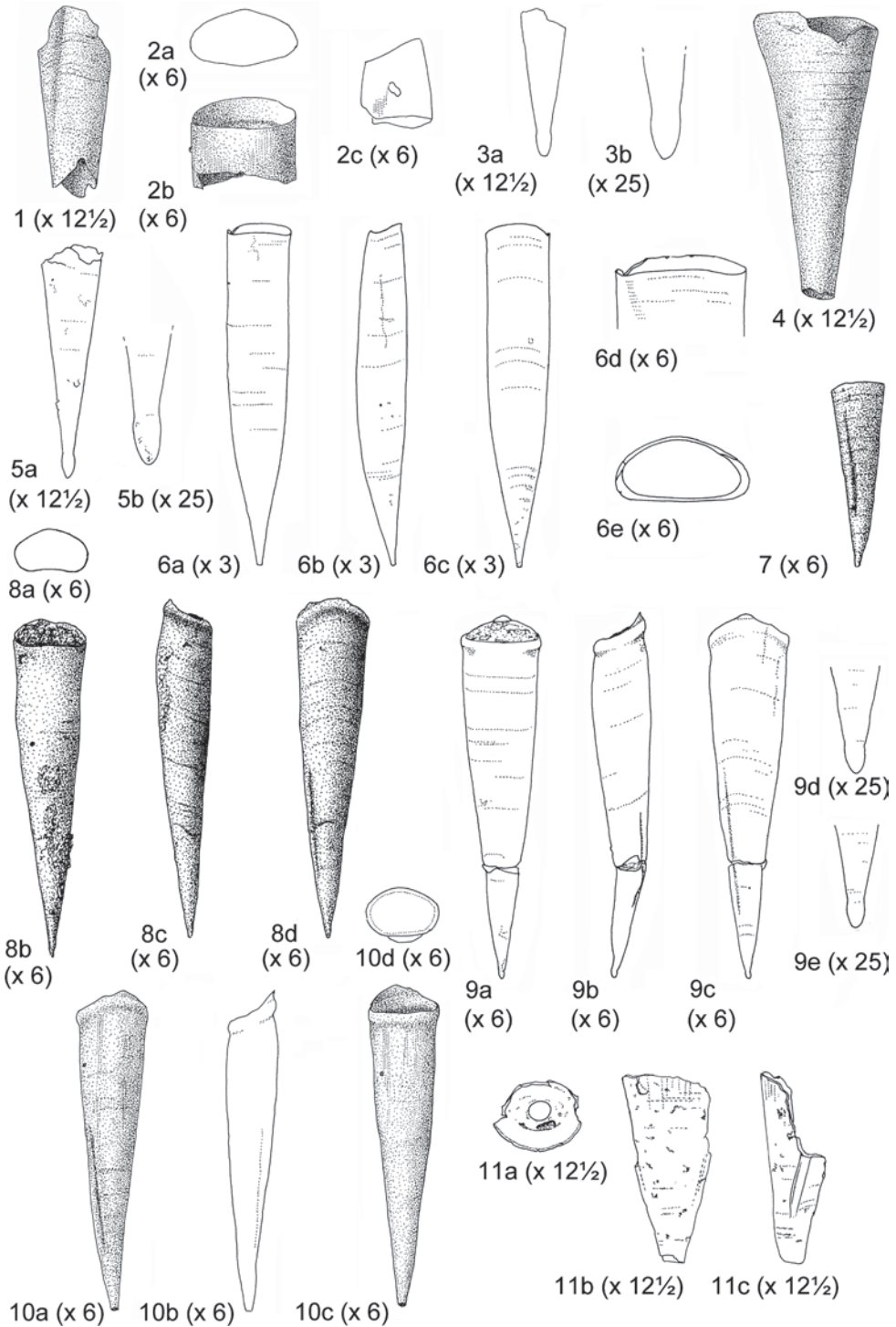


Plate 19

Spoelia torquayensis A.W. Janssen, 1990

Fig. 1. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 427. Dorsal view.

Fig. 2. Saint-Paul-lès-Dax (Abesse), FSUB (A. Cluzaud collection) typothèque 51-4-27. a, apertural. b, frontal. c, lateral view.

Fig. 3. Saint-Paul-lès-Dax (Bezoye), MNHN A32113. a, frontal. b, lateral view.

Fig. 4. Peyrehorade (Peyrère), paratype, RGM 229 505. a, frontal. b, left or right lateral. c, right or left lateral view. d, apical shell part.

Fig. 5. Peyrehorade (Peyrère), paratype, RGM 229 506. a, frontal, b. lateral view. c, apical shell part.

Fig. 6. Bélus (Marcon), MNHN A32112. a, left or right lateral. b, frontal. c, right or left lateral view (specimen with a lateral carina on one side only).

Cuvierinidae sp. nov.?

Fig. 7. Saint-Paul-lès-Dax (Abesse), MNHN A32114. a, apertural. b, dorsal. c, left lateral view.

Cuvierinidae sp. 1

Fig. 8. Saint-Etienne-d'Orthe (Verdun), MNHN A32115. a, frontal. b, lateral view.

Cuvierinidae sp. 2

Fig. 9. Saint-Paul-lès-Dax (Cabanes), MNHN A32116. a, apertural. b, ventral. c, left lateral view. d, apical shell part from ventral. e. identical, from lateral.

Fig. 10. Saint-Paul-lès-Dax (Cabanes), MNHN A32117. a, apertural. b, frontal. c, lateral view.

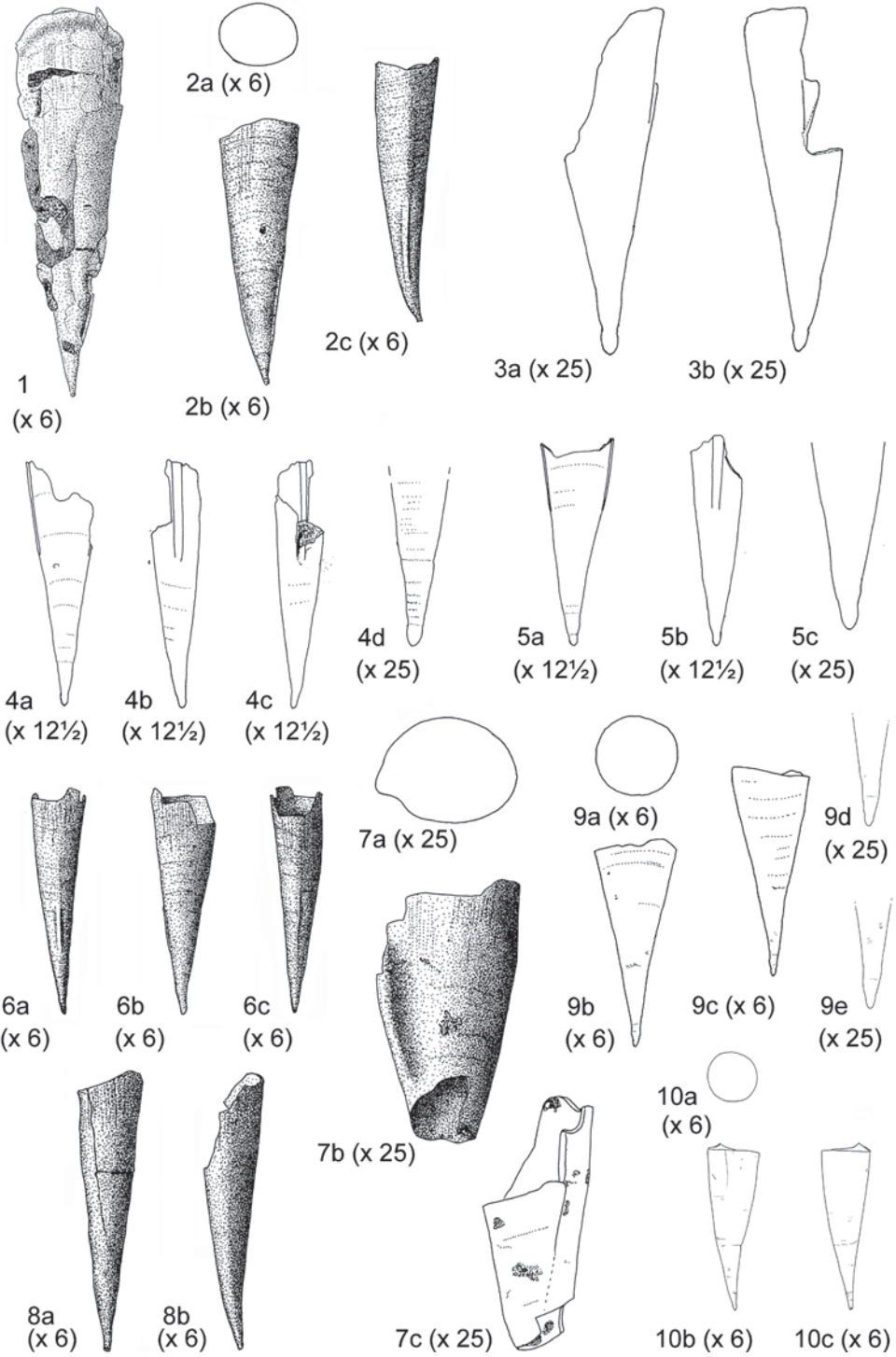


Plate 20*Spoelia torquayensis* Janssen, 1990

Fig. 1. Saint-Etienne-d'Orthe (Lartigaou), RGM 569 465. Apical fragment, lateral view.

Fig. 2. Saint-Etienne-d'Orthe (Lartigaou), RGM 569 466. Apical fragment. a, lateral view. b, protoconch enlarged.

Clio sp. 1

Fig. 3. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 441. Apical fragment retaining protoconch.

Clio sp. nov.?

Fig. 4. Saint-Jean-de-Marsacq (Pinot), RGM 569 468. a, apical fragment, lateral view. b, idem, enlarged.

Fig. 5. Saint-Jean-de-Marsacq (Pinot), RGM 569 469. Apical fragment. a, frontal view. b, protoconch enlarged.

Vaginella austriaca Kittl, 1886

Fig. 6. Saint-Jean-de-Marsacq (Pinot), RGM 541 391b. Apical fragment retaining protoconch, ventral view.

Fig. 7. Saint-Jean-de-Marsacq (Pinot), RGM 541 391c. Apical fragment retaining protoconch, right lateral view.

Fig. 8. Saint-Jean-de-Marsacq (Pinot), RGM 541 391d. Apical fragment retaining protoconch, right lateral view.

Vaginella depressa Daudin, 1800

Fig. 9. Saint-Paul-lès-Dax (Cabanes), RGM 541 364, juvenile specimen in pre-metamorphosis stage. a, frontal view. b, protoconch enlarged. c, microornament on protoconch-2.

Vaginella tricuspadata Zorn & Janssen, 1993

Figs. 10-11. Saint-Etienne-d'Orthe (Lartigaou): RGM 541 448c-d, apical fragments. a, frontal views. b, protoconchs enlarged.

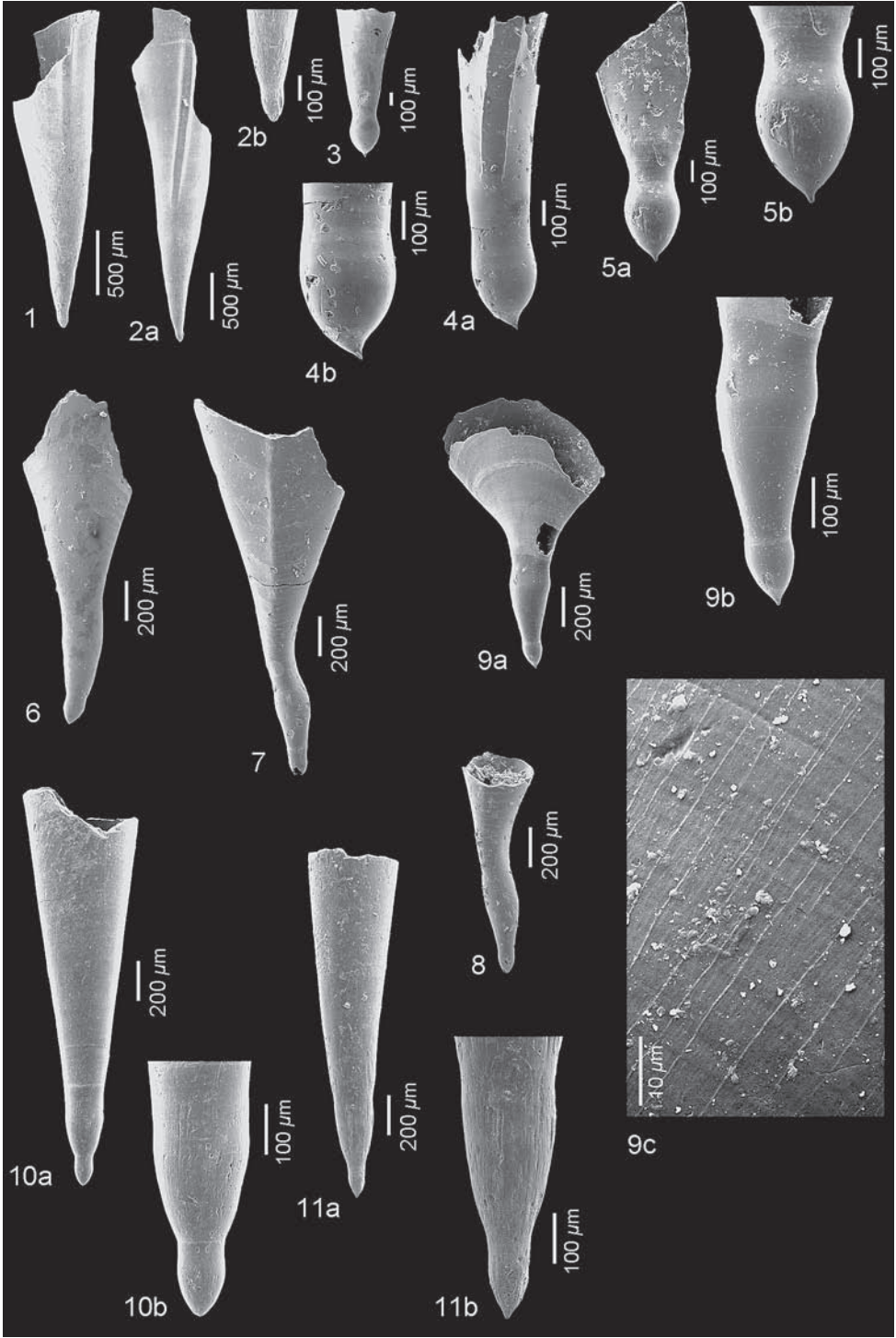


Plate 21*Clio lozoueti* sp. nov.

Fig. 1. Bélus (Marcon), holotype, MNHN A32118. a, apertural. b, dorsal. c, right lateral view. d, apical shell part from dorsal. e, identical, from lateral.

Fig. 2. Bélus (Marcon), paratype, MNHN A32119. a, dorsal. b, right lateral. c, ventral view. d, apical shell part from dorsal. e, identical, from lateral.

Fig. 3. Peyrehorade (Peyrère), paratype, RGM 541 407. a, apertural. b, dorsal. c, left lateral view.

Clio nielseni A.W. Janssen, 1990

Fig. 4. Saint-Etienne-d'Orthe (Verdun), MNHN A32120. a, dorsal. b, right lateral. c, ventral view.

Clio ortheziana (Benoist, 1889)

Fig. 5. Orthez (Le Paren), holotype (specimen lost, drawings copied from Benoist, 1889, pl. 2, fig. 3b-c). a, ventral. b, dorsal view.

Clio vasconiensis sp. nov.

Fig. 6. Saint-Etienne-d'Orthe (Lartigaou), holotype, RGM 541 430. Ventral or dorsal view.

Fig. 7. Saint-Etienne-d'Orthe (Lartigaou), paratype (crushed), RGM 541 431. a, ventral or dorsal view. b, apical shell part.

Fig. 8. Saint-Etienne-d'Orthe (Lartigaou), paratype (drawn from wax cast), RGM 541 435. Ventral or dorsal view.

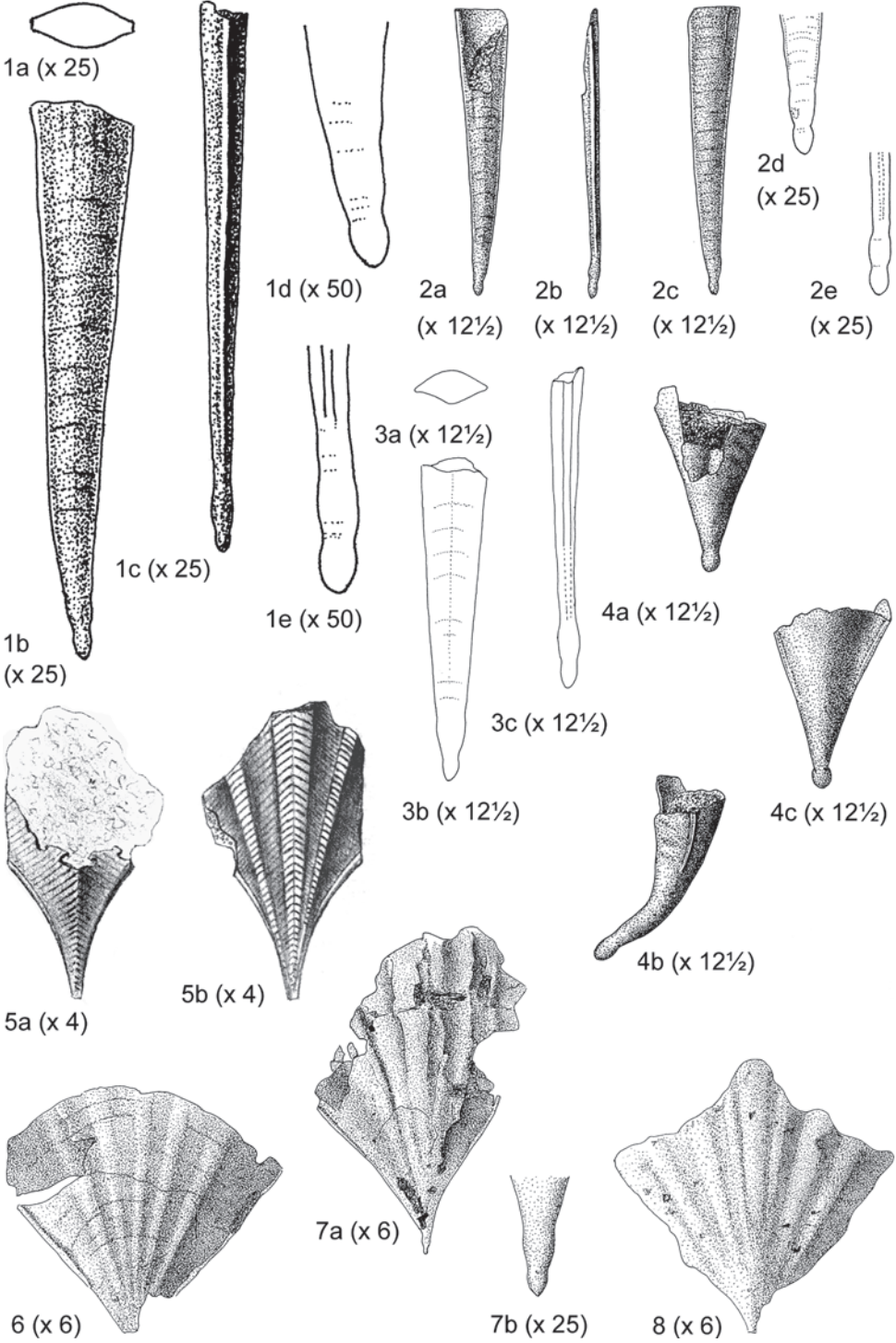


Plate 22*Clio* sp. nov.?

Fig. 1. Saint-Jean-de-Marsacq, MNHN A32123. a, apertural. b, dorsal. c, right lateral. d, ventral view.

Fig. 2. Saint-Jean-de-Marsacq (Pinot), RGM 569 467. a, dorsal. b, apertural. c, left lateral view.

Clio sp. 1

Fig. 3. Saint-Etienne-d'Orthe (Lartigaou), RGM 541 442. a, dorsal. b, right lateral view.

Clio sp. 2

Fig. 4. Saubrigues (Tauziets), RGM 541 606. a, dorsal. b, right lateral. c, ventral view.

Fig. 5. Saint-Martin-de-Hinx (Secat), MNHN A32124. a, dorsal. b, apertural. c, left lateral view.

Fig. 6. Saint-Martin-de-Hinx (Secat), RGM 395 404. a, dorsal. b, right lateral view.

Cavolinia zamboninii Checchia-Rispoli, 1921

Fig. 7. Saint-Martin-de-Hinx (Secat), RGM 541 058. Dorsal view.

Diacrolinia aurita (Bellardi, 1873)

Fig. 8. Saint-Martin-de-Hinx (Secat), MNHN A32125. a, dorsal. b, left lateral. c, ventral view (specimen in pre-metamorphosis stage).

Diacrolinia cluzaudi sp. nov.

Fig. 9. Meilhan (Vives), holotype, FSUB (A. Cluzaud collection) typothèque 52-4-8. a, dorsal. b, right lateral. c, larval shell part from ventral. d, identical from right lateral.

Fig. 10. Meilhan (Vives), paratype, FSUB (A. Cluzaud collection) typothèque 52-4-9. a, dorsal. b, right lateral. c, ventral view.

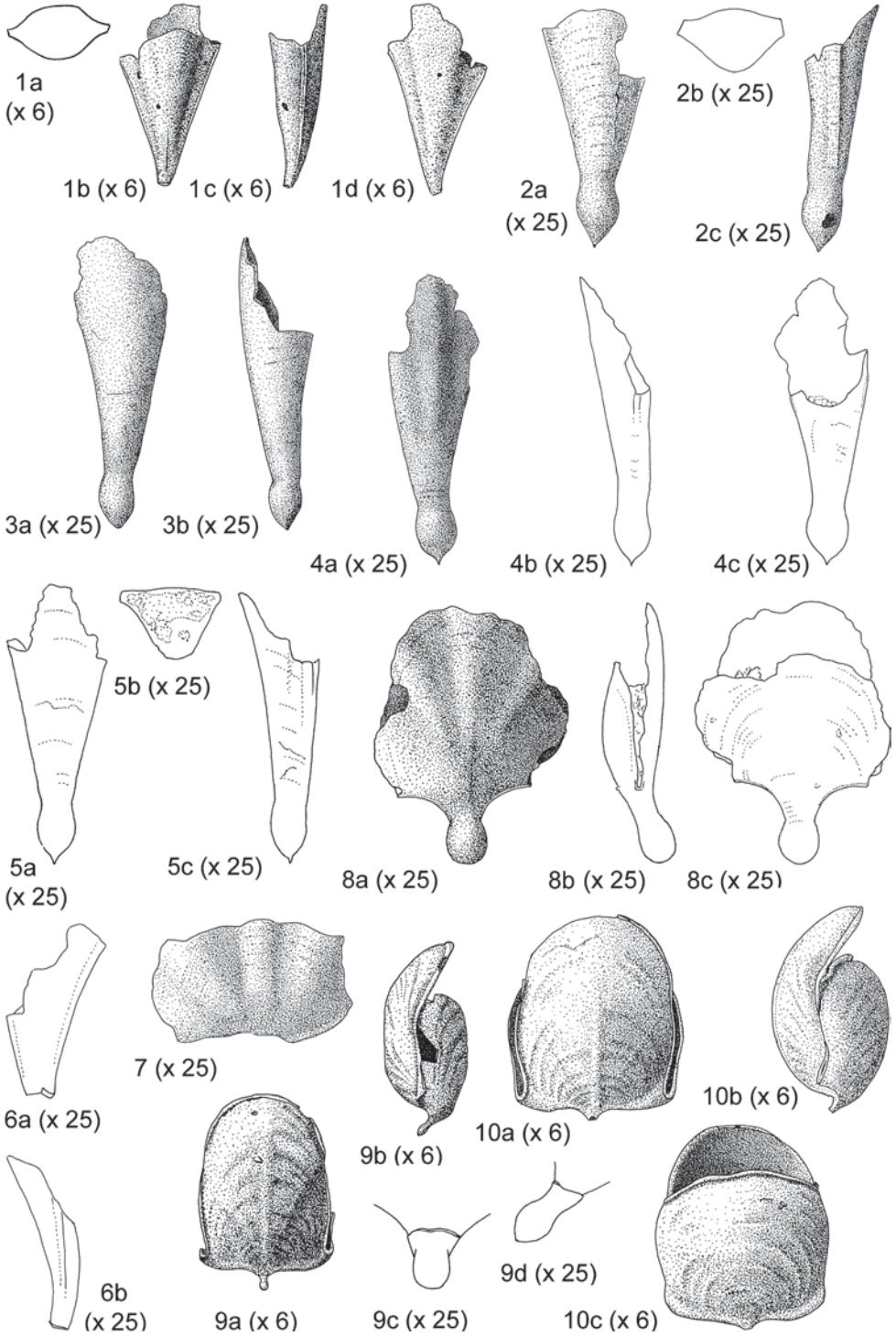


Plate 23

Diacrolinia aquensis (Grateloup, 1827)

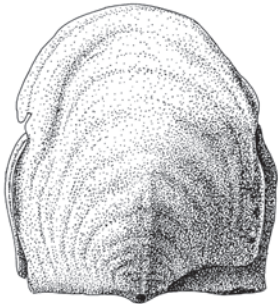
Fig. 1. Saucats (Coquillière), neotype, RGM 541 320. a, dorsal. b, left lateral, c, ventral view.

Diacrolinia orbigny (Rang, 1827)

Fig. 2. Saint-Paul-lès-Dax (Cabanes), neotype, MNHN-A28097, P. Lozouet collection. a, dorsal. b, left lateral, c, ventral view.

Fig. 3. Saint-Paul-lès-Dax (Cabanes), RGM 541 375. a, dorsal. b, right lateral, c, ventral view.

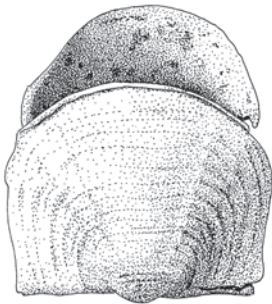
Fig. 4. Saint-Paul-lès-Dax (Cabanes), RGM 541 374. a, dorsal. b, left lateral, c, ventral view (same specimen as Plate 24, fig. 1).



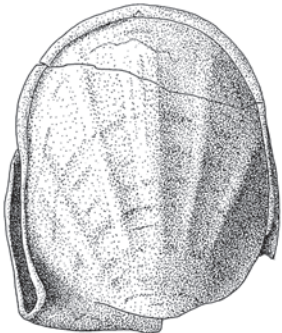
1a (x 6)



1b (x 6)



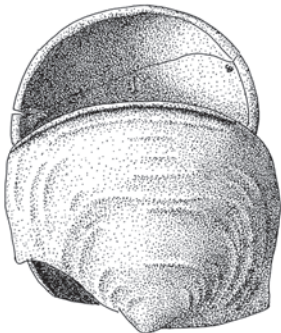
1c (x 6)



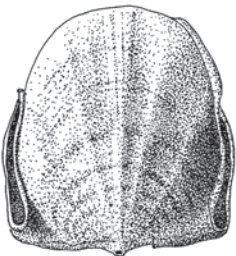
2a (x 6)



2b (x 6)



2c (x 6)



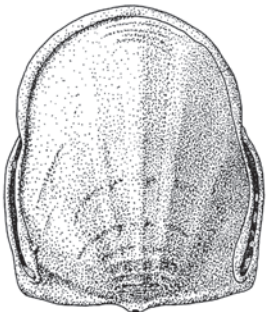
3a (x 6)



3b (x 6)



3c (x 6)



4a (x 6)



4b (x 6)



4c (x 6)

Plate 24

Diacrolinia orbigny (Rang, 1827)

Fig. 1. Saint-Paul-lès-Dax (Cabanes), RGM 541 374. a, adapical. b, adapertural view (same specimen as Pl. 23, fig. 4).

Fig. 2. Saint-Paul-lès-Dax (Cabanes), RGM 541 361. a, left lateral. b, ventral view.

Edithinella caribbeana (Collins, 1934)

Fig. 3. Salles (Moulin Ruiné), RGM 393 122. a, dorsal. b, right lateral. c, ventral view.

Edithinella varanica (Sirna, 1968)

Fig. 4. Orthez (Le Paren), SMF 332812/1. a, frontal. b, right lateral. c, apertural view.

Gamopleura taurinensis (Michelotti, 1847)

Fig. 5. Meilhan (Vives), FSUB (A. Cluzaud collection) typothèque 52-4-10. a, ventral. b, right lateral view.

Vaginella austriaca Kittl, 1886

Fig. 6. Saint-Jean-de-Marsacq (Lahitet), MNHN A32127. a, ventral. b, left lateral view.

Fig. 7. Saint-Jean-de-Marsacq (Lahitet), MNHN A32128. a, apical shell part from left lateral. b, identical from ventral.

Vaginella chattica R. Janssen, 1979

Fig. 8. Peyrehorade (Peyrère), FSUB typothèque 23-4-18, Peyrot collection. a, ventral. b, left lateral. c, dorsal view.

Vaginella depressa Daudin, 1800

Fig. 9. Léognan, neotype, MNHN A28096 (ex RGM 396 088, old collection). a, apertural. b, ventral. c, left lateral. d, dorsal view.

Fig. 10. Martillac (Barreau), RGM 227 565, specimen in premetamorphosis stage. a, ventral. b, apertural. c, left lateral view.

Fig. 11. Uzeste (Gamachot), RGM 396 115, apical shell part showing wrinkles. a, lateral. b, frontal view.

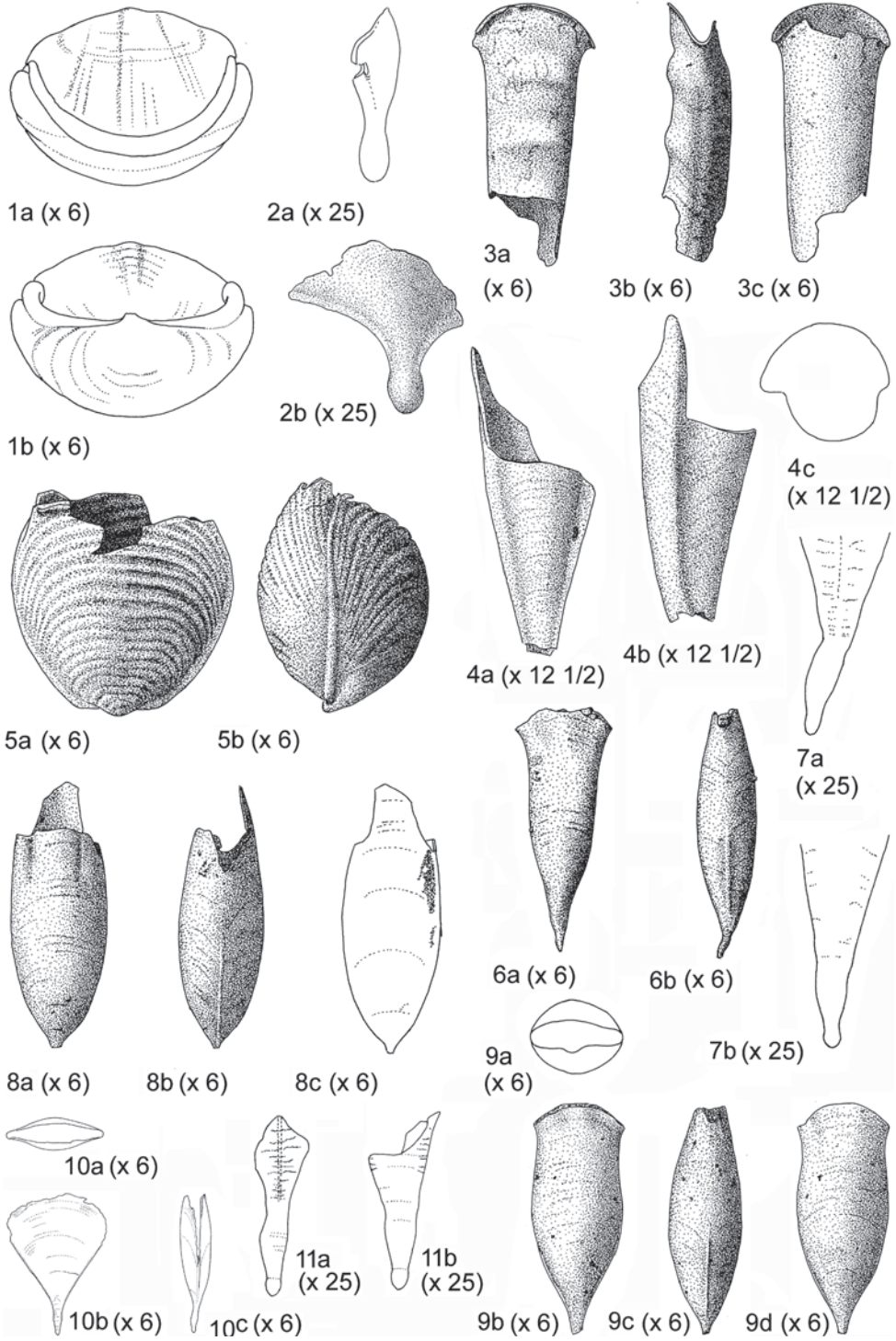


Plate 25

Vaginella depressa Daudin, 1800

Léognan (Coquillat), MBB unnumbered, ventral or dorsal views of 30 selected specimens to demonstrate variability, from sample of 6,022. Specimens are arranged according to increasing H/W-ratio, all magnified $\times 6$.

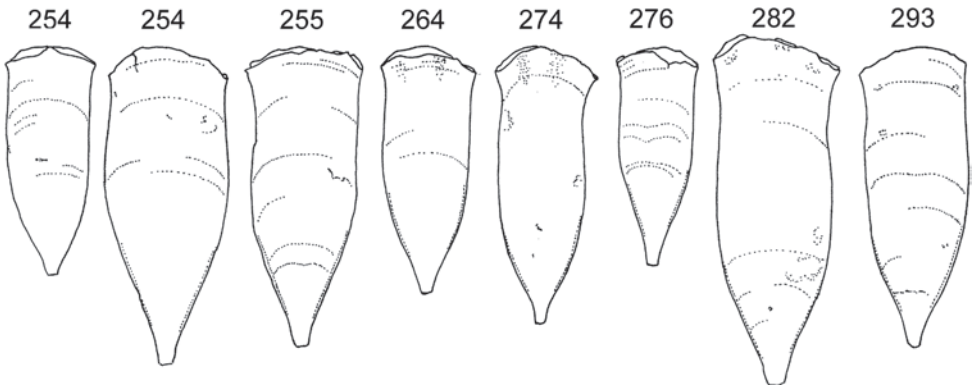
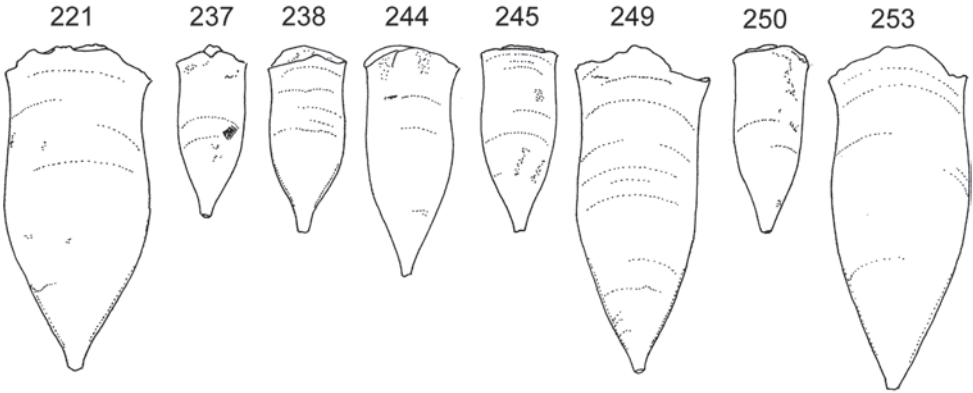
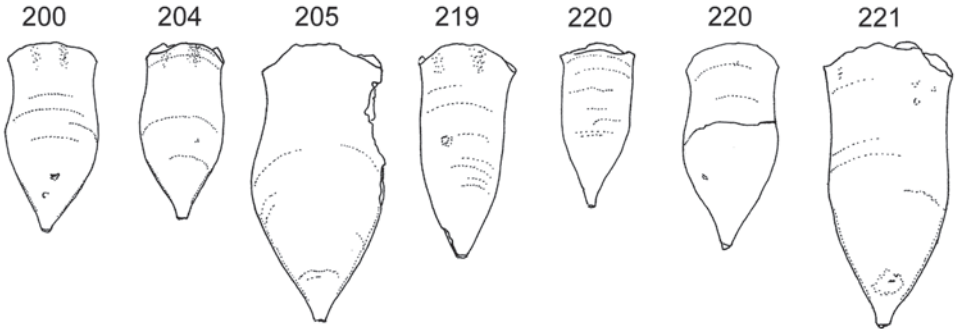
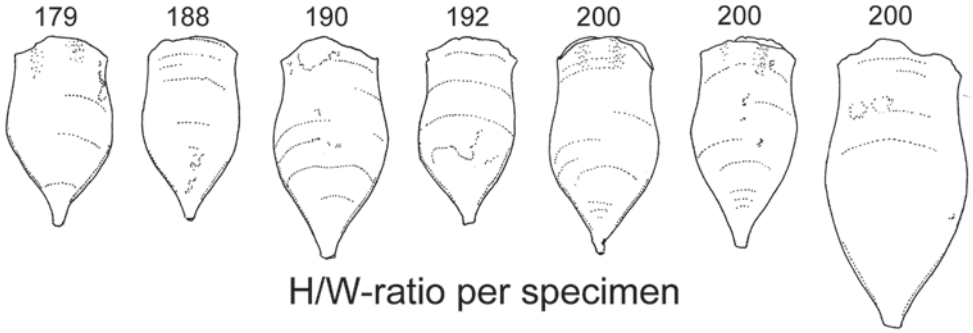


Plate 26*Vaginella depressa* Daudin, 1800

Fig. 1. Cestas (Pré-Cazeaux), FSUB typotheque 33-4-9, A. Magne collection. a, ventral. b, right lateral. c, dorsal view.

Fig. 2. Martillac (Barreau), RGM 227 568. a, apertural. b, ventral. c, left lateral view.

Fig. 3. Saint-Paul-lès-Dax (Cabanes), RGM 396 094. a, ventral. b, left lateral view.

Fig. 4. Uzeste (Gamachot), RGM 396 116, apical shell part with larval shell and wrinkles at the side of the basal teleoconch. a, ventral. b, left lateral view.

Fig. 5. Saucats (Pont-Pourquey), MNHN A32129, transitional to *V. austriaca*. a, ventral. b, left lateral view.

Vaginella gaasensis sp. nov.

Fig. 6. Gaas (Espibos), holotype, RGM 541 402. a, apertural. b, ventral. c, left lateral. d, dorsal view.

Vaginella lapugyensis Kittl, 1886

Fig. 7. Saint-Martin-de-Hinx (Secat), MNHN A32130, apical fragment with larval shell. a, apertural. b, ventral. c, right lateral view.

Fig. 8. Saint-Martin-de-Hinx (Secat), MNHN A32131. a, apertural. b, ventral. c, left lateral view.

Vaginella tricuspidata Zorn & Janssen, 1993

Figs. 9 (holotype), 10-13 (paratypes). Saint-Etienne-d'Orthe (Lartigaou). 9-11, 13. ventral views. 12. dorsal view.

Vaginella cf. *tricuspidata* Zorn & Janssen, 1993

Fig. 14. Saint-Paul-lès-Dax (Estoti), apical shell part, FSUB (A. Cluzaud collection) typotheque 32-4-37. a, frontal. b, apertural. c, lateral view.

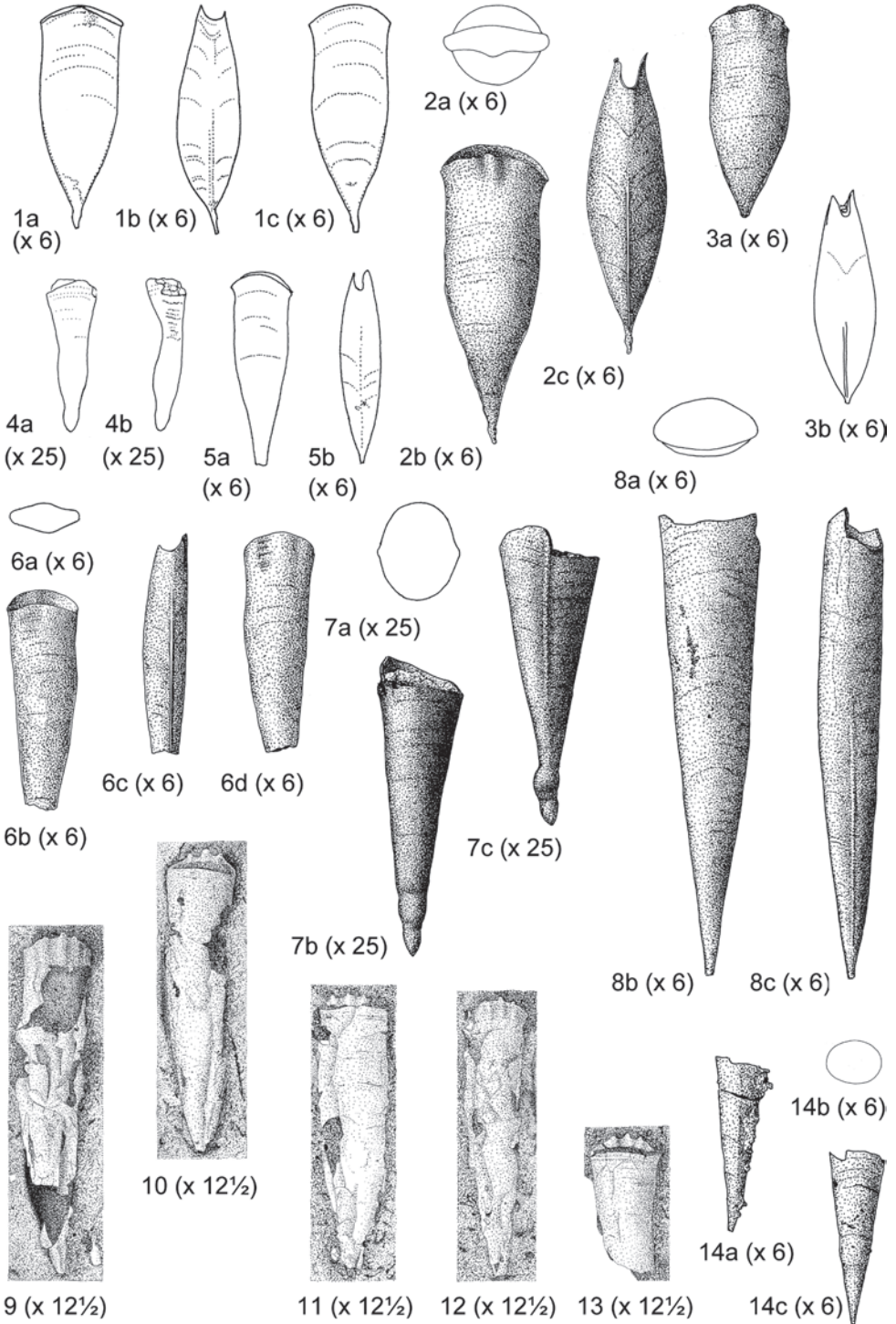


Plate 27

Vaginella victoriae A.W. Janssen, 1990a

Fig. 1. Saint-Paul-lès-Dax (Cabanes), RGM 541 366. a, apertural. b, ventral. c, left lateral. d, dorsal view. e, detail of apertural margin.

Fig. 2. Saint-Paul-lès-Dax (Cabanes), FSUB (A. Cluzaud collection) typothèque 25-4-10. a, apertural. b, dorsal. c, right lateral. d, ventral view.

Fig. 3. Saint-Paul-lès-Dax (Cabanes), MNHN A32132. a, left lateral. b, dorsal. c, apertural. d, ventral view.

Hameconia edmundi A. W. Janssen, 2008b

Fig. 4. Saint-Etienne-d'Orthe (Lartigaou), holotype, RGM 541 444. a, left lateral. b, frontal view (with dorsal side of larval shell and ventral side of teleoconch visible).

Peracle sp.

Fig. 5. Saint-Etienne-d'Orthe (Église C), MNHN A32136. a, apertural. b, apical. c, lateral view.

Gymnosomata sp.

Fig. 6. Saint-Paul-lès-Dax (Cabanes), RGM 541 367. Frontal view.

