The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, north west France), 2. Caenogastropoda*

Frank Van Dingenen[1], Luc Ceulemans[2] & Bernard M. Landau[3, 4]

[1] *Cambeenboslaan A 11, B-2960 Brecht, Belgium; email: fvd@telenet.be*
[2] *Avenue Général Naessens de Loncin 1, B-1330 Rixensart, Belgium; email: luc.ceulem@skynet.be*
[3] *Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands; Instituto Dom Luiz da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal; and International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal; email: bernielandau@sapo.pt*
[4] *Corresponding author*

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In this paper we review the Caenogastropoda of the Zanclean lower Pliocene assemblage of Le Pigeon Blanc, Loire-Atlantique department, which we consider the 'type' locality for Assemblage III of Van Dingenen *et al*. (2015). Ninety-one species are recorded, of which 17 are new: *Bittium lozoueti* nov. sp., *Bittium gliberti* nov. sp., *Tympanotonos redoniensis* nov. sp., *Oligodia palumbina* nov. sp., *Cochlis robbai* nov. sp., *Cochlis pedrialii* nov. sp., *Payraudeautia pigeonblancensis* nov. sp., *Alvania calasi* nov. sp., *Alvania dissensia* nov. sp., *Alvania merlei* nov. sp., *Alvania zbyszewskii* nov. sp., *Crisilla ariejansseni* nov. sp., *Rissoa pouweri* nov. sp., *Caecum aartseni* nov. sp., *Nystia guillotini* nov. sp., *Aclis pacaudi* nov. sp., *Niso dollfusi* nov. sp. This includes the first European Neogene record for the genus *Tympanotonos*. *Macromphalina bouryi* (de Morgan, 1915) is a secondary homonym of *Macromphalina bouryi* (Dautzenberg, 1912) and renamed *Macromphalina massicardi* nom. nov. Based on the data presented here, we suggest that average Sea Surface Temperatures off the NW French coast in the Zanclean early Pliocene may have been warmer than they are at these latitudes today, possibly similar to those found today off the southern Portuguese coasts.

Key words: northwestern France, lower Pliocene, Caenogastropoda, new taxa

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al*., 2014, 2016; Van Dingenen *et al*., 2014, 2015). Gastropods of the subclass Caenogastropoda are revised, and the study is restricted to the locality of Le Pigeon Blanc, which we consider to be the 'type locality' for Assemblage III of Van Dingenen *et al*., 2015.
In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded 42 Caenogastropoda species from Le Pigeon Blanc, some of which were described as new. However, as the thesis was never published, these names do not comply with article 13 of the ICZN code (1999) and must be considered *nomina nuda*.

Geological setting and Material and methods

(see Ceulemans *et al*., 2016, pp. 51-52).

Abbreviations:

MNHN.F	Muséum national d'Histoire naturelle (collection de Paléontologie), Paris (France).
NHMW	Naturhistorisches Museum Wien collection, Vienna (Austria).
FVD	Frank Van Dingenen private collection, Brecht (Belgium).
LC	Luc Ceulemans private collection Rixensart (Belgium).

* For nr 1 in this series see Ceulemans et al. (2016), *Cainozoic Research* 16(1): 51-100.
For nr 3 in this series see Ceulemans, L., Van Dingenen, F., Merle, D. & Landau, B.M. 2016. The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, northwest France). Part 3 – Muricidae. *Vita Malacologica* 15: 35-55.

Correction: In part 3 of this series, p. 45 paratype 1 of *Ocinebrina lauriatrageae* numbered A35352, should read A57352.

Systematic palaeontology

Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Cerithiidae Fleming, 1822
Subfamily Cerithiinae Fleming, 1822
Genus *Thericium* Monterosato, 1890

Type species (by original designation) – *Cerithium vulgatum* Bruguière, 1792, present-day, Mediterranean.

1890 *Thericium* Monterosato, p. 163.
1895a *Vulgocerithium* Cossmann *in* Sacco, p. 77. Type species (by subsequent designation, Cossmann, 1906): *Cerithium vulgatum* Bruguière, 1792, present-day, Mediterranean.

Thericium bronni (Hörnes, 1856)

Plate 1, figs 1-3

1854 *Cerithium Inconditum* Millet, p. 163 (*nomen nudum*).
*1856 *Cerithium Bronni* Partsch, Hörnes, p. 407, pl. 42, fig. 12.
1865 *Cerithium inconditum* Millet, p. 594.
1889 *Cerithium heptagonum* Mayer-Eymar, p. 207, pl. 5, fig. 7.
1895a *Cerithium* (*Ptychocerithium*) *Bronni* var. *tauroplanata* Sacco, p. 26, pl. 2, figs 43, 44.
1895a *Cerithium* (*Ptychocerithium*) *Bronni* var. *transiens* Sacco, p. 26, pl. 2, fig. 45.
1906 *Cerithium* (*Ptychocerithium*) *Bronni* Partsch – Cossmann, p. 81, pl. 4, fig. 2.
1911 *Cerithium* (*Ptychocerithium*) *Bronni* Partsch – Vignal, p. 148, pl. 7, fig. 8.
1921 *Cerithium* (*Ptychocerithium*) *heptagonum* (Mayer-Eymar) – Cossmann & Peyrot, p. 204, pl. 5, figs 74, 75.
1949 *Cerithium* (*Ptychocerithium*) *bronni heptagonum* Mayer, 1889 – Glibert, p. 147, pl. 9, fig. 11.
1964 *Cerithium* (*Ptychocerithium*) *bronni* Partsch *in* Hörnes, 1845 – Brébion, p. 239, pl. 6, figs 16-20.
1998 *Cerithium* (*Ptychocerithium*) *bronni* Partsch – Schultz, p. 58, pl. 22, fig. 2.

Material and dimensions – Maximum height 28.4 mm (all incomplete). NHMW 2015/0133/0203-0205 (3), NHMW 2015/0133/0103 (4); LC (10); FVD (12). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Cossmann & Peyrot (1921) separated the Atlantic lower and middle Miocene specimens under the name *Cerithium* (*Ptychocerithium*) *heptagonum* from *Thericium bronni* (Hörnes, 1856) based on the shells being smaller, thinner and more elongated, and on small sculptural details. Glibert (1949) considered them a subspecies of *T. bronni*, the only constant difference between them being the smaller size of the Atlantic specimens. Brébion (1964) stressed the enormous variability in the material he had at hand and pointed out that some NW French specimens were larger than those from the Paratethys, and concluded that it was not easy to characterise *T. bronni*. However, if the Atlantic form should turn out to be distinct from that of the Paratethys, the name *Cerithium inconditum* Millet, 1865 has priority over *Cerithium heptagonum* Mayer-Eymar, 1889, at least for the Assemblage I populations.
Based on the scant and imperfectly preserved material from Le Pigeon Blanc, we echo Brébion's conclusion. Each of the fragments at hand varies slightly in spiral angle, sculpture, number of axial ribs and their development. We also agree with the above authors that we cannot separate them from the Paratethian shells.
Brébion (1964, p. 241) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, Chalonnes, Reneauleau, Beaulieu) and Assemblage III (Le Pigeon Blanc, Palluau). The latter Zanclean records are the stratigraphically earliest for the species.

Distribution – Lower Miocene: Atlantic (Burdigalian), Aquitaine Basin, France (Vignal, 1911; Cossmann, 1906; Cossmann & Peyrot, 1921); Proto-Mediterranean, Italy (Sacco, 1895a). Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949), Aquitaine Basin, France (Cossmann & Peyrot, 1921); Paratethys, Austria (Hörnes, 1856; Schultz, 1998). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Genus *Colina* H. Adams & A. Adams, 1854

Type species (by subsequent designation, Cossmann, 1889) – *Cerithium macrostoma* Hinds, 1844, present-day, Indonesia.

1854 *Colina* H. Adams & A. Adams, p. 286.

Note – At Le Pigeon Blanc, material ascribed to the genus *Colina* H. Adams & A. Adams 1854 by Brébion (1964) is fragmentary. In the Assemblage I localities this material is more plentiful and better preserved. Whether these NW French Atlantic Miocene and Pliocene species are monophyletic with the present-day *Cerithium macrostoma* Hinds, 1844, type species of the genus *Colina*, is doubtful. Some of the French specimens have strongly varicose later adult whorls, which distort the shell and sculpture. It is also possible that these shells are not members of the Cerithiidae Fleming, 1822, but Cerithiopsidae Forbes & Hanley, 1850, as the sculpture is also similar to that of members of the genus *Krachia* Bałuk, 1975 (see Bouchet & Warén, 1993, p. 605). We hope that the better preserved material from Assemblage I will have the protoconch preserved, which would help us place these shells. Provisionally they are recorded here, but will be discussed and compared in more detail in the paper covering Assemblage I localities.

***Colina jucunda* (Millet, 1865)**
Plate 1, figs 4-7

1854 *Cerithium Jucundum* Millet, p. 163 (*nomen nudum*).
*1865 *Cerithium jucundum* Millet, p. 594.
1964 *Colina jucunda* Millet, 1854 [*sic*] – Brébion, p. 236, pl. 6, figs 13-14.

Material and dimensions – Maximum height 13.2 mm (incomplete). NHMW 2015/0133/0277-0279 (2 fragments); LC (40 fragments); FVD (31 incomplete/fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Colina jucunda* (Millet, 1865) is characterised by having flat-sided whorls, sculpture consisting of narrow close-set ribs and four or five subequal spiral cords on each whorl, with small tubercles develop at the sculptural intersections. The last two adult whorls become strongly varicose and inflated, distorting the shell shape and further spiral ribs develop on this inflated portion (Pl. 1, fig. 4).
Colina jucunda differs from *C. puymoriae* (Mayer, 1862), from the middle Miocene Loire Basin of France, in having flattersided whorls, finer sculpture, with four or more cords on intermediate spire whorls, whereas in *C. puymoriae* only the penultimate and last whorl have four cords. In both species the fourth cord appears between the first and second cord. Neither the specimen of *C. puymoriae* figured by Glibert (1949, pl. 9, fig. 9), nor specimens at hand from Thenay (Loire-et-Cher, France) show any varices.
Millet (1865, p. 595) recorded this species from from Assemblage I (Reneauleau, Sceaux-d'Anjou, Thorigné). Brébion (1964, p. 238) added several further Assemblage I localities (St-Michel, Les Pierres Blanches, Chalonnes, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné, Le Temple du Cerisier, Moulin de Carcé) and Assemblage III (Le Pigeon Blanc, Le Girondor, La Gauvinière, La Dixmerie, Palluau).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Colina petitiana* (Millet, 1865)**
Plate 1, fig. 8

1854 *Cerithium Petitianum* Millet, p. 164 (*nomen nudum*).
*1865 *Cerithium Petitianum* Millet, p. 595.
1964 *Colina petitiata* Millet, 1854 [*sic*] – Brébion, p. 235, pl. 6, figs 11-12.

Material and dimensions – Maximum height 13.0 mm (incomplete). NHMW 2015/0133/0280 (1 fragment); LC (2 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Colina petitiana* (Millet, 1865) is characterised by having sculpture consisting of narrow close-set ribs and five or six spiral cords on each whorl, the 3-4 adapical cords weaker, often alternate in strength, the abapical two cords more strongly developed and having prominent tubercles at the sculptural intersections.
Millet (1865, p. 595) recorded this species from Assemblage I (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Michel). Brébion (1964, p. 238) added several further Assemblage I localities (Les Pierres Blanches, St-Clément-de-la-Place).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Subfamily Bittiinae Cossmann, 1906
Genus *Bittium* Gray, 1847

Type species (by subsequent designation, Gray, 1847b [November]) – *Strombiformis reticulatum* Da Costa, 1778, present-day, Europe.

1847a *Bittium* Gray, p. 270 [October].
1869 *Cerithiolum* Tiberi, p. 263. Type species (by subsequent designation, Houbrick, 1993): *Strombiformis reticulatum* Da Costa, 1778, present-day, Europe.
1917 *Inobittium* Monterosato, p. 20. Type species (by monotypy): *Cerithium lacteum* Philippi, 1836, present-day, Europe.
1917 *Manobittium* Monterosato, p. 20. Type species (by original designation): *Cerithium latreillii* Payraudeau, 1826, present-day, Europe.
1971 *Dahlakia* Biggs, p. 221. Type species (by original designation): *Dahlakia leilae* Biggs, 1971 [= *Bittium proteum* (Jousseaume, 1930)], present-day, Red Sea.
1976 *Rasbittium* Gründel, p. 53. Type species (by original designation): *Cerithium latreillii* Payraudeau, 1826, present-day, Europe. Junior objective synonym of *Manobittium*.
1976 *Scabrobittium*, Nordsieck, p. 8. Type species (by original designation): *Murex scabrum* Olivi, 1792, present-day, Mediterranean.

Note – The genus is well represented in the Le Pigeon Blanc assemblage by five species that are impossible to confuse. The greatest affinity is with the Plio/Pleistocene of the North Sea Basin and the Atlantic British Isles with which it shares two species, with no affinity with any Atlantic or Mediterranean fossil assemblages further south. It is interesting that three out of the five species, in which the protoconch is known, they are all paucispiral, whereas today most *Bittium* species have multispiral protoconchs. Paucispiral protoconchs are suggestive of non-planktotrophic larval development, which is associ-

ated with stratigraphically short-lived and geographically narrowly distributed species. This may explain the endemicity of these NW French Zanclean *Bittium* species.

***Bittium courtillerianum* (Millet, 1865)**
Plate 1, fig. 9; Plate 2, fig. 4

1854	*Cerithium Courtillerianum* Millet, p. 164 (*nomen nudum*).
*1865	*Cerithium courtillerianum* Millet, p. 595.
1907	*Cerithium courtillerianum* Millet – Couffon, p. 192.
1915	*Cerithium courtillerianum* Millet – Couffon, p. 46.
1964	*Bittium reticulatum* var. *courtillerianum* Millet, 1854 (emend) [*sic*] – Brébion, p. 225, pl. 5, figs 24-26.

Material and dimensions – Maximum height 10.5 mm. NHMW 2015/0133/0104 (1), NHMW 2015/0133/0111 (1), NHMW 2015/0133/0105 (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Bittium courtillerianum* (Millet, 1865) is characterised by its paucispiral protoconch composed of 1.5-1.75 whorls, with a large bulbous nucleus (dp = 290 μm), its teleoconch consists of about ten straight-sided whorls, with spiral sculpture consisting of narrow, elevated, rounded cords, two on the first two teleoconch whorls, a third appearing above the upper cord on the third, quickly gaining in strength to become equal to the earlier cords, and axial sculpture consisting of about 13 slightly opisthocline rounded ribs, about equal in width to their interspaces, forming an evenly reticulated sculpture. Small rounded knobs are developed at the sculptural intersections. The concave base is sharply delimited by two peribasal cords, with a bifid periumbilical cord.
Couffon (1907) considered *Cerithium courtillerianum* a synonym of *B. scabrum* (Olivi, 1792) and later (1915) of *B. reticulatum* (Da Costa, 1778). We note that *B. scabrum* is now considered a junior synonym of *B. reticulatum* (Gofas, 2015a). Brébion (1964, p. 225) considered this taxon a subspecies of *B. reticulatum* with three instead of four primary spirals, but *B. reticulatum* has a multispiral protoconch (van der Linden & Wagner, 1990). It is with *Bittium lacteum* (Philippi, 1836) that this species has the closest affinity, with which it shares the characters of a paucispiral protoconch and three primary spiral cords. Brébion (1964, p. 225) did compare his material with *B. lacteum*, saying it was very similar, but differed in having less regular sculpture with less prominent tubercles formed at the intersection and pointed out differences in the strength and disposition of the basal cords. It is indeed true and consistent that the cords are narrower and the tubercles less strongly developed than in the lower upper Pliocene shell illustrated by Landau *et al*. (2004a, pl. 2, fig. 2) from Estepona, southern Spain or the present-day shells illustrated by Giannuzzi-Savelli *et al*. (1996, fig. 75). In these specimens the sculpture is predominantly tuberculose, whereas in the French fossil shells the sculpture is openly reticulated, with the spiral sculpture very slightly predominant. There are also slightly fewer axial ribs in the French shells than in any *B. lacteum* seen, which is the cause of the more open reticulation. It is also true that the tubercles formed at the intersections are far smaller in the French fossil shells than in any *B. lacteum* seen.
Bittium lacteum has an inexplicably poor fossil record. Even the recent revision by Chirli (2006) on the Italian Pliocene did not report this species in the Mediterranean. In the extant Atlantic faunas we have not been able to find any reliable records for *B. lacteum* north of Portugal. This French fossil form is also present in the stratigraphically younger NW French Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la Place; NHMW coll.) and Brébion (1964, p. 226) reported it from Assemblages I-IV. In view of the shell differences described above, the chronological gap (with exception of the Assemblage IV records that need to be verified) and the geographical separation, these NW French specimens could be considered a subspecies of *B. lacteum*. However, their presence in the Assemblage IV localities would signify a stratigraphical overlap. Moreover, we cannot be certain of a direct phylogenetic link between the two forms. We therefore prefer to consider them distinct at full species rank, the NW French form being *Bittium courtillerianum* (Millet, 1865).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Bittium crassicostatum* (Etheridge & Bell *in* Bell, 1898)**
Plate 1, fig. 10

*1898	*Cerithium* (*Bittium*) *reticulatum* var. *crassicostata* Etheridge & Bell *in* Bell, p. 143.
1920	*Bittium crassicostatum* (Etheridge & Bell) – Harmer, p. 525, pl. 47, fig. 4.
1964	*Bittium crassicostatum* Etheridge & Bell, 1898 – Brébion, p. 229, pl. 5, figs 32, 33.

Material and dimensions – Maximum height 9.4 mm (incomplete). NHMW 2015/0133/0106 (1), NHMW 2015/0133/0107 (5); LC (13); FVD (5). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Bittium crassicostatum* (Etheridge & Bell *in* Bell, 1898) is quite unlike most of its European congeners in having predominantly axial sculpture composed of only five or six very broad, rounded axial ribs, roughly aligned along the shell axis, but interrupted by the suture. The spiral sculpture is subordinate, but also composed of relatively broad cords, which overrun the axial ribs. The only significant difference between the shells from

Le Pigeon Blanc and the specimen from St. Erth figured by Harmer (1920, pl. 47, fig. 4) is that the French shells have slightly more opisthocline axial ribs, which tend to broaden towards the abapical suture, but these differences are minor. The only species with which *B. crassicostatum* can be compared is *B. robustum* Harmer, 1918 from the upper Pliocene Red Crag of England, but also reported from Belgium (Glibert, 1958, p. 6, pl. 2, fig. 2), but this is a much larger-shelled species, with more numerous axial ribs (11-14 vs. 5-6). *Bittium crassicostatum* was recorded by Brébion (1964, p. 230) only from Le Pigeon Blanc.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964). Lower Pleistocene: St. Erth, England (Bell, 1898; Harmer, 1920).

***Bittium lozoueti* nov. sp.**
Plate 1, figs 11-14; Plate 2, fig. 5

1964 *Bittium reticulatum* var. *lecointrei* nov. var. Brébion, p. 227, pl. 5, figs 27, 28 (*nomen nudum*).

Type material – Holotype MNHN.F.A53621, height 11.0 mm; paratype 1 MNHN.F.A53622, height 9.1 mm; paratype 2 NHMW 2015/0133/0108, height 9.7 mm, paratype 3 NHMW 2015/0133/0115, height 10.6 mm; paratype 4 NHMW 2015/0133/0116, height 11.2 mm; paratype 5 NHMW 2015/0133/0109, height 8.5 mm.

Other material – Maximum height 10.0 mm. NHMW 2015/0133/0110 (20); FVD (17). Type locality.

Etymology – Named for Pierre Lozouet of the MNHN (Paris), in recognition of his work on French fossil gastropods. *Bittium* gender neuter.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Bittium* species with a paucispiral protoconch, two spiral cords on first teleoconch whorl, a third appearing adapically on second whorl, a fourth cord between cords 1 and 2 on third whorl, a fifth between cords 1 and 2 on penultimate whorl, axial sculpture of about 13 narrow ribs, small tubercles developed at the intersections, and a base with two peribasal cords and a further 4-5 cords medially.

Description – Shell small, turriculate, with tall, slender spire. Protoconch consisting of 1.5-2 convex whorls, with large nucleus (dp= 322 μm). Junction with teleoconch sharply delimited. Teleoconch consisting of 10-11 convex whorls, with periphery mid-whorl. Suture superficial. Spiral sculpture consisting of elevated, rounded cords, two on first teleoconch whorl, a third appears above upper cord on second, a fourth cord between cords 1 and 2 on third teleoconch whorl. From third teleoconch whorl a further narrower cord placed immediately above suture. On penultimate whorl a further cord appears adapically between cords 1 and 2. Axial sculpture consisting of about 13 slightly prosocline narrow rounded ribs, about half the width of their interspaces. Spiral sculpture overruns axial ribs, forming small rounded knobs at intersections. Last whorl convex, strongly constricted at base, bearing five cords above peribasal cord, cord 2 being weaker, the rest subequal in strength. Last whorl bearing a single varix in most specimens, occasional specimens with a further varix on penultimate or third from last whorl. Base imperforate, concave, bearing two peribasal cords and a further 4-5 non-beaded cords. Aperture ovate, outer lip thin, convex, ending in short siphonal canal. Columella slightly thickened, almost rectilinear. Columellar callus narrow, closely appressed.

Discussion – It is quite understandable that Brébion (1964, p. 227) considered this a subspecies of *Bittium reticulatum* (Da Costa, 1778), as the teleoconch sculpture is superficially similar. However, if the criteria considered to be important in distinguishing *Bittium* species are used; *i.e.* 1) protoconch type, 2) number of spiral cords, 3) order in which they appear (Landau *et al*., 2004a, p. 10), this position is untenable. The French fossil species has a paucispiral protoconch, whereas in *B. reticulatum* it is multispiral (van der Linden & Wagner, 1990). Indeed, the character of the protoconch separates *Bittium lozoueti* nov. sp. from most of the other present-day congeners such as *B. latreillei* (Payraudeau, 1826), *B. reticulatum* (Da Costa, 1778) [= *B. scabrum* (Olivi, 1792)], *B. jadertinum* (Brusina, 1865), which all have a multispiral protoconch (van der Linden & Wagner, 1990). Specimens at hand of *Bittium miocaenicum* Peyrot, 1938 from the middle Miocene Loire Basin (Thenay; NHMW coll.) have a protoconch of just over two whorls with a smaller nucleus than either *B. courtillerianum* (Millet, 1865) or *B. lozoueti* nov. sp. Its teleoconch sculpture is similar to that of *B. reticulatum*, with four primary spiral cords, but *B. reticulatum* has three protoconch whorls.
Bittium larieyensis Vignal, 1911 from the lower Miocene Aquitanian of France is similar in having five spiral cords on the last whorls, but in this species the fifth cord appears above the suture on the fifth whorl as opposed to between cords 1 and 2 on the penultimate whorl. Specimens at hand from Corbleu (Landes, France), do not have the protoconch well preserved, but it seems to be composed of more than two whorls.
Brébion (1964, p. 227) recorded this species only from the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Bittium gliberti* nov. sp.**
Plate 2, figs 1-3, 6

1964 *Bittium turritelloides* Dollfus mss. – Brébion, p. 230, pl. 6, figs 1-5 (*nomen nudum*).

Type material – Holotype MNHN.F.A53623, height 10.5 mm; paratype 1 MNHN.F.A53624, height 10.7 mm; paratype 2 MNHN.F.A53625, height 9.4 mm; paratype 3 MNHN.F.A53626, height 7.5 mm; paratype 7 NHMW 2015/0133/0112, height 12.8 mm, paratype 8 NHMW 2015/0133/0113, height 8.7 mm; paratype 9 NHMW 2015/0133/0201, height 11.5 mm; paratype 10 NHMW 2015/0133/0202, height 9.7 mm.

Other material – Maximum height 12.7 mm. NHMW 2015/0133/0114 (50+); FVD (50+). Type locality.

Etymology – Named for Maxime Glibert (1905-1984), curator at the Institut Royal des Sciences Naturelles de Belgique (Brussels), in recognition of his enormous contribution to European Cainozoic molluscan taxonomy. *Bittium* gender neuter.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Bittium* species with a paucispiral protoconch, three spiral cords on first teleoconch whorl, further cords added abapically, later teleoconch whorls with 7-10 irregular cords, axial sculpture of about 13 narrow ribs weakening abapically and absent on last two whorls in many specimens, without tubercles formed where the spiral cords overrun the ribs, and a poorly delimited base bearing spiral cords.

Description – Shell small, turriculate, with tall, slender spire. Protoconch consisting of 1.5 convex whorls, with large nucleus (dp = 290 μm). Junction with teleoconch sharply delimited. Teleoconch consisting of 12 convex whorls, with periphery below mid-whorl. Suture impressed. Spiral sculpture consisting of elevated cords, three on first teleoconch whorl, mid-cord slightly wider; a fourth cord appears between cord 1 and 2 on third whorl; a fifth cord between cords 3 and 4 on fourth whorl; two further cords on whorl five, one between cords 1 and 2, one between cords 2 and 3. In some specimens cords become subequal in strength and disposition, so that subsequent spire whorls bear seven subequal cords, in others further cords appear irregularly in interspaces on penultimate and last whorls. Axial sculpture consisting of 8-10 narrow, opisthocline ribs weakening abapically, obsolete, or almost so on last three whorls in some specimens, in others continuing onto last whorl. Spiral sculpture overruns axial ribs without forming tubercles at intersections. Last whorl evenly convex, hardly constricted at base, bearing 7-10 cords above base, with secondary cords in some interspaces in some specimens. A varix present on last whorl in some specimens. Base imperforate, concave, hardly delimited by two peribasal cords and a further 4-5 cords. Aperture ovate, outer lip thin, convex, ending in short siphonal canal. Columella slightly thickened, almost rectilinear. Columellar callus narrow, closely appressed.

Discussion – *Bittium gliberti* nov. sp. is separated from its congeners by having the tallest and most slender shell of all the Le Pigeon Blanc *Bittium* species, and in having subdued axial sculpture that disappears on the last two whorls in many specimens. After the fifth whorl the spiral sculpture is highly variable; some specimens have fewer (minimum 7) relatively broad and flattened, subequal cords separated by narrow interspaces, whilst other have more numerous (up to 10) narrower cords of irregular or alternating strength. The axial sculpture of narrow opisthocline ribs is more regular, but in about half of the specimens weakens and disappears on the last two or three whorls, whilst in half of the specimens the ribs persist onto the last whorl, but not on to the base. *Bittium duvergieri* Cossmann & Peyrot, 1921 from the middle Miocene of the Aquitaine and Loire basins also has predominant spiral sculpture, but differs in having a less slender shell, fewer spiral cords and no axial sculpture.
Brébion (1964, p. 231) recorded this species only from Assemblage III localities (Le Pigeon Blanc, Le Girondor).

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Bittium robustum **Harmer, 1918**
Plate 2, figs 7, 8

*1918	*Bittium robustum* Harmer, p. 417, pl. 41, figs 9, 10.
non 1955	*Bittium robustum* Harmer, 1918 – van Regteren Altena *et al*., p. 30, pl. 6, fig. 60.
1958	*Bittium robustum* Harmer, 1918 – Glibert, p. 6, pl. 2, fig. 1.
2012	*Bittium robustum* Harmer, 1918 – Wesselingh *et al*., p. 41, figs 19-20.

Material and dimensions – Maximum height 15.7 mm (all incomplete). NHMW 2015/0133/0119 (1), 2015/0133/0281 (1), NHMW 2015/0133/0120 (4); LC (9 fragments); FVD (3 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Bittium robustum* Harmer, 1918 is characterised by its unusually large size for the genus, robust shell, deep sutures and coarse sculpture. The specimens from Le Pigeon Blanc are indeed robust and although none of the shells are complete, they have a total reconstructed height of about 17 mm, similar to that of the North Sea Basin specimens. They are, however, slightly different in having more convex whorls and in having a fifth cord on the spire whorls, with, in the occasional specimen, a secondary weaker spiral intercalated in some of the interspaces. In spite of these small differences, this large *Bittium* is so conspicuous amongst its congeners that we provisionally consider them to be a single species.
Harmer (1920, p. 526, pl. 47, fig 5) described a much smaller shell, *B. dissimile*, from the Gelasian Pleistocene of St. Erth, England. Apart from the obvious size difference (maximum height 5 mm vs. 17 mm), the sculpture is identical. We have not seen these shells from St. Erth to

comment further. The shell illustrated by van Regteren Altena *et al*. (1955, pl. 6, fig. 60) as *B. robustum* has a much wider apical angle and a very superficial suture, and does not seem to be this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Upper Pliocene: Red Crag, England (Harmer, 1918); Belgium (Glibert, 1958), The Netherlands (Wesselingh *et al*., 2012).

Family Dialidae Kay, 1979
Genus *Gibborissoia* Cossmann *in* Sacco, 1895

Type species (by original designation) – *Bulimus costellatus* Grateloup, 1828, Miocene, France.

1895b *Gibborissoia* Cossmann *in* Sacco, p. 34.
1915 *Touzinia* Cossmann, p. 62. Type species (by original designation): *Phasianella prevostina* de Basterot, 1825, Miocene, France.
1921 *Gibborissoa* Cossmann, p. 53. Unjustified emendation of *Gibborissoia*.

Note – Lozouet *et al*. (2001, p. 25) stressed that *Phasianella prevostina* de Basterot, 1825 was a synonym of *Bulimus costellatus* Grateloup, 1828 [= *Gibborissoia varicosa* (de Basterot, 1825)]. Therefore, the genus *Touzinia* Cossmann, 1915, which has as type species *P. prevostina* is a synonymy of *Gibborissoia* Cossmann *in* Sacco, 1895b. We would agree with Reid (1989) that the shell is too thin for placement in the Littorinidae Children, 1834, as suggested by Cossmann (1915) and Glibert (1949).

***Gibborissoia morgani* (Cossmann & Peyrot, 1918)**
Plate 2, fig. 9

*1918 *Littorina* (*Touzinia*) *Morgani* Cossmann & Peyrot, p. 435, pl. 17, figs 94, 95.
1949 *Littorina* (*Littorinopsis*) *morgani* Cossmann & Peyrot, 1918 – Glibert, p. 88, pl. 5, fig. 6.

Material and dimensions – Maximum height 6.2 mm. NHMW 2015/0133/0188 (1), NHMW 2015/0133/0189 (4); LC (6); FVD (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Gibborissoia morgani* (Cossmann & Peyrot, 1918) differs from the hugely polymorphic and widespread lower-middle Miocene *Gibborissoia varicosa* (de Basterot, 1825) in its 1) lack of varices, 2) lack of spiral sculpture, 3) inflated last whorl, and 4) angular periphery to the last whorl. It is more similar to the Langhian middle Miocene *G. angulosa* Landau, Harzhauser, İslamoğlu & Silva, 2013 from the Karaman Basin of Turkey, but this species 1) is more slender, 2) has a deeper, V-shaped suture, and 3) the base is less depressed. The protoconch of *G. morgani* is dome-shaped, composed of three whorls, with a small nucleus, whereas in *G. angulosa* it is composed of just under two whorls.

Distribution – Middle Miocene: Loire Basin, France (Cossmann & Peyrot, 1918; Glibert, 1949). Lower Pliocene: Atlantic, NW France (this paper).

Family Potamididae H. Adams & A. Adams, 1854
Genus *Tympanotonos* Schumacher, 1817

Type species (by monotypy) – *Murex fuscatus* Linnaeus, 1758, present-day, West Africa.

1817 *Tympanotonos* Schumacher, p. 211.
1846 *Tympanotonus* Agassiz, p. 382. Unjustified emendation of *Tympanotonos*.
1884 *Tympanotomus* Fischer, p. 681. Unjustified emendation of *Tympanotonos*.

***Tympanotonos redoniensis* nov. sp.**
Plate 2, figs 10-13

?1964 *Potamides basteroti* Marcel de Serres, 1829 – Brébion, p. 219, pl. 5, fig. 19.

Type material – Holotype MNHN.F.A57392, height 24.2 mm, width 11.6 mm; paratype 1 NHMW 2015/0133/0206, height 17.5 mm; paratype 2 NHMW 2015/0133/0207, height 29.4 mm; paratype 3 NHMW 2015/0133/0208, height 21.2 mm; paratype 3 NHMW 2015/0133/0117, height 13.4 mm.

Other material – Maximum height 32.6 mm (all incomplete). NHMW 2015/0133/0118 (4); LC (30 fragments); FVD (19 fragments). Type locality.

Etymology – Named after the 'Redonian' stage, the name used until recently for these NW French post-middle Miocene assemblages. *Tympanotonos* gender masculine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Tympanotonos* species with two tuberculose cords running just below mid-whorl on early teleoconch whorls, cords coalescing abapically so that later whorls sculptured by ten prominent tubercles mid-whorl.

Description – Shell of medium size and thickness, turriculate, with strongly nodular sculpture. Protoconch and earliest teleoconch whorls not preserved. Teleoconch consisting of about 12 low whorls bearing strong tubercles mid-whorl. Suture linear, impressed. Sculpture from fourth or fifth teleoconch whorl (first whorl on which sculpture preserved) consisting of two elevated, close-set, nodular spiral cords placed just below mid-whorl and

a single narrow smooth cord placed immediately above and below suture. In one specimen cord placed just below suture also nodular, but not as strongly developed as other two cords. Axial sculpture consisting of close-set comma-shaped growth lines. Abapically the two mid-whorl cords coalesce forming a single row of ten distinct rounded tubercles placed mid-whorl. Last whorl short, bearing two strong peribasal cords. Base strongly constricted, convex, bearing two weaker cords. Aperture not preserved (description based on holotype and paratypes).

Discussion – Unfortunately all our material is incomplete, but we are convinced that the apical fragments bearing two close-set nodular cords and the apical section correspond to the same species as the fragments consisting of only adult whorls with a single row of strong tubercles mid-whorl, as this abrupt sculptural change is also seen in the present-day West African type species; *Tympanotonos fuscatus* (Linnaeus, 1758). We do not, however, have any specimens showing this sculptural transition. We therefore provisionally place this new species in the genus *Tympanotonos*, although the ornament on the early teleoconch whorls is coarser than in *T. fuscatus*.
It is difficult to clearly separate *Tympanotonos redoniensis* nov. sp. from *T. fuscatus*, as the living species is extremely variable; as illustrated by Ardovini & Cosignani (2004, p. 91). Indeed, some specimens also show a single row of strong tubercles on the later whorls. However, in all specimens of *T. fuscatus* seen the beading on the cords on the early whorls is finer and the difference in strength between the adapical cord and the two lower cords less pronounced than in the French fossil species. On the later whorls of *T. fuscatus* there is a beaded cord bordering the suture, whereas this is not seen on the later whorls in *T. redoniensis*.
Reid *et al.* (2008, p. 693) wrote: '*Although the living West African* Tympanotonos fuscatus *has been considered the sole relict of a formerly pantropical genus..., we have found no evidence of this genus in the European fossil record*'. Therefore, its presence in the Le Pigeon Blanc assemblage is interesting, as it is the stratigraphically earliest European Neogene fossil record. *Tympanotonos* is indicative of sheltered muddy shores and often mangrove habitat (Reid *et al*., 2008). Therefore its presence in northwestern France suggests that it is possible that at least relict pockets of mangrove may have survived here into the Zanclean early Pliocene, much later than the previously thought latest occurrence of middle Miocene (Reid *et al*., 2008, p. 681). Mangrove forests today are found in saline coastal sediment habitats in the tropics and subtropics, mainly between latitudes 25° N and 25° S. This would suggest warmer SSTs than those found along the northwestern French coast today.
Brébion (1964, p. 220) recorded this species from Assemblage III (Le Pigeon Blanc, La Dixmerie) and Assemblage IV (St-Jean-la-Poterie) localities.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

Family Siliquariidae Anton, 1838
Genus *Tenagodus* Guettard, 1770
Subgenus *Tenagodus s. str.*

Type species (by subsequent designation, Sacco, 1896b) – *Serpula anguina* Linnaeus, 1758, present-day, Indian Ocean.

1770 *Tenagodus* Guettard, p. 128.
1789 *Siliquaria* Bruguière, pl. xv. Type species (by subsequent monotypy, Lamarck, 1799): *Serpula anguina* Linnaeus, 1758, present-day, Indian Ocean. Junior objective synonym of *Tenagodus*, with the same type species.
1807 *Siliquarigenus* Renier, 1807, pl. VIII. Not available: published in a work placed on the Official Index by Opinion 427 (ICZN, 1956).
1808 *Agathirses* de Montfort, p. 399. Type species (by original designation): *Agathirses furcellus* de Montfort, 1808, Eocene, France.
1810 *Siliquarius* de Montfort, p. 38. Unjustified emendation of *Siliquaria* Bruguière, 1789.
1817 *Anguinaria* Schumacher, p. 262. Substitute name for *Siliquaria* 'Lamarck' [= Bruguière, 1789], by Schumacher treated as a junior homonym of '*Silicaria*" [= *Siliquaria* Schumacher, 1817] [Bivalvia]. Junior homonym of *Anguinaria* Lamarck, 1816 [Bryozoa].
1861 *Pyxipoma*, Mörch, p. 409. Type species (by subsequent designation, Bieler, 1996): *Siliquaria lactea* Lamarck, 1818, present-day, Philippines.
1885 *Tenagodes* Fischer, p. 692. Unjustified emendation of *Tenagodus*.

***Tenagodus* (*Tenagodus*) *obtusus* (Schumacher, 1817)**
Plate 2, fig. 14

*1817 *Anguinaria obtusa* Schumacher, p. 262.
1854 *Siliquaria terebella* Lamk. – Millet, p. 158.
1964 *Tenagodus terebellus* Lamarck, 1818 – Brébion, p. 213.
2004a *Tenagodus* (*Tenagodus*) *obtusus* (Schumacher, 1817) – Landau *et al*., p. 14, pl. 2, fig. 7 (*cum syn*.).
2006 *Tenagodus obtusus* (Schumacher, 1817) – Chirli, p. 115, pl. 44, figs 1-4.
2012 *Tenagodus obtusus* (Schumacher, 1817) – Wesselingh *et al*., p. 46, fig. 40.
2013 *Tenagodus* (*Tenagodus*) *obtusus* (Schumacher, 1817) – Landau *et al*., p. 58, pl. 5, fig. 8 (*cum syn*.).

Material and dimensions – Maximum height 27.8 mm (all incomplete). NHMW 2015/0133/0121 (1), NHMW 2015/0133/0122 (6); FVD (12). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The presence of a continuous shell slit places this species in *Tenagodus sensu stricto*. There is agreement in the literature that the early Pliocene to Recent Eu-

ropean specimens represent a single species *Tenagodus* (*Tenagodus*) *obtusus* (Schumacher, 1817) (= *Tenagodus anguinus* auct. *non* Linnaeus, 1758, which is a tropical Indo-Pacific species). The same cannot be said about the Miocene forms. Most authors report them under the name *Tenagodus anguinus miocaenicus* Cossmann & Peyrot, 1921 (Glibert, 1949; Kojumdgieva & Strachimirov, 1960; Strausz, 1966; Bałuk, 1975), although as pointed out by Lozouet *et al*. (2001, p. 28), they should be referred to by the earlier name *Tenagodus terebellus* (Lamarck, 1818). This separation is made mainly on the basis of size, the Miocene specimens being smaller (Glibert, 1949). As pointed out by Landau *et al*. (2013) this chronospecific separation is unjustified as the specimens from the middle Miocene Karaman Basin of Turkey are just as large as most Pliocene specimens. Having said this, it is particularly striking in the northwestern French outcrops that specimens from the Tortonian Assemblage I localities are consistently smaller than those found in Assemblage III at Le Pigeon Blanc. Specimens from the middle Miocene Langhian of the Loire Basin (Ferrière-Larçon: NHMW coll.) are intermediate in size. We therefore continue to consider the Miocene to present-day forms a single species.

Brébion (1964, p. 214) recorded this species from Assemblage I (Reneauleau, Sceaux-d'Anjou, Thorigné, Chalonnes, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné) and Assemblage III (Le Pigeon Blanc, Contigné, Palluau).

Today, it occurs in the Mediterranean and West Africa, but not along the European Atlantic frontage. Therefore, its increased range in the lower Pliocene, including the northern coast of France, suggests warmer waters prevailed than those found at this latitude today. Marquet (1997a, 1998) also reported *Tenagodus* in the North Sea Basin of Belgium, from the base of the Kattendijk Fomation, also lower Pliocene, but not in stratigraphically younger beds. These records suggest that the cooling occurred during the end of the early Pliocene, as *Tenagodus* is not found in the northwestern French Assemblage IV localities, nor is it in the younger North Sea Basin assemblages.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Landau *et al*., 2004a). Middle Miocene: northeastern Atlantic (Aquitanian-Serravallian): Aquitaine Basin, (Cossmann & Peyrot, 1921), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Bulgaria (Kojumdgieva & Strachimirov, 1960), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Vienna Basin, Austria (Schultz, 1998); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al*., 2013). Upper Miocene: northeastern Atlantic (Tortonian and Messinian), Loire Basin, France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964); North Sea Basin, Belgium (Marquet, 1997a); western Mediterranean, Estepona Basin, Spain, (Landau *et al*., 2004a); central Mediterranean, Italy (Anfossi *et al*., 1983; Chirli, 2006). Lower upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); central Mediterranean, Italy (Sacco, 1896b; Malatesta, 1974; Chirli, 1988; Cavallo & Repetto, 1992). Present-day: Mediterranean to West Africa, 100-300 m depth (Poppe & Goto, 1991).

Family Turritellidae Lovén, 1847
Subfamily Turritellinae Lovén, 1847

Note – In this work we follow Landau *et al*. (2013) and have tried to use a more restricted concept of monophyletic genera. We are not aware of any molecular phylogenetic work on the group to date. Marwick (1957) reviewed the genera of the Turritellidae and drew special attention to the shape of the outer lip trace, using the terms lateral sinus for the trace on the whorl sides and the basal sinus for the trace on the base. He also highlighted the importance in the order of appearance of the cords on the neanic whorls and used a lettering system for the spiral cords in which B was the medial primary, D the peribasal primary generally involved with the suture, A was the first to appear adapical to B and C the first to appear abapical to B, between B and D (Marwick, 1957, p. 148). We have adopted this descriptive nomenclature in this section. We stress that the generic attributions here are provisional pending an in-depth review of the European Neogene turritellids and molecular phylogenetic work on the extant species, which is beyond the scope of this work.

Genus *Haustator* de Montfort, 1810

Type species (by monotypy) – *Haustator gallicus* de Montfort, 1810 [= *Haustator imbricatara* Lamarck, 1804)], Eocene, France.

1810 *Haustator* de Montfort, p. 182.

***Haustator incrassata* (J. Sowerby, 1814)**
Plate 3, fig. 1

*1814 *Turritella incrassata* J. Sowerby, p. 111, pl. 51, fig. 6.
1845 *Turritella triplicata* Br. – Nyst, p. 400, pl. 37, figs 7, 8 (*non* Brocchi, 1814).
1848 *Turritella incrassata* J. Sow. – Wood, p. 75, pl. 9, fig. 7.
1878 *Turritella incrassata* J. Sow. – Nyst, pl. 6, fig. 12a, b.
1878 *Turritella incrassata* var. *planispira* S. Wood – Nyst, pl. 6, fig. 12c.
1878 *Turritella incrassata* var. *imbricataria* S. Wood – Nyst, pl. 6, fig. 12f.
1882 *Turritella incrassata* J. Sowerby – Nyst, p. 82.
1882 *Turritella incrassata* var. *bicincta* Nyst, p. 82.

1918 *Turritella* (*Haustator*) *incrassata* (J. Sowerby) – Harmer, p. 446, pl. 42, figs 1-3, 5-7, pl. 43, fig. 16.
1918 *Turritella* (*Haustator*) *triplicata* (Brocchi) – Harmer, p. 448, pl. 42, figs 11, 13, 14 (*non* Brocchi, 1814).
1918 *Turritella* (*Haustator*) *erthensis* Harmer, p. 451, pl. 42, fig. 4.
1918 *Turritella* (*Haustator*) *biplicata* (Bronn) – Harmer, p. 455, pl. 43, figs 17, 18 (*non* Bronn, 1831).
1924 *Turritella incrassata* Sow. – Guillaume, p. 311, pl. 11, figs 10, 12-17.
1955 *Turritella* (*Haustator*) *triplicata* (Brocchi, 1814) + vars. – van Regteren Altena *et al*., p. 27, fig. 51 (*non* Brocchi, 1814).
1964 *Turritella* (*Haustator*) *incrassata* var. *obsoleta* nov. var. Brébion, p. 193, pl. 5, figs 3, 4 (*nomen nudum*).
1997b *Turritella* (*Haustator*) *incrassata incrassata* J. Sowerby, 1814 – Marquet, p. 11, pl. 1, fig. 3.
1998 *Turritella* (*Haustator*) *incrassata incrassata* J. Sowerby, 1814 – Marquet, p. 54, fig. 29.

Material and dimensions – Maximum height 20.5 mm. NHMW 2015/0133/0282 (1), NHMW 2015/0133/0283 (1); LC (3); MNHN.F.A53617 (Palluau). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – We have placed this species in the genus *Haustator* de Montfort, 1810, which is characterised by having the neanic whorls tricostate, the primaries starting in the order C–B–A. On the second teleoconch whorl secondaries appear in the interspaces and a weaker cord D appears above the suture. Fine irregular tertiary cords cover the entire whorl surface from the fourth whorl. It is quite understandable why Brébion (1964, p. 193) described the NW French Pliocene forms a distinct variety '*obsoleta*', as the sculpture is much weaker than that of specimens of *Haustator incrassata* (J. Sowerby, 1814) at hand from the upper Pliocene of Belgium. Nevertheless, the position of the primaries is the same and the number of varieties described of this species suggests a high degree of variability. Of the material illustrated by Brébion, we could only track down the fragmentary specimen from Palluau (1964, pl. 5, fig. 4; here reillustrated Pl. 3, fig. 2).
Haustator incrassata is uncommon at Le Pigeon Blanc, with only a few specimens available. They are much smaller than the specimens from the British and Belgian North Sea Basin Pliocene and, as mentioned above, have much weaker sculpture. Brébion (1964, p. 193) recorded this species from Assemblage III localities (Le Pigeon Blanc, Palluau) and Assemblage IV (Gourbesville). Guillaume (1924) added the Assemblage IV locality of Le Bosq d'Aubigny.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1918). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1918); Oorderen and Kruisschans, Belgium (Marquet, 1998). Lower Pleistocene: St Erth, England (Harmer, 1918). Pleistocene (indeterminate): The Netherlands (van Regteren Altena *et al*., 1955).

Genus *Oligodia* Handmann, 1882

Type species (by subsequent designation, Landau *et al*., 2013) – *Turritella bicarinata* Eichwald, 1830. Neogene, Paratethys.

1882 *Oligodia* Handmann, p. 212.
1896a *Torculoidella* Sacco, p. 28. Type species (by original designation): *Turbo varicosus* Brocchi, 1814, Pliocene, Italy.
1933 *Eichwaldiella* Friedberg, p. 22. Type species (by monotypy): *Turritella bicarinata* Eichwald, 1830, Miocene, Europe. Junior homonym of *Eichwaldiella* Whitley, 1930 [Pisces].

Note – This group is characterised by shells in which the medial primary B and the peribasal D dominate strongly. Marwick (1957) synonymised *Eichwaldiella* Friedberg, 1933 (type species: *Turritella bicarinata* Eichwald, 1830, by monotypy) with *Torculoidella* Sacco, 1896. *Eichwaldiella* Friedberg, 1933 is preoccupied by *Eichwaldiella* Whitley, 1930 [Pisces]. Landau *et al*. (2013, p. 62) pointed out that all authors had overlooked the earlier name *Oligodia* Handmann, 1882, and designated *Turritella bicarinata* Eichwald, 1830 as the type species for *Oligodia*. Therefore *Eichwaldiella* Friedberg, 1933 (*non* Whitley, 1930) is a junior synonym of *Oligodia*. Landau *et al*. (2013, p. 62) commented that the genus *Torculoidella* might also be a junior synonym of *Oligodia*. We have now had the opportunity to examine the neanic whorls of the type species of *Torculoidella*, *Turbo varicosus* Brocchi, 1814 (Pliocene, San Gimignano, Pietrafitta, Siena, Italy; NHMW coll.). The early neanic whorls are strongly angulated mid-whorl by a well-developed cord B. Peribasal cord D develops from the second teleoconch whorl, strengthening abapically, but remaining much weaker than cord B. Therefore, we confirm the observations given by Marwick (1957) for the genus *Torculoidella*; *i.e*. the predominance of medial primary B and peribasal D, and do not find them to differ from those of the genus *Oligodia*. We therefore place *Torculoidella* in synonymy with *Oligodia*.

***Oligodia guillaumei* (Brébion, 1989)**
Plate 3, figs 3-5

1924 *Turritella subangulata* Br. – Guillaume, p. 296, pl. 11, fig. 18 [*non Oligodia subangulata* (Brocchi, 1814) = *O. spirata* (Brocchi, 1814)].
1964 *Turritella (Zaria) subangulata* var. *simillima* Dollfus, mss. – Brébion, p. 196, pl. 5, figs 7, 8 (*nomen nudum*).
*1989 *Turritella* (*Zaria*) *guillaumei* Brébion *in* Lauriat-Rage *et al*., p. 132, pl. 8, fig. 10.

Material and dimensions – Maximum height 44.2 mm. Syntype MNHN.F.R52784 (coll. Viaud), La Limouzinière, Loire-Atlantique, France. MNHN.F.A53616, A53619 (2).
NHMW 2015/0133/0123-0124 (2), 2015/0133/0125 (13); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Revised description – Shell medium sized, solid, relatively broad, turriculate. Protoconch not preserved. Teleoconch of up to 12 whorls. Early teleoconch whorls strongly carinate, with medial primary B, placed mid-whorl, strongly developed and elevated, peribasal cord D weaker, but well-developed. Numerous narrow, close-set secondary cords fill interspaces. Abapically, on intermediate whorls, cord B weakens, becomes less elevated, similar in strength to cord D on ninth or tenth whorl, whorl profile on either side of cord B weakly concave. Last 2-3 whorls slightly concave above mid-whorl, weakly swollen above suture; cords B and D hardly discernable, overrun by secondary spiral sculpture. Last whorl angled at base; base weakly convex, bearing fine secondary cords. Aperture ovate, outer lip damaged in all specimens. Columella smooth, thin callus wash over base in parietal area. Basal and lateral sinuses typical for genus (see Marwick, 1957, p. 146, fig. 4).

Discussion – Brébion (*in* Lauriat-Rage *et al*., 1989) based the nominal taxon on a figure and descriptive comment given by Guillaume (1924, p. 296). Whilst discussing the 'Groupe de *T. subangulata* Br.', Guillaume wrote: '*Vers l'Ouest et le Nord, elle gagne au Redonien les faluns de Touraine (où elle est représentée par une intéressante race locale dont les derniers tours deviennent plans ou même concaves)*'. The differentiating comment is repeated on the plate caption (1924, p. 311). Although the erection of this species complies with Art. 13.1.2 (ICZN, 1999), we consider it useful to provide a fuller description.
It is surprising that this form was confused, or considered a subspecies of *Oligodia subangulata* (Brocchi, 1814) [= *O. spirata* (Brocchi, 1814)] for so long, as the resemblance is superficial. *Oligodia guillaumei* (Brébion, 1989) is thicker-shelled. The early teleoconch whorls of both species look similar, with a strongly elevated medial primary cord B angulating the whorls, but in *O. guillaumei* peribasal cord D is present from the first teleoconch whorl, which is not the case with *O. spirata*. In this respect *O. guillaumei* is more typical of the genus. The later teleoconch whorls in *O. guillaumei*, with their concave portion above mid-whorl and swollen lower portion, is quite different from any of the many morphotypes of *O. spirata* (*i.e*., see Chirli, 2006, pl. 40, figs 9-15).
At Le Pigeon Blanc this species is common and is further separated from *O. spirata* by its larger size, as *O. spirata* in the Pliocene NW of France does not attain the large size of some of the Pliocene Mediterranean shells. Brébion (1964, p. 198) recorded this species from Assemblage III localities (Le Pigeon Blanc, Palluau, La Dixmerie, Les Cléons, Le Girondor, La Gauvinière) and some Assemblage IV localities (St-Jean-la-Poterie, Gourbesville).

Distribution – Lower Pliocene: Atlantic, NW France (Guillaume, 1924; Brébion, 1964, 1989). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Oligodia palumbina* nov. sp.**
Plate 3, figs 6, 7

1964 *Turritella* (*Haustator*) *laevispira* nov. sp. Brébion, p. 190, pl. 5, fig. 2 (*nomen nudum*).

Type material – Holotype NHMW 2015/0133/0129, height 70.2 mm; paratype 1 NHMW 2015/0133/0130, height 54.3 mm.

Other material – Maximum height 78.0 mm. LC (2), FVD (11). Type locality.

Etymology – From Latin '*palumbes*, *palumbis*', noun, wood-pigeon, ringdove; a reference to the type locality of Le Pigeon Blanc (the white pigeon). *Torculoidella* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Oligodia* species with a very tall slender spire, primary cords only stronger than secondaries on the earliest teleoconch whorls; with a weak, hardly elevated, medial primary B placed slightly above mid-whorl and a weak peribasal cord D; adapically whorls flat-sided, weakly inflated abapically and slightly overhanging suture, with all cords narrow, weak and of subequal strength.

Description – Shell medium-sized, solid, slender, turriculate, tall spired. Protoconch not preserved. Teleoconch of up to 15 whorls. First two teleoconch whorls weakly carinate, with medial primary B, placed slightly above mid-whorl, weakly developed and hardly elevated, peribasal cord D weak. Numerous narrow, close-set secondary cords fill interspaces, only slightly weaker than primary cords. Adapically, whorls flat-sided, cords crowded, narrow, of subequal strength, whorl weakly inflated abapically, slightly overhanging suture. Last whorl angled at base; base flattened, bearing fine secondary cords. Aperture ovate, outer lip damaged in all specimens. Columella smooth, thin callus wash over base in parietal area. Basal and lateral sinuses typical for genus (see Marwick, 1957, p. 146, fig. 4).

Discussion – This species illustrates the importance of spiral sculpture on the neanic whorls. Brébion (1964, p. 190) placed this species in the genus *Haustator* de Montfort, 1810 probably due to the general shape of the shell being similar to the type species *H. imbricataria*

(Lamarck, 1804) from the Eocene of France: tall slender spire with flat-sided whorls, the abapical portion slightly overhanging the suture. However, in *Haustator* the neanic whorls are tricostate, the primaries starting in the order C–B–A, whereas in this species the first teleoconch whorl has B–D; features of the genus *Oligodia* Handmann, 1882.

Oligodia palumbina nov. sp. differs from all of its European Neogene congeners in that the primary cords are only weakly developed and stronger than the rest of the crowded secondary cords on the first two or three teleoconch whorls. A superficially similar species occurs in the lower Pliocene Kattendijk Formation of Belgium; *Haustator vanderfeeni* (Brakman, 1937). The sculpture on the later teleoconch whorls and whorl profile are very similar, but in specimens at hand from Verrebroekdok (Kallo; NHMW coll.) the shells are smaller (up to 30 mm), the apical angle is wider and on the first preserved whorl (the second teleoconch whorl) C–B–A are developed. Although we cannot say in which order they appear, as the first teleoconch whorl is missing, placement in the genus *Haustator* is reasonable.

Brébion (1964) suggested that some shells illustrated by Harmer (1918, pl. 43, figs 9-11) from the upper Pliocene Red Crag of England may represent the same species. These were identified by Harmer as *Turritella* (*Haustator*) *marginalis* (Brocchi). We have not seen *Haustator marginalis*, but a specimen illustrated by Chirli (2006, pl. 42, figs 8, 9) shows tricostate neanic whorls, so placement in *Haustator* is probably correct. The whorl shape of the fragments illustrated by Harmer certainly agrees with corresponding whorls in *O. palumbina*, but the apical whorls are missing. We exclude these shells from the synonymy until better material is available.

Brébion (1964, p. 190) reported this species from Assemblage III localities (Le Pigeon Blanc, Palluau, Les Cléons) and possibly Assemblage IV (Gourbesville). In the Le Pigeon Blanc assemblage *O. palumbina* is uncommon and easily separated from its congeners *O. guillaumei* (Brébion, 1989), which has a wider apical and cords B–D persisting onto intermediate whorls and *O. spirata* (Brocchi, 1814) in which cord B forms a carina mid-whorl on all whorls.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964). ?Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Oligodia spirata* (Brocchi, 1814)**
Plate 3, fig. 8

*1814	*Turbo spiratus* Brocchi, p. 369, pl. 6, fig. 19.
1814	*Turbo subangulatus* Brocchi, p. 374, pl. 6, fig. 16.
1964	*Turritella (Zaria) subangulata* var. *subacutangula* d'Orbigny, 1852 – Brébion, p. 195, pl. 5, figs 5, 6.
2004a	*Turritella spirata* (Brocchi, 1814) – Landau *et al*., p. 17, pl. 2, fig. 11, pl. 3, fig. 7 (*cum syn*.).
2006	*Archimediella spirata* (Brocchi, 1814) – Chirli, p. 104, pl. 40, figs 9-15.
2010	*Turritella spirata* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 20, 31 1st row right.

Material and dimensions – Maximum height 24.2 mm. NHMW 2015/0133/0126 (1), NHMW 2015/0133/0127 (1), 2015/0133/0128 (29); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Oligodia spirata* (Brocchi, 1814) is characterized by a multispiral protoconch (although this is not preserved in the material from Le Pigeon Blanc) and in having medial primary B strongly developed making the early whorls angular, with a single carina, placed just below mid-whorl. The sculpture of the adult whorls is variable with two main morphotypes: *spirata*, with a strongly developed cord B, giving an angular whorl profile and the secondary cords always much weaker; morphotype *subangulata* has a weaker central cord, the whorls are more convex and some of the secondary spiral cords more developed almost equal in strength to cord B. However, intermediate forms can be found and most recent authors consider these two morphotypes of a single species (for discussion on synonymy and name preference, see Caprotti, 1975).

The specimens from Le Pigeon Blanc are of the *spirata* morphotype, with a strongly developed cord B, whilst the other spiral cords remain of secondary strength. Brébion (1964, p. 196) recorded this species from all Assemblage III localities (Le Pigeon Blanc, Palluau, Corcoué-sur-Logne, La Dixmerie, Les Cléons, Le Girondor).

Distribution – Middle Miocene: Atlantic, Loire Basin , France (Cossmann & Peyrot, 1924; Glibert, 1949); Proto-Mediterranean, NE Spain (Solsona, 1998); Paratethys, Poland (Bałuk, 1975), Austria (Hörnes, 1855), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966). Upper Miocene: Atlantic (Tortonian and Messinian), NE France (Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1896a; Robba, 1968). Lower Pliocene: Atlantic, NW France (Brébion, 1964); western Mediterranean, NE Spain, (Solsona, 1998); Roussillon, France (Fontannes, 1879; Martinell & Domènech, 1986); central Mediterranean, Italy (Sacco, 1896a; Palla, 1967; Caprotti, 1970, 1974, 1975; Anfossi *et al*., 1983; Bernasconi, 1990); Atlantic, Morocco (Brébion, 1979). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Ruggieri *et al*., 1959; Malatesta, 1974; Caprotti, 1975; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010); Tunisia (Fekih, 1975); Atlantic, Morocco (Lecointre, 1952). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912).

Order Littorinimorpha Golikov & Starobogatov, 1975
Superfamily Calyptraeoidea Lamarck, 1809
Family Calyptraeidae Lamarck, 1809
Genus *Calyptraea* Lamarck, 1799

Type species (by monotypy) – *Patella chinensis* Lin-

naeus, 1758, present-day, Mediterranean.

1799 *Calyptraea* Lamarck, p. 78.
1847b *Galerus* Gray, p. 157. Type species (by original designation): *Patella chinensis* Linnaeus, 1758, present-day, Mediterranean.

***Calyptraea chinensis* (Linnaeus, 1758)**
Plate 4, fig. 1

*1758 *Patella chinensis* Linnaeus, p. 1257.
1854 *Caliptraea* [*sic*] *Mamillaris* Millet, p. 165 (*nomen nudum*; *non* Broderip, 1834).
1864 *Caliptraea* [*sic*] *mamillaris* Millet, p. 680 (*non* Broderip, 1834).
1964 *Calyptraea chinensis* Linné, 1766[*sic*] – Brébion, p. 313.
2013 *Calyptraea chinensis* (Linnaeus, 1758) – Landau *et al*., p. 95, pl. 9, fig. 7, pl. 61, fig. 6 (*cum syn*.).

Material and dimensions – Maximum diameter 19.3 mm. NHMW 2015/0133/0213 (1), 2015/0133/0214 (7); LC (4); FVD (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species in extremely variable in both sculpture and profile, although most specimens are relatively constant within a population. The specimens from Le Pigeon Blanc are small and only moderately elevated, with finely squamose surface sculpture.
Brébion (1964, p. 315) recorded this species from Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu), Assemblage III localities (Le Pigeon Blanc, Le Girondor, La Gauvinière, Palluau) and Assemblage IV localities (St-Jean-la-Poterie, La Dixmerie, Gourbesville, Le Bosq d'Aubigny).

Distribution – Lower Miocene: Paratethys (Aquitanian): Vienna Basin, Austria (Schaffer, 1912); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964), Netherlands (Janssen, 1984). Middle Miocene: Atlantic (Langhian-Serravallian): Aquitaine Basin, France, (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1923; Bałuk, 1975), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966), Ukraine (Zelinskaya *et al*., 1968), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Burdigalian-Langhian): northeastern Spain (Solsona, 1998), (Serravallian): Karaman Basin, Turkey (Fischer, 1866; Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), Cacela Basin, Portugal (Glibert, 1963); Proto-Mediterranean Sea (Tortonian and Messinian): Italy (Sacco, 1896b; Venzo & Pelosio, 1963). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1916), Belgium (Glibert, 1958; Marquet, 1998); Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011) Morocco (Lecointre, 1952); northeastern Spain (Martinell, 1979), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974), Tunisia (Fekih, 1975). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1916), Belgium (Glibert, 1958; Marquet, 1998); Atlantic, Pombal Basin, Portugal (Silva, 2001), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Malatesta, 1974; Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: Atlantic, British Isles (Glibert, 1963), Morocco (Lecointre, 1952); central Mediterranean, Italy (Cerulli-Irelli, 1912; Taviani *et al*., 1998), Sicily (Glibert, 1963). Present-day: northeastern Atlantic, British Isles to Zaire, Madeira and Canaries, Mediterranean, Black Sea (Poppe & Goto, 1991).

Genus *Crepidula* Lamarck, 1799

Type species (by monotypy) – *Patella fornicata* Linnaeus, 1758, present-day, European.

1799 *Crepidula* Lamarck, p. 78.
1847b *Crypta* Gray, p. 157. Type species (by monotypy): *Patella fornicata* Linnaeus, 1758, present-day, European.
1857 *Garnotia* Gray, p. 117. Type species (by monotypy): *Crepidula solida* Hinds, 1844 (= *Crepidula adunca* G.B. Sowerby I, 1825), present-day, eastern Pacific.
1852 *Ianacus* Mörch, p. 146. Type species (by subsequent designation, Wenz, 1940): *Crepidula plana* Say, 1822, present-day, northwest Atlantic.
1853 *Jenacus* Mörch, p. 75. Unjustified emendation of *Ianacus*.
1940 *Janacus* Wenz, p. 905. Incorrect subsequent spelling

***Crepidula gibbosa* Defrance, 1818**
Plate 4, fig. 2

*1818 *Crepidula gibbosa* Defrance, p. 397.
1854 *Crepidula Mutabilis* Millet (*pars*), p. 166 (*nomen nudum*).
1865 *Crepidula mutabilis* Millet (*pars*), p. 598.
1964 *Crepidula gibbosa* Defrance, 1818 – Brébion, p. 316.
2013 *Crepidula gibbosa* Defrance, 1818 – Landau *et al*., p. 96, pl. 9, figs 8, 9 (*cum syn*.).

Material and dimensions – Maximum diameter 23.8 mm, height 6.8 mm. NHMW 2015/0133/0152 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Crepidula gibbosa*, Defrance, 1818 has a more elevated, convex dorsum than *C. unguiformis*, which usually has a concave dorsum. Moreover, *C. gibbosa* has a straight septum and lacks the central depression seen in *C. unguiformis*. For further discussion see Landau *et al*. (2004a, p. 72).
Brébion (1964, p. 316) recorded this species from numerous Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Beaulieu) and Assemblage IV (Bosq-d'Aubigny), we record it from Assemblage III (Le Pigeon Blanc).

Distribution – Middle Miocene: Atlantic: (Langhian and Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): NW France (Glibert, 1964); Proto-Mediterranean Sea, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (this paper); Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011). Lower upper Pliocene: Atlantic, Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Glibert, 1963). Present-day: Mediterranean, below low tide line, often on other molluscs (Poppe & Goto, 1991).

***Crepidula unguiformis* Lamarck, 1822**
Plate 4, fig. 3

*1822	*Crepidula unguiformis* Lamarck, p. 25.
1854	*Crepidula Mutabilis* Millet (*pars*), p. 166 (*nomen nudum*).
1865	*Crepidula mutabilis* Millet (*pars*), p. 598.
1964	*Crepidula* (*Janacus*) *crepidula* Linné 1766 [*sic*] – Brébion, p. 317.
2004a	*Crepidula unguiformis* Lamarck, 1822 – Landau *et al*., p. 73, pl. 15, fig. 5 (*cum syn*.).
2011	*Crepidula unguiformis* Lamarck, 1822 – Landau *et al*., p 15, pl. 4, fig. 13 (*cum syn*.).
2013	*Crepidula unguiformis* Lamarck, 1822 – Landau *et al*., p 96, pl. 9, fig. 10 (*cum syn*.).

Material and dimensions – Maximum diameter 23.0 mm (incomplete). NHMW 2015/0133/0274 (1); LC (7); FVD (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Crepidula unguiformis* Lamarck, 1822 is often found inside the aperture of other shells. Its shape is therefore very variable, determined by the living substrate. Some specimens develop a corrugated shell, following the contour of internal lirae, if present inside the aperture of their host shell. The specimens from Le Pigeon Blanc are all smooth and almost completely flat. For further discussion see Landau *et al*., (2004a, p. 73).
Brébion (1964, p. 317) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel), Assemblage III (Le Pigeon Blanc, Palluau) and Assemblage IV (Bosq-d'Aubigny).

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1919). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964), Netherlands (Janssen, 1984). Middle Miocene: northeastern Atlantic (Langhian and Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Proto-Mediterranean Sea, northeastern Spain (Solsona, 1998), Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), (Tortonian): Cacela Basin, Portugal (NHMW collection); Proto-Mediterranean Sea, Po valley, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011); western Mediterranean, Roussillon Basin, France (Fontannes, 1879), northeastern Spain (Solsona, 1998); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967), Tunisia (Fekih, 1975). Lower-upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a), central Mediterranean, Italy (Sacco, 1896b; Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Lower-upper Pleistocene: central Mediterranean, Sicily (Glibert, 1963). Present-day: Mediterranean, below low tide line to 100 m depth, often on other molluscs (Poppe & Goto, 1991).

Superfamily Capuloidea Fleming, 1822
Family Capulidae Fleming, 1822
Genus *Capulus* de Montfort, 1810

Type species (by original designation) – *Patella ungarica* Linnaeus, 1758, present-day, Mediterranean.

1810	*Capulus* de Montfort, p. 54.
1822	*Pileopsis* Lamarck, p. 16. Type species (by subsequent designation, Children, 1923): *Patella ungarica* Linnaeus, 1758, present-day, Mediterranean.
1823	*Actita* Fischer von Waldheim, p. 234. Unnecessary substitute name for *Capulus* de Montfort 1810 and *Pileopsis* Lamarck 1822.
1828	*Brocchia* Bronn, p. 538. Type species (by monotypy): *Patella sinuosa* Brocchi, 1814, Pliocene, Italy.
1840	*Capulis* Swainson, p. 243. Incorrect subsequent spelling of *Capulus*.

***Capulus ungaricus* (Linnaeus, 1758)**
Plate 4, fig. 4

*1758	*Patella ungarica* Linnaeus, p. 782.
1854	*Capulus Obliquatus* Millet, p. 165 (*nomen nudum*).
1865	*Capulus obliquatus* Millet, p. 598.
1964	*Capulus ungaricus* var. *neglectus* Michelotti, 1847 – Brébion (*partim*), p. 309.
2004a	*Capulus ungaricus* (Linnaeus, 1758) – Landau *et al*., p. 68, pl. 14, fig. 1 (*cum syn*.).
2008	*Capulus ungaricus* (Linné, 1758) – Chirli, p. 26, pl. 6, figs 8-15.
2008	*Capulus ungaricus* (Linné, 1758) – Chirli & Richard, p. 26, pl. 4, fig. 1.
2011	*Capulus ungaricus* (Linnaeus, 1758) – Landau *et al*., p. 14, pl. 4, fig. 7 (*cum syn*.).

Material and dimensions – Maximum diameter 20.5 mm, height 8.3 mm. NHMW 2015/0133/0212 (1); LC (20 fragments); FVD (11 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Both Glibert (1949) and Brébion (1964) separated the French middle Miocene to lower Pliocene Loire Basin specimens as a separate subspecies *Capulus ungaricus* var. *neglectus* Michelotti, 1847. According to Cossmann & Peyrot (1918, p. 507) this subspecies differs from the type by its smaller, thinner, almost smooth shell and having the apex strongly deviated off-centre. The specimens from Le Pigeon Blanc are indeed smaller and have a thinner shell than Pliocene specimens of *C. ungaricus* from other Mediterranean localities. However, ribs are present and the protoconch of two whorls (Pl. 4, fig 4b), or just under, is similar to that illustrated by Fretter & Graham (1981, fig. 225).
The Assemblage I specimens from NW France are not *C. ungaricus*. They have a paucispiral protoconch and plicae on the right hand side of the umbo when seen from above, and are ascribed to *C. partimsinuosus* (Wood, 1848). This species will be discussed more fully in the relevant paper. The North Sea Basin Pliocene *Capulus* species were fully discussed by Marquet & Landau (2006).
Brébion (1964, p. 309) recorded this species from Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, Les Pierres Blanches), Assemblage III localities (Le Pigeon Blanc, Le Girondor, Palluau) and Assemblage IV localities (Gourbesville). The Assemblage I records refer to *C. partimsinuosus* and are excluded from the distribution. The Assemblage IV records are provisionally included, but need to be verified.

Distribution – Middle Miocene: Paratethys, Poland (Bałuk, 1975), Vienna (Hörnes, 1856); Proto-Mediterranean, Italy (Sacco, 1896b); Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1919), Loire Basin, France (Glibert, 1949). Upper Miocene: Proto-Mediterranean (Tortonian), Italy (Sacco, 1896b). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1916), Kattendijk Formation, Belgium (Glibert, 1958; Marquet, 1998); Atlantic, NW France (Brébion, 1964), Guadalquivir basin, Spain (Landau *et al*., 2011); central Mediterranean, Italy (Chirli, 2008). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1916), Oorderen Sands, Belgium (Glibert, 1958; Marquet, 1998); Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1896b; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914; Brambilla *et al*., 1988; Di Geronimo & La Perna, 1997); Atlantic, Morocco (Lecointre, 1952). Present-day: Atlantic, Iceland to West Africa, North America to Florida, Mediterranean. Not present in the North Sea (Fretter & Graham, 1981). Sublittoral to 850 m depth, on stones and shells (Poppe & Goto, 1991).

Superfamily Vetulinoidea Gray, 1840
Family Triviidae Troschel, 1863
Subfamily Triviinae Troschel, 1863
Genus *Trivia* Gray, 1837

Type species (by subsequent designation, Gray, 1847b) – *Cypraea europaea* Montagu, 1808, present-day, British Isles.

1837	*Trivia* Gray, p. 256.

***Trivia coccinelloides* (J.D.C. Sowerby, 1823)**
Plate 4, fig. 5

*1823	*Cypraea coccinelloides* J.D.C. Sowerby, p. 107, pl. 378, fig. 1.
1964	*Trivia coccinelloides* Sowerby, 1823 – Brébion, p. 326.
2003	*Trivia coccinelloides* (J. de C. Sowerby, 1823) – Fehse & Landau, p. 87, fig. 1/1a-c (*cum syn*.).
2011	*Trivia coccinelloides* (J. de C. Sowerby, 1823) – Landau *et al*., p. 17, pl. 6, fig. 8.

Material and dimensions – Maximum height 9.6 mm. NHMW 2015/0133/0236 (1), 2015/0133/0237 (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Trivia coccinelloides* (J.D.C. Sowerby, 1823) is characterised by the aperture being well to the right of the ventral mid-line, the fossula not delimited from the columella and the inner border of the columella and fossula not covered by the outer lip when seen in ventral view. The shells vary slightly in the development of the dorsal hump, and in the number of dorsal ribs and labial teeth.
Fehse & Landau (2003) stated that this species had been found in the lower Pliocene Kattendijk Formation of Bel-

gium, quoting Marquet (1998) as source. This seems to be an error, as Marquet records *T. coccinelloides* only from the upper Pliocene Lillo Formation. In the lower Pliocene Kattendijk Formation he records T. *coccinelloides parvula* Schilder, 1933, which differs in having coarser sculpture. *Trivia coccinelloides* does, however, occur in the lower Pliocene Coralline Crag of England (Wood, 1848; Harmer, 1920), which makes subspecies status undesirable, as they both occur in the lower Pliocene North Sea Basin. It would be better to consider them distinct at full species level, if they are indeed distinct.
Brébion (1964, p. 327) recorded this species from the Assemblage IV locality of St-Jean-la-Poterie. It is interesting that he did not recognise this species at Le Pigeon Blanc, where it is very common.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); Guadalquivir Basin, S. Spain (Landau *et al*., 2011); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1920); Lillo Formation, Belgium (Glibert, 1958; Marquet, 1998); Atlantic, Pombal Basin, Portugal (Silva, 2001); western Mediterranean, Estepona, S. Spain (Fehse & Landau, 2003); central Mediterranean, Italy (Sacco, 1894). Upper Pliocene-Pleistocene: NW France (Brébion, 1964).

***Trivia pisolina* (Lamarck, 1811)**
Plate 4, fig. 6

*1811	*Cypraea pisolina* Lamarck, p. 108.
1854	*Cypraea Pisolina* Lmk. – Millet, p. 158.
?1914	*Trivia pisolina* (Lamarck) – Harmer, p. 50, pl. 2, fig. 17.
non 1924	*Trivia* cf. *pisolina* Lamarck – Cossmann & Peyrot, p. 388, pl. 11, figs 2, 3.
1938	*Trivia pisolina* Lamarck – Peyrot, p. 170, pl. 4, figs 2, 8, 9.
1964	*Trivia pisolina* Lamarck, 1810 [*sic*] – Brébion, p. 322, pl. 7, figs 31-33.

Material and dimensions – Maximum height 9.3 mm. NHMW 2015/0133/0305 (1); LC (1 fragment). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Trivia pisolina* (Lamarck, 1811) is a very distinctive species, characterised by its smooth dorsum, devoid of ribs and the coarse apertural dentition. Few European Neogene triviids have a smooth dorsum. *Trivia perobsoleta* Sacco, 1894, from the Mediterranean Pliocene also lacks ribs, but differs in being larger shelled and having finer apertural dentition.
The shell figured by Harmer (1914, pl. 2, fig. 17) from the English Crag seems to be an internal mould. We are uncertain if it is *T. pisolina* and exclude it from the distribution. The shell identified as *Trivia* cf. *pisolina* by Cossmann & Peyrot (1924, pl. 11, figs 2, 3) from the lower Miocene Aquitaine Basin is not this species. It is probably a subadult specimen of another triviid.
Millet (1854, p. 158) recorded this species from Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place). Brébion (1964, p. 324) added Les Pierres Blanches and Beaulieu, and Assemblage II (Apigné, Chalonnes, Carcé). We add Assemblage III (Le Pigeon Blanc), where it is exceedingly rare.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Peyrot, 1938; Brébion, 1964). Lower Pliocene: Atlantic, NW France (this paper).

Genus *Niveria* Jousseaume, 1884

Type species (by subsequent designation, Jousseaume, 1884c) – *Cypraea nivea* G.B. Sowerby I, 1832, present-day, Caribbean.

1884b	*Niveria* Jousseaume, p. 415.
1933a	*Sulcotrivia* Schilder, p. 18. Type species (by original designation): *Cypraea dimidiata* Bronn, 1831, Pliocene, Italy.
1979	*Circumscapula* Cate, p. 109. Type species (by original designation): *Trivia myrae* Campbell, 1961, present-day, Gulf of California.

***Niveria testudinella* (Wood, 1842)**
Plate 4, fig. 7

*1842	*Trivia testudinella* Wood, p. 543.
1843	*Cypraea avellana* J. Sow. – Nyst, p. 608, pl. 45, fig. 13 [*non Niveria avellana* (J. Sowerby, 1823)].
1848	*Cypraea avellana* J. Sow. – Wood, p. 15, pl. 2, fig. 5 [*non Niveria avellana* (J. Sowerby, 1823)].
1878	*Cypraea avellana* J. Sow. – Nyst, pl. 5, fig. 1 [*non Niveria avellana* (J. Sowerby, 1823)].
1882	*Cypraea avellana* J. Sow. – Nyst, p. 58 [*non Niveria avellana* (J. Sowerby, 1823)].
1920	*Trivia affinis* (Dujardin) – Harmer, p. 510, pl. 45, fig. 13, ?12. [*non* Dujardin, 1837, = *Niveria dimidiatoaffinis* (Sacco, 1894)].
1933a	*Trivia* (*Sulcotrivia*) *testudinella* Wood – Schilder, p. 14.
1946	*Trivia* (*Sulcotrivia*) *testudinella* Wood, 1848 [*sic*] – Beets, p. 67.
1956	*Trivia* (*Sulcotrivia*) *testudinella* S.V. Wood, 1842 – van Regteren Altena *et al*., p. 86, pl. 10, fig. 104.
1958	*Trivia* (*Sulcotrivia*) *testudinella* Wood, 1842 – Glibert, p. 28.
1997b	*Trivia* (*Sulcotrivia*) *testudinella* Wood, 1842 – Marquet, p. 75, pl. 2, fig. 3.
1998	*Trivia* (*Sulcotrivia*) *testudinella* Wood, 1842 – Marquet, p. 86, fig. 61.

Material and dimensions – Maximum height 13.7 mm. NHMW 2015/0133/0238-0239 (2), 2015/0133/0240 (3); LC (8); FVD (4). Le Pigeon Blanc, Le Landreau, Nantes

area, Loire-Atlantique department, NW France.

Discussion – In the British Crags *Niveria avellana* (J. Sowerby, 1823) and *Niveria testudinella* (Wood, 1842) have been confused. Specimens at hand from the Red Crag of Walton-on-the-Naze, Essex (NHMW coll.) show *N. avellana* has an even larger and more globose shell than *N. testudinella*, the dorsal sulcus is wider and the ribbing is slightly less dense. *Niveria dimidiatoaffinis* (Sacco, 1894) (= *Cypraea affinis* Dujardin, 1837; *non* Gmelin, 1791), common in the middle Miocene Loire Basin differs in having a more slender shell, with the siphonal and anal canals more produced. The dorsal sulcus more sharply bisects the dorsal ribs. *Niveria excoccinella* (Sacco, 1894), also common in the Loire Basin Miocene has much wider and less regular ribs.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1920); Lillo Formation, Belgium (Glibert, 1958); Pliocene (indeterminate): Belgium (Marquet, 1997b, 1998).

Subfamily Eratoinae Gill, 1871
Genus *Erato* Risso, 1826

Type species (by monotypy) – *Voluta cypraeola* Brocchi, 1814, Pliocene, Italy.

1826 *Erato* Risso, p. 240.

***Erato andecavica* Schilder, 1933**
Plate 4, fig. 8

*1933b *Erato incrassata andecavica* Schilder, p. 250, 254, 260, 282, 283, fig. 73.
2002 *Erato andecavica* Schilder, 1933 – Fehse & Landau, p. 94, figs 10, 11, 14, 30, 33/2.

Material and dimensions – Maximum height 11.1 mm. NHMW 2015/0133/0232 (1), 2015/0133/0233 (7). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Erato andecavica Schilder, 1933 is characterised by its strongly inflated shape, dimple on the anterior end of the dorsum and greatly thickened, basally flattened outer lip, with an angular margin and strong denticles. The species is constant in shape, but varies greatly in the character of the denticles on the columella. *Erato andecavica* is closely similar to the chronologically slightly older *E. gallica* Schilder, 1933 from the middle Miocene Loire Basin, but differs in having an even more inflated shell, with fewer and coarser denticles on the outer lip. The columellar denticles are strongly developed in the abapical third, obsolete adapically, forming a callosity along the parietal edge. In *E.gallica* the columellar teeth usually persist further adapically.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (this paper).

***Erato britannica* Schilder, 1933**
Plate 4, fig. 9

1848 *Erato laevis* Don. – Wood, p. 18, pl. 2, fig. 10a, b [*non Marginella laevis* Donovan, 1804 = *Erato voluta* (Montagu, 1803)].
1920 *Erato laevis* (Donovan) – Harmer, p. 511, pl. 45, fig. 1 [*non Marginella laevis* Donovan, 1804 = *Erato voluta* (Montagu, 1803)].
*1933a *Erato* (*Erato*) *cypraeola britannica* Schilder, p. 7.
1933b *Erato* (*Erato*) *spiralis britannica* Schilder – Schilder, p. 250, 254, 259, 261.
1958 *Erato* (*Erato*) *cypraeola britannica* Schilder, 1933 – Glibert, p. 26, pl. 2, fig. 25.
2002 *Erato britannica* Schilder, 1933 – Fehse & Landau, p. 92, figs 20, 25, 27, 29, 33/1.

Material and dimensions – Maximum height 8.9 mm. NHMW 2015/0133/0234 (1), 2015/0133/0235 (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Erato britannica Schilder, 1933 is characterised by its high spire, elongated shape, the knob-like denticles on the basally flattened outer lip, deeply concave fossula and large number of strongly developed folds on the anterior portion of the base. The species is constant in shape, varying only slightly in number of denticles. As discussed by Fehse & Landau (2002) the shape, size and aperture of this species resemble *E. voluta* (Montagu, 1803), whereas the dentition, columella, fossula, and terminal ridge are similar to *E. cypraeola* (Brocchi, 1814). For comparison to other similar species see Fehse & Landau (2002, p. 94, table 2).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920), Kattendijk Formation, Belgium (Schilder, 1933a). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1920); Lillo Formation, Belgium (Glibert, 1958).

***Erato cooperi* Fehse & Landau, 2002**
Plate 4, fig. 10

*2002 *Erato cooperi* Fehse & Landau, p. 95, figs 18, 23, 24, 31, 33/3.

Material and dimensions – Maximum height 5.7 mm. NHMW 2015/0133/0230 (1), 2015/0133/0231 (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-

Atlantique department, NW France.

Discussion – *Erato cooperi* Fehse & Landau, 2002 belongs to a group of small, squat eratoiids, including *E. pernana* Sacco, 1894, *E. praecedens* Schilder, 1933, *E. exmaugeriae* Schilder, 1933 and *E. scaldisia* Schilder, 1933 and, placed by Schilder (1933b) in the subgenus *Eratopsis* Hoernes & Auinger, 1880. However, this name should be considered a full genus rank and reserved for species in which the columellar teeth cover the venter. Apart from the small size and squat appearance, this species is characterised by its strongly developed terminal ridge, which is bifid. The shape in some specimens is slightly more elongated, less inflated, the strength and number of denticles on either side of the aperture is variable. Both *Erato exmaugeriae* and *E. scaldisia* from the upper Pliocene Oorderen Sands of Belgium differ in having a less globose shell and finer labial and columellar dentition. *Erato pernana* from the Pliocene Mediterranean has again more numerous teeth and *E. praecedens* has coarser dentition. For further discussion see Fehse & Landau (2002, p. 97, 98, table 4).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (this paper).

Superfamily Cypraeoidea Rafinesque, 1815
Family Cypraeidae Rafinesque, 1815
Subfamily ?Zonariinae Schilder, 1932
Genus *Schilderia* Tomlin, 1930

Type species (by typification of replaced name) – *Cypraea infernoi* Cerulli-Irelli, 1911, Pleistocene, Italy. *Nom. nov. pro Globulina* Cerulli-Irelli, 1911, *non* d'Orbigny, 1839 [Foraminifera], *non* Wagner, 1905 [Helicinidae]. Tomlin cited *Cypraea utriculata* Lamarck, 1811 as the type species of *Schilderia*, but this is not valid under Art. 67.8 (ICZN, 1999).

1911 *Globulina* Cerrulli-Irelli, p. 272. Type species (by monotypy): *Cypraea infernoi* Cerulli-Irelli, 1911, Pleistocene, Italy. Junior homonym of *Globulina* d'Orbigny, 1839 [Foraminifera] and *Globulina* Wagner, 1905 [Helicinidae].
1930 *Schilderia* Tomlin, p. 24.

***Schilderia* sp.**
Plate 5, fig. 1

Material and dimensions – Length 41.7 mm (dorsum missing). FVD (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species is represented in the Le Pigeon Blanc assemblage by a single specimen in which the dorsum is missing. The shell is characterised by its relatively produced siphonal and anal canals, although there is hardly any constriction delimiting the siphonal protruberance when viewed aperturally, its greatly callused outer lip bearing 24 denticles, which are restricted to the inner edge and about 15 denticles on the columella, restricted to the angulation, weakening adapically; the posterior third of the columella is smooth, devoid of denticles.
The genus *Schilderia* is well represented in the middle and upper Miocene of NW France (Glibert, 1952a; Dolin & Lozouet, 2004 respectively). It is difficult to identify this species with the scant material available, but of the Tortonian upper Miocene species from NW France *S. andegavensis* (Defrance, 1826) has a strong constriction between the dorsum and the anterior protruberance, teeth along the entire length of the columella and about 21 labral teeth; *S. veronicata* Dolin & Lozouet, 2004 differs in having less produced protruberances and fewer teeth on the inner margin of the outer lip (18 + 2); *S. lauriatae* Dolin & Lozouet, 2004 has a more globose shell, the siphonal constriction is more prominent, it has less developed, smaller teeth on the columella and fewer but stronger teeth on the outer lip (16 + 3); *S. incognita* Dolin & Lozouet, 2004 has 13 strong triangular teeth on the columella and fewer teeth on the outer lip (18 + 2); *S. fasciolaria* Dolin & Lozouet, 2004 has a similar ventral profile, but more numerous teeth on the columella (20) and fewer on the outer lip (20 + 3); *S. brebioni* Dolin & Lozouet, 2004 is probably the most similar to the shell from Le Pigeon Blanc, with a similar ventral profile, 16 columellar teeth and 20 small labial teeth. Dolin & Lozouet (2004) give no indication of intraspecific variability for their taxa.
No specimens of *Schilderia* were found by Brébion (1964, p. 335), but he comments on a specimen in manuscript notes of Dollfus from other Assemblage III localities La Dixmerie and Le Girondor, about 49 mm x 31 mm, with about 30 teeth on the outer lip.
Although we cannot identify this species, these records serve to show that the relatively thermophile genus *Schilderia* was far less prolific in the lower Pliocene of NW France, both in numbers and species, than it was in the Tortonian upper Miocene. Today, the genus is not found north of Vigo, Spain (latitude 42º N) (Poppe & Goto, 1992), again suggesting warmer water previailed in the lower Pliocene than found off the coast of NW France today.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Ovulidae Fleming, 1822
Genus *Neosimnia* Fischer, 1884

Type species (by monotypy) – *Bulla spelta* Linnaeus, 1758, present-day, Mediterranean.

1884 *Neosimnia* Fischer, p. 664.
1878 *Velox* Monterosato, p. 319. Type species (by monotypy): *Bulla spelta* Linnaeus, 1758, present-day, Mediterranean.

***Neosimnia spelta* (Linnaeus, 1758)**
Plate 5, fig. 2.

*1758	*Bulla spelta* Linnaeus, p. 1182.
non 1920	*Ovula spelta* (Linné) – Harmer, p. 506, pl. 45, fig. 7 [= *Neosimnia leathesii* (J. Sowerby, 1824)].
non 1985	*Neosimnia spelta* (Linneo, 1758) – Inzani, p. 7, pl. 5, fig. 1 [= *Neosimnia pliomajor* (Sacco, 1894)].
1996	*Neosimnia spelta* (Linnaeus, 1758) – Giannuzzi-Savelli *et al*., p. 180, figs 727a-731.
?*non* 2008	*Neosimnia spelta* (Linné, 1758) – Chirli, p. 50, pl. 17, figs 6-8 [?= *Neosimnia pliomajor* (Sacco, 1894)].
2009	*Neosimnia spelta* (Linnaeus, 1758) – Lorenz & Fehse, p. 98, pl. 124, A216-A218.
2010	*Neosimnia pliomajor* (Sacco, 1894) – Sosso & Dell'Angelo, p. 25, unnumbered fig. p. 34 bottom left (*non* Sacco, 1894).

Material and dimensions – Height 10.7 mm. NHMW 2015/0133/0408 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Not only is the identification of ovulid shells difficult due to the lack of morphological shell features and in some cases the shells of distinct species seem identical until the animal and radula are examined (Landau & Fehse, 2004), but the reverse is also true. Reijnen *et al*. (2010) showed that within Caribbean *Cyphoma* Röding, 1798, some species that could be distinguished based on shell character and mantle colour, were all conspecific based on genetic analysis. Therefore, we approach the classification of fossil ovulids with ever increasing trepidation.
The genus *Neosimnia* Fischer, 1884 was synonymised with *Simnia* Risso, 1826 by WoRMS (Gofas, 2010). Lorenz & Fehse (2009, pl. 122-132) considered the two genera distinct and figured many species of each genus. Certainly, based on the generic attributions of these authors, there seem to be clear differences in shell morphology between *Neosimnia* and *Simnia* species; *Neosimnia* being thicker shelled with a thickened outer lip, whereas *Simnia* species have a wider aperture abapically and an outer lip devoid of varix. Until further molecular data is available, we prefer to consider the two distinct.
The genus *Neosimnia* is represented in the Le Pigeon Blanc by a single somewhat abraded specimen. We have provisionally attributed it to the living Mediterranean *N. spelta* (Linnaeus, 1758) based on its solid shell, considerably thickened outer lip and the flattening of the inner lip between the ventral keel and the cardinal ridge (see Landau & Fehse, 2004, p. 19). The shell is on the small side of the size range for the present day specimens (9-15 mm: Lorenz & Fehse, 2009, p. 98) and somewhat more slender than usual. However, *N. spelta* is variable in shape and similarly slender specimens occur today in the Mediterranean (see Giannuzzi-Savelli *et al*., 1996, fig. 728).
Neosimnia semen (Defrance 1825) from the middle and upper Miocene of north western France differs in being thinner-shelled, in lacking the flattened area on the venter of the last whorl between the ventral keel and the cardinal ridge and in having spiral sculpture along the entire length of the last whorl, whereas in *N. spelta* spiral grooves are restricted to the extremities. The surface sculpture in the Le Pigeon Blanc specimen is abraded, but the shell shape and thickness is that of *N. spelta* rather than *N. semen*. In the Pliocene Mediterranean and adjacent Atlantic *N. pliomajor* (Sacco, 1894) has a rounded venter and is thinly callused, like *N. semen*, spiral sculpture is restricted to the terminals, like *N. spelta*, but differs in having more produced terminals than either *N. semen* or *N. spelta* (Landau & Fehse, 2004). *Neosimnia leathesii* (J. Sowerby, 1824) from the Pliocene North Sea Basin of England, Belgium and The Netherlands is broader-shelled than *N. semen* or *N. pliomajor*. Specimens at hand from England and Belgium (NHMW coll.) are solid shelled, with a groove rather than flattened area between the ventral keel and the cardinal ridge and seem even broader than the broad form of *N. spelta*; a consistent feature in the North Sea Basin Pliocene form. As far as we are aware, this is stratigraphically the earliest record for *N. spelta*, although the shell illustrated by Sosso & Dell'Angelo (2010, p. 34) as *N. pliomajor* from the upper Zanclean to lower Piacenzian of Italy is, in our opinion, more like *N. spelta*, with a short posterior terminal and a greatly thickened and flattened columellar callus.
We provisionally consider these Neogene forms distinct, but in view of the unexpected molecular data of Reijnen *et al*. (2010) discussed above all these forms could represent a single species. We await further genetic data on present-day ovulids to see if the findings by Reijnen *et al*., (2010) are isolated to *Cyphoma* or widespread amongst ovulids.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Lower-upper Pliocene: central Mediterranean, Italy (Sosso & Dell'Angelo, 2010). Present-day: Mediterranean and adjacent Atlantic (Lorenz & Fehse, 2009).

Superfamily Littorinoidea Children, 1834
Family Littorinidae Children, 1834
Subfamily Littorininae Children, 1834
Genus *Eula* Kadolsky, 1973

Type species (by typification of replaced name) – *Paludestrina pendula* Wood, 1872, Pliocene, British Isles.

1872	*Eulimene* Wood, p. 64. Type species (by subsequent designation, Cossmann, 1921): *Paludestrina pendula* Wood, 1872, Pliocene, British Isles. Junior homonym of *Eulimene* Risso, 1826 [Crustacea].
1973	*Eula* Kadolsky, p. 33.

Note – The shell characters of *Eula* Kadolsky, 1973 do not fit with those of the Littorininae and probaby not the Littorinidae either. We have not seen any specimen with the protoconch intact, which might help with its place-

ment, nor have other specialist workers contacted (David Reid, Dietrich Kadolsky personal communication BL, 2016). We provisionally follow the traditional placement of this genus within the Littorinidae (*i.e.* Marquet, 1997a, 1998; Moerdijk & Janse, 2015), but doubt this is correct.

***Eula terebellata* (Nyst, 1835)**
Plate 5, fig. 3

*1835	*Melania terebellata* Nyst, p. 24, pl. 4, fig. 9.
1845	*Melania terebellata* Nyst – Nyst, p. 38, fig. 12.
1848	*Paludestrina* (*?*) *terebellata* Nyst – Wood, p. 109, pl. 12, fig. 7.
1872	*Eulimene terebellata* Nyst – Wood, p. 65.
1878	*Littorina terebellata* Nyst – Nyst, pl. 6, fig. 22.
1882	*Littorina terebellata* Nyst – Nyst, p. 95.
1915	*Littorinopsis* (*Touzinia*) *terebellata* Nyst – Cossmann, p. 63, pl. 3, figs 11, 12.
1921	*Eulimene terebellata* (Nyst) – Harmer, p. 594, pl. 50, fig. 23.
1954	*Eulimene terebellata* (Nyst, 1835) – van Regteren Altena *et al*., p. 62, pl. 3, fig. 31.
1957	*Littorinopsis* (*Eulimene*) *terebellata* Nyst, 1835 – Glibert, p. 22, pl. 1, fig. 21.
1997a	*Eula terebellata* (Nyst, 1835) – Marquet, p. 12, pl. 1, fig. 6.
1998	*Eula terebellata* (Nyst, 1835) – Marquet, p. 57, fig. 32.
2015	*Eula terebellata* (Nyst, 1835) – Moerdijk & Janse, p. 22, fig. 8.

Material and dimensions – Maximum height 6.9 mm. NHMW 2015/0133/0270 (1); LC (10); FVD (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The specimens from Le Pigeon Blanc are identical to that figured by Marquet (1997a, pl. 1, fig. 6) from the upper Pliocene of Belgium. Kadolsky (1973) placed the genus in the Eulimidae. In his revision of the family, Warén (1984) did not include *Eula* in the Eulimidae. Marquet (1997a) suggested placement in the Littorinidae, a position followed here.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Upper Pliocene: Red Crag, England (Wood, 1848, 1872; Harmer, 1921); Oorderen & Kruisschans Sands, Belgium (Marquet, 1997a; 1998); The Netherlands (van Regteren Altena *et al*., 1954; Moerdijk & Janse, 2015). Lower Pleistocene: St. Erth, England (Bell, 1893; Etheridge & Bell, 1898; Harmer, 1921).

Genus *Melarhaphe* Mühlfeld *in* Menke, 1828

Type species (Established in synonymy of *Paludina*) – *Turbo caerulescens* Lamarck, 1822, present-day, Europe.

1828	*Melarhaphe* Mühlfeld *in* Menke, p. 23.
1836	*Melaraphis* Philippi, p. 189. Incorrect subsequent spelling.
1846	*Melarhaphis* Agassiz, p. 54. Incorrect subsequent spelling.
1854	*Melaraphe* H. Adams & A. Adams, p. 314. Incorrect subsequent spelling.

Note – The name *Melarhaphe* was introduced by Menke (1828, p. 23) in the synonymy of *Paludina glabrata* Ziegler *in* C. Pfeiffer (1828, p. 46) and was based on a manuscript name of Megerle von Mühlfeld. The spelling *Melaraphe* does not occur in Menke's paper, but was frequently used by later authors. As transliteration of the greek character *ρ* as occurring in Gr. *ραφε* is either done as *r* or *rh* in Latin, the confusion is understandable. We have not been able to find out who was the first to use *Melaraphe*, but anyway this was an unjustified emendation and Menke's spelling has to be maintained. In 'Nomenclator Zoologicus' Neave, (1940, p. 91) erroneously listed *Melaraphe*, referring to Menke's paper and adding 'also as *Melarhaphe'*. This wrong citation may have been the source of later confusion continuing to the present-day, as is *e.g.* clearly demonstrated in Queiroga *et al*. (2011) who used *Melaraphe* in their texts, but *Melarhape* in their figure captions. In WoRMS (Bouchet & Reid, 2011) the correct name is listed.
Species belonging to the genus *Melarhaphe* Mühlfeld *in* Menke, 1828 are characterised by their relatively thick pyramido-conical shells, flattened or convex whorls, a moderately high pointed spire, a long, straightened columellar inner edge and most importantly by the lack of macroscopic spiral grooves (Kadolsky, 1973; Rosewater, 1981; Reid, 1989).

***Melarhaphe gibbosa* (Etheridge & Bell, 1893)**
Plate 5, fig. 4

*1893	*Littorina gibbosa* Etheridge & Bell *in* Bell, p. 630.
1898	*Littorina gibbosa* Eth. & Bell – Bell, p. 154, pl. 3, fig. 1.
1921	*Littorina gibbosa* Etheridge & Bell – Harmer, p. 664, pl. 53, fig. 24.
1997b	*Littorina* (*Melaraphe* [*sic*]) *gibbosa* – Marquet, p. 12, pl. 1, fig. 4.
1998	*Littorina* (*Melaraphe* [*sic*]) *gibbosa* – Marquet, p. 55, fig. 30.

Material and dimensions – Maximum height 3.8 mm. NHMW 2015/0133/0131 (1), 2015/0133/0132 (8); LC (8); FVD (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The shells from Le Pigeon Blanc of this tiny species of *Melarhaphe* are identical to that figured by Harmer (1921, pl. 53, fig. 24) for *Littorina gibbosa* Etheridge & Bell, 1893 from the Gelasian Pleistocene of St. Erth, Cornwall (England), but also reported by Harmer from the upper Pliocene Red Crag of eastern England and Marquet (1997a, 1998) from the Kattendijk Formation of

Belgium. There is nothing to add to the description given by Harmer (1921, p. 665) and there is little intraspecific variability.

The genus is not speciose in the European Pliocene. *Melarhaphe suboperta* (J. Sowerby, 1813) from the upper Pliocene North Sea Basin Red Crag of England and Kruisschans Sands of Belgium is larger, taller-spired, with a rounded periphery on the last whorl. *Melarhaphe silvae* Landau, Marquet & Grigis, 2004 from the lower upper Pliocene of the Estepona Basin, southern Spain, is most similar to *M. gibbosa* and also has a peripheral keel on the last whorl, but the Spanish species is larger-shelled and the keel is even more accentuated and protruding. *Melarhaphe sacyi* (Cossmann & Peyrot, 1919) from the Atlantic lower Miocene Aquitaine Basin of France is also small-shelled, but more globose, with a rounded last whorl lacking a peripheral keel. *Littorina ariesensis* (Fontannes, 1880) from the Pliocene Mediterranean, placed by some authors in *Melarhaphe*, belongs within the genus *Echinolittorina* Habe, 1956 (see Landau *et al*., 2004a).

This genus is represented by a single living species *M. neritoides* (Linnaeus, 1758). This modern species occurs from Norway to Mauritania, in the Azores and throughout the Mediterranean and Black Sea (Rosewater, 1981). It lacks any trace of a peripheral keel.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Kattendijk Formation, Belgium (Marquet, 1997b; 1998). Upper Pliocene: Red Crag, England (Harmer, 1921). Lower Pleistocene: St. Erth, England (Etheridge & Bell, 1893; Bell, 1898; Harmer, 1921).

***Melarhaphe* sp.**
Plate 5, fig. 5

Material and dimensions – Maximum height 3.9 mm. NHMW 2015/0133/0276 (1); LC (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – We tentatively assign this species to the genus *Melarhaphe* Mühlfeld *in* Menke, 1828, although it has a thinner shell than most *Melarhaphe* species. It is somewhat similar to the Pliocene North Sea Basin *M. suboperta* (J. Sowerby, 1813), but that species is larger and thicker shelled and has a regularly conical spire rather than distinctly shouldered as seen in the Le Pigeon Blanc species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Superfamily Naticoidea Guilding, 1834
Family Naticidae Guilding, 1834
Subfamily Naticinae Guilding, 1834
Genus *Cochlis* Röding, 1798

Type species (by subsequent designation, Hedley, 1916) – *Nerita vittata* Gmelin, 1791, present-day, Morocco.

1798 *Cochlis* Röding, p 146.

Note – In this section we have followed Pedriali & Robba (2005) for our species descriptions. The shell characters are described as defined by these authors (2005, p. 111, fig. 2) and the measurements taken using their method where:

DHW = diameter of first half protoconch whorl;
PD = diameter of protoconch;
PW = number of protoconch whorls;
H = height of shell;
D = maximum diameter;
SH = height of spire;
AH = height of aperture;
AW = width of aperture;
UW = width of umbilicus;
WUC = width of the umbilical callus;
WAB = width of the abapical sulcus;
IS = inner lip slope;
SA = spire angle;
DFW = diameter first protoconch whorl.

We have not found it easy to find the protoconch/teleoconch boundary in our material, so we have added a further measurement, which is DFW = diameter first protoconch whorl. We are greatly endebted to Luca Pedriali and Elio Robba for having examined our material and given us some helpful comments.

***Cochlis robbai* nov. sp.**
Plate 5, figs 6, 7

1964 *Natica plicatelloides* var. *cossmanni* Brébion, p. 344, pl. 8, fig. 3 (*nomen nudum*).

Type material – Holotype, MNHN.F.A53620, height 23.0 mm; paratype 1 NHMW 2015/0133/0333, height 21.8 mm; paratype 2 NHMW 2015/0133/0334, height 30.0 mm; paratype 3 NHMW 2015/0133/0335, height 21.7 mm; paratype 4 NHMW 2015/0133/0336, height 20.3 mm; paratype 5 NHMW 2015/0133/0337, height 33.1 mm.

Other material – Maximum height 34.5 mm. NHMW 2015/0133/0338 (23); FVD (40). Type locality.

Etymology – Named after Elio Robba of the Università degli Studi di Milano-Bicocca, Italy, in recognition of his excellent works on Italian naticids. *Cochlis* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium sized *Cochlis* species with a pau-

cispiral protoconch composed of about 1.75 whorls, an inflated shell, which is not expanded at the outer lip, an umbilicus mostly filled by funicle, a large, broad, rounded funicle, no visible colour pattern, and an operculum bearing a single flattened marginal ridge not delimited by a marginal groove.

Description – Protoconch paucispiral, composed of about 1.75 whorls (junction not clearly preserved), nucleus medium sized. Shell globose, moderately depressed, solid. Spire low-conical, depressed, whorls moderately convex. Suture linear, adpressed. Last whorl inflated, somewhat depressed, moderately produced but not inflated towards aperture, with weakly delimited, gently sloping subsutural shelf. Aperture D-shaped, height averaging 1.3 times width. Parietal callus thick, flattened, subquadrangular, narrowing strongly abapically below basal fasciole; anterior lobe hardly delimited by furrow that can be felt rather than seen. Umbilicus wide, largely filled by funicle. Funicle very stout, strongly rounded, separated from basal fasciole by slit-like furrow. Umbilical callus large to very large, very thick, with prominently arched outline, placed just below mid-columella, separated from parietal callus by deep, reverse J-shaped notch. Basal fasciole blunt, of medium-width, poorly delimited. Surface covered with fine, dense, prosocline growth lines, stronger over subsutural shelf and basal fasciole. No colour pattern preserved.
Operculum moderately thick. Inner margin straight. Inner surface almost flat, with more or less distinct transverse ridges, nucleus not protruding. Outer surface slightly concave. Central callus well developed, elongate, tongue-shaped, curved towards inner margin. A single, flat-topped marginal ridge present, slightly elevated but not delimited by groove.

Discussion – *Cochlis robbai* nov. sp. has a very characteristic shell, with its globose, but not expanded last whorl and its wide umbilicus almost filled by a raised funicle. There is little intraspecific variability; as the shells increase in size the funicle becomes more raised and the umbilical callus thicker. In shell character *C. robbai* is most similar to *Cochlis undata* (Sassi, 1827) from the Pliocene of Italy, which has the same shaped last whorl, expanded but not inflated towards the outer lip and also has the umbilicus mostly filled by a large funicle, but differs most notably by the character of the operculum, which in *C. undata* has two marginal ridges and respective grooves, whereas in *C. robbai* there is a a single, flat-topped marginal ridge, slightly elevated but not delimited by groove. Indeed, none of the many opercula illustrated by Robba & Pedriali lack a groove medial to the ridge as seen in the Pigeon Blanc species.
Brébion (1964, 344) considered this form a subspecies of *Natica plicatelloides* Cossmann & Peyrot, 1919, but as Brébion correctly pointed out, it differs from this species by its much larger funicle. He recorded this species exclusively from the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Cochlis pedrialii* nov. sp.**
Plate 6, figs 1, 2

1964 *Natica millepunctata* var. *sornayi* Brébion, p. 341, pl. 8, fig. 2 (*nomen nudum*).

Type material – Holotype NHMW 2015/0133/0339, height 21.8 mm; paratype 1 NHMW 2015/0133/0340, height 30.0 mm; paratype 2 NHMW 2015/0133/0341, height 21.7 mm; paratype 3 NHMW 2015/0133/0342, height 20.3 mm; paratype 4 NHMW 2015/0133/0343, height 33.1 mm; paratype 5 NHMW 2015/0133/0344, height 33.1 mm; paratype 6 MNHN.F.A57189, height 21.7 mm; paratype 7 MNHN.F.A57190, height 21.7 mm.

Other material – Maximum height 33.5 mm. NHMW 2015/0133/0345 (15); FVD (32). Type locality.

Etymology – Named after Luca Pedriali of Ferrara, Italy, in recognition of his excellent works on Italian naticids. *Cochlis* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium sized *Cochlis* species with a paucispiral protoconch composed of about 1.75 whorls, an inflated shell, which is not expanded at the outer lip, a wide umbilicus that is almost completely open, a very low, broad funicle, a colour pattern of medium-sized

DHW	PD	H	D	SH	AH	AW
270-350 μm	-	21.7-33.1 mm	21.9-32.5 mm	3.8-6.3 mm	15.4-24.9 mm	12.0-19.0 mm
310	-	25.0	25.3	5.1	19.2	14.4

UW	WUC	WAD	WAB	IS	SA	DFW
4.0-7.1 mm	3.2-5.7 mm	0.06-0.12 mm	0.05-0.09 mm	18.4-29.9º	123.3-129.6º	610-630 μm
4.9	4.1	0.09	0.07	25.1	127.3	620

Table 1. Dimensions of *Cochlis robbai* nov. sp., measurements based on type series, taken following Pedriali & Robba (2005).

spots, and an operculum bearing two marginal grooves delimiting a single rounded marginal ridge.

Description – Protoconch paucispiral, composed of about 1.75 whorls, nucleus small. Shell globose, moderately depressed, solid. Spire low-conical, depressed, whorls moderately convex. Suture linear, adpressed. Last whorl inflated, somewhat depressed, moderately produced but not inflated towards aperture, with weakly delimited, gently sloping, slightly concave subsutural shelf. Aperture D-shaped, height averaging 1.3 times width. Parietal callus thick, flattened, subquadrangular, narrowing evenly abapically below basal fasciole; anterior lobe not delimited. Umbilicus very wide, open. Funicle broad, but hardly elevated. Umbilical callus narrow, thick, placed just below middle of columella, in most specimens hardly delimited from narrowing abapical portion of parietal callus. Basal fasciole hardly developed. Surface covered with fine, dense, inconspicuous prosocline growth lines, in most specimens only visible over subsutural shelf and basal fasciole. Colour pattern of medium-sized reddish spots preserved.
Operculum moderately thick. Inner margin straight. Inner surface almost flat, with more or less distinct transverse ridges, nucleus not protruding. Outer surface flat. Central callus moderately wide, rounded, tongue-shaped, with straight inner margin. Two marginal grooves and one ridge; outer groove rather wide, moderately deep, inner usually narrower and shallower. Outer ridge between grooves moderately wide, round-topped.

Discussion – The *Cochlis* species from Le Pigeon Blanc are easily separated in two groups; those with an umbilicus almost filled by the funicle: *C. robbai* (see above), and those with a wide, open umbilicus, the funicle reduced to a low but broad rounded swelling: *C. pedrialii* nov. sp. Neither species shows any significant intraspecific variability. Several Italian Pliocene species also have a low funicle. *Cochlis depressofuniculata* (Sacco, 1891) has a much narrower funicle, which although low, is more distinct than that of *C. pedrialii*. The operculum of *C. depressofuniculata* differs in having two marginal ridges. *Cochlis raropunctata* (Sassi, 1827) also has a wide open umbilicus, but with a narrow, low funicle running through as opposed to the much broader funicle in *C. pedrialii*. Again the operculum of *C. raropunctata* differs in having two marginal ridges.
Brébion (1964, p. 342) recorded this species from Assemblage III localities (Le Pigeon Blanc, Palluau).

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Subfamily Poliniceinae Finlay & Marwick, 1937
Genus *Euspira* Agassiz *in* J. Sowerby, 1837

Type species (by subsequent designation, Bucquoy *et al*., 1883) – *Natica glaucinoides* J. Sowerby, 1812, Pliocene, British Isles.

1837 *Euspira* Agassiz *in* J. Sowerby, p. 14.
1847b *Lunatia*, Gray, p. 149. Type species (by original designation): *Natica ampullaria* Lamarck, 1822 [= *Euspira heros* (Say, 1822)], present-day, north eastern Atlantic.
1919 *Labellinacca* Cossmann, p. 188. Type species (by original designation): *Natica labellata* Lamarck, 1804, Eocene, France.

***Euspira bononiensis* (Foresti, 1884)**
Plate 6, fig. 3

*1884 *Natica bononiensis* Foresti, p. 312, pl. 1, figs 8, 9.
1964 *Euspira exvarians* Sacco, 1891 – Brébion, p. 351, pl. 8, figs 13-15.
2009 *Euspira bononiensis* (Foresti, 1884) – Pedriali & Robba, p. 388, pl. 1, figs 1-3, pl. 3, figs 1, 2, 21, 22 (*cum syn.*).
2011 *Euspira bononiensis* (Foresti, 1884) – Landau *et al*., p. 16, pl. 5, fig. 10.

Material and dimensions – Maximum height 26.1 mm. NHMW 2015/0133/0346 (1), 2015/0133/0347 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Euspira bononiensis* (Foresti, 1884) is characterised by having a protoconch of 2-2.2 whorls, a deep umbilicus, a broad markedly depressed funicle and a deep inner furrow. The shell can vary widely both in inflation and in thickness. The shells from Le Pigeon Blanc are not perfectly preserved and are missing the protoconch. However, the teleoconch characters are those of the species.
Euspira bononiensis was fully discussed and compared with its congeners *E. catena* (Da Costa, 1778) and *E.*

DHW	PD	H	D	SH	AH	AW
140-150 μm	930 μm	21.7-29.1 mm	23.4-28.8 mm	5.1-7.9 mm	15.3-21.4 mm	13.7-17.3 mm
145		25.6	26.0	6.4	19.3	15.1

UW	WUC	WAD	WAB	IS	SA	DFW
3.9-6.5 mm	2.0-3.6 mm	0.07-0.16 mm	0.07-0.12 mm	26.3-30.1º	129-133º	370-430 μm
4.7	2.6	0.1	0.09	26.5	129.3	40

Table 2. Dimensions of *Cochlis pedrialii* nov. sp., measurements based on type series, taken following Pedriali & Robba (2005).

helicina (Brocchi, 1814) by Pedriali & Robba (2009). They considered *Natica* (*Naticina*) *catena* var. *exvarians* Sacco, 1891 a synonym, which extended the range of this previously Mediterranean species to the Pliocene of the North Sea Basin, by including references to *Euspira exvarians* by Marquet (1997b, 1998). Landau *et al*. (2011) also recorded it from the Lower Pliocene Atlantic Guadalquivir Basin of Spain. These NW French records help to fill the geographical gap between the southern and northern records. Pedriali & Robba (2009, p. 390) suggested this species became extinct during the late Pliocene. Brébion (1964) recorded it from Assemblage IV localities (Gourbesville, Bosq d'Aubigny), which are late Pliocene-Pleistocene. We also note that two species described by Harmer (1921); *Natica* (*Lunatia*) *cavellii* and *N.* (*L.*) *assimilis*, considered subjective synonyms of *Euspira exvarians* by Marquet (1997b, 1998), are also Pleistocene species. If these synonymies are correct, it seems that the species survived into the Pleistocene at the northern end of its wider Pliocene distribution.

Distribution – Upper Miocene: Proto-Mediterranean (Tortonian): Italy (Pedriali & Robba, 2009). Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, Spain (Landau *et al*., 2011); North Sea Basin, Coralline Crag, England (Harmer, 1921); central Mediterranean, Italy (Pedriali & Robba, 2009). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1921), Oorderen Sands, Belgium (Marquet, 1998); central Mediterranean, Italy (Pedriali & Robba, 2009). Upper Pliocene-Pleistocene: NW France (Brébion, 1964).

***Euspira guillemini* (Payraudeau, 1826)**
Plate 6, fig. 4

*1826	*Natica guillemini* Payraudeau, p. 119, pl. 5, figs 25, 26.
1997	*Euspira guillemini* (Payraudeau, 1826) – Giannuzzi-Savelli *et al*., p. 194, figs 786-788, p. 220, fig. 822.
2009	*Euspira guillemini* (Payraudeau, 1826) – Pedriali & Robba, p. 392, pl. 1, figs 10, 11, pl. 3, fig. 7, pl. 4, figs 7-9 (*cum syn.*).
2013	*Euspira guillemini* (Payraudeau, 1826) – Landau *et al*., p. 103, pl. 12, fig. 4, pl. 62, fig. 5.

Material and dimensions – Maximum height 3.0 mm. NHMW 2015/0133/0348 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The only specimen we can ascribe to *Euspira guillemini* (Payraudeau, 1826) is very small, although it may not be fully grown. Landau *et al*. (2013) noted that the Serravallian middle Miocene Turkish specimens were also considerably smaller than the mean height of just over 10 mm given by Pedriali & Robba (2009, p. 393). Apart from its small size, it is characterised by its rather elevated spire, broad and strongly depressed funicle, an umbilicus bearing a broad inner furrow and no internal spiral sculpture. The species is most easily recognised by its paucispiral protoconch consisting of about 1.5 smooth whorls with a large nucleus. The protoconch measurements of the Le Pigeon Blanc shell (dp = 970 μm, dn = 330 μm) are similar to those given by Pedriali & Robba (2009, p. 393; dp = 740-900 μm, dn = 250-280 μm).

Distribution – Middle Miocene: Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Lower Pliocene: Atlantic, NW France (this paper). Pliocene (unspecified): central Mediterranean, Italy (Pedriali & Robba, 2009). Pleistocene (unspecified): central Mediterranean, Italy (Pedriali & Robba, 2009). Present-day: north eastern Atlantic from Great Britain to Canary Islands, Mediterranean (Pedriali & Robba, 2009).

***Euspira varians* (Dujardin, 1837)**
Plate 6, fig. 5

*1837	*Natica varians* Dujardin, p. 281, pl. 19, fig. 6.
1919	*Natica* (*Lunatia*) *varians* var. *meridionalis* Cossmann & Peyrot, p. 430, pl. 11, figs 35-38.
1952a	*Polynices* (*Euspira*) *varians* Dujardin, 1837 – Glibert, p. 248, pl. 1, fig. 7.
1964	*Euspira varians* Dujardin, 1837 – Brébion, p. 347.
?1969	*Polinices* (*Euspira*) *helicinus varians* (Dujardin, 1837) – Janssen, p. 165, pl. 5, figs 8, 9.

Material and dimensions – Maximum height 19.2 mm. NHMW 2015/0133/0349 (1); NHMW 2015/0133/0350 (40); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Euspira varians* (Dujardin, 1837) is closely similar to *E. helicina* (Brocchi, 1814), from which it differs by being thicker-shelled, having a more elevated spire, and having the umbilicus almost filled by callus (Glibert, 1952a). As noted by Cossmann & Peyrot (1919), the shell adjacent to the suture is often eroded, giving the spire an exaggeratedly scalate appearance; this is not so in well-preserved specimens. Having said that, there is some variability within the specimens from Le Pigeon Blanc at to height of spire, inflation of the last whorl and the degree to which the callus fills the umbilicus. Indeed some of the specimens approximate to some of the slenderer forms of *E. helicina* illustrated by Pedriali & Robba (2009, pl. 1, fig. 13). Nevertheless, they can be easily separated based on protoconch characters. *Euspira helicina* has a multispiral protoconch of 2.5-2.75 whorls, whereas the specimens here identified as *E. varians* have a paucispiral protoconch with a large nucleus. The protoconch/teleoconch boundary is not easily seen (Pl. 6, fig. 5d), but it is composed of about 1.25 whorls (PD ≈ 500 μm, DHW ≈ 120 μm) (there is a crack at just over two whorls, but we do not believe this to be the protoconch/teleoconch boundary. There is a change in shell colour and texture at about 1.25 whorls, but as stated above, the exact position of the boundary is unclear). We have not seen the

protoconch of the German Miocene material from Dingden identified as *E. varians* by Janssen (1969), and we provisionally exclude it from the distribution, as almost no species are common to these two assemblages.
Brébion (1964, p. 348) recorded this species from Assemblage I (Reneauleau, Les Pierres Blanches, Thorigné, Contigné), Assemblage III (Le Pigeon Blanc, Palluau, Le Girondor, La Gauvinière, La Dixmerie) and Assemblage IV (St-Jean-la-Poterie).

Distribution – Middle Miocene: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1919), Loire Basin, France (Glibert, 1952a). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Euspira* sp.**
Plate 7, fig. 1

Material and dimensions – Height 7.4 mm. NHMW 2015/0133/0358 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – A single specimen of a small *Euspira* species is at hand, which is characterised by its moderately elevated, stepped conical spire composed of convex whorls, its strongly inflated last whorl, its wide umbilicus bearing a very fine rib abapically, but no funicle is developed. The umbilical callus is thickened, but narrow, continuous with the small anterior lobe of the parietal callus, which is totally detached from the almost non-existant posterior lobe. The basal fasciole is not delimited, broad and rounded. The protoconch is preserved (Pl. 7, fig. 1d); it seems to consist of about two whorls, but we cannot be sure of the position of the protoconch/teleoconch boundary. The presence of the abapical umbilical rib led us to place this species in the genus *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, 1883 (see below). However, in view of the absence of a funicle, placement in *Euspira* might be more appropriate [Robba and Pedriali, personal communication (BL), 2015]. We can find no species with which to compare this species.

Distribution – Lower Pliocene: NW France (this paper).

Genus *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, 1883

Type species (by original designation) – *Nerita intricata* Donovan, 1804, present-day, British Isles.

1883 *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, p. 137, 149.

Note – Based on molecular data, Huelsken *et al*. (2008, 2012) synonymised *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, 1883 with *Euspira* Agassiz *in* J. Sowerby, 1837. We follow Robba *et al.* (2016) in retaining *Payraudeautia* as valid on account of its distinctive open umbilicus with an inner spiral ridge or cord abapical to the funicle.

***Payraudeautia pigeonblancensis* nov. sp.**
Plate 6, figs 6, 7

Type material – Holotype NHMW 2015/0133/0351, height 8.9 mm; paratype 1 NHMW 2015/0133/0352, height 7.7 mm; paratype 2 NHMW 2015/0133/0353, height 7.0 mm; paratype 3 NHMW 2015/0133/0354, height 7.5 mm; paratype 4 NHMW 2015/0133/0354, height 7.5 mm; paratype 5 NHMW 2015/0133/0355, height 6.2 mm; paratype 6 MNHN.F.A57191, height 6.7 mm; paratype 7 MNHN.F.A57192, height 5.7 mm.

Other material – Maximum height 6.0 mm. NHMW 2015/0133/0357 (16); LC (15); FVD (8). Type locality.

Etymology – Named after the type locality of Le Pigeon Blanc. *Payraudeautia* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Payraudeautia* species with a protoconch of 2.6 whorls, a slightly stepped spire, an incised suture, a wide umbilicus, a moderately depressed funicle, a short umbilical callus and a prominent umbilical rib.

Description – Protoconch multispiral, turbiniform, composed of 2.6 convex whorls, with small nucleus. Teleoconch globose, slightly depressed, solid. Spire low, conical, moderately depressed, whorls convex, giving spire slightly stepped aspect. Suture linear, incised. Last whorl inflated, somewhat depressed, hardly expanded towards aperture; subsutural shelf poorly differentiated, narrow; periphery mid-whorl. Aperture D-shaped, peristome rather thick, height 1.3 times width. Parietal callus thickened, but narrow, with concave outer border; anterior lobe ending at basal fasciole; posterior lobe hardly developed, reduced to thickening adjacent to lip insertion. Umbilicus deep, very large, bounded by rounded basal fasciole, markedly excavated within, bearing two rib-like structures: lower is a prominent, elevated, round-topped spiral ridge terminating in a semielliptical, asymmetric plug on abapical part of columella; upper rib is funicle, which is narrow, moderately depressed, separated from inner spiral ridge by broad, deep groove. Umbilical callus relatively thick, merging with anterior lobe of parietal callus. Basal fasciole poorly differentiated. Surface covered with faint growth lines.

Discussion – Two species within the genus *Payraudeautia* were recognised by Pedriali & Robba (2009) in the Italian Pliocene: *P. fasciolata* (Sacco, 1890) and *P. intri-*

DHW	PD	H	D	SH	AH	AW
85μm	1000 μm	6.2-8.9 mm	6.5-8.5 mm	1.7-2.5 mm	4.6-6.4 mm	3.4-4.6 mm
		7.5	7.4	2.0	5.5	3.9

UW	WUC	WAD	WAB	IS	SA	DFW
1.9-2.3 mm	-	-	1.2-1.5 mm	24.1-34.6º	120-135.6º	260 μm
2.1	-	-	1.4	28	127.5	

Table 3. Dimensions of *Payraudeautia pigeonblancensis* nov. sp., measurements based on type series, taken following Pedriali & Robba (2005). WUC and WAD could not be measured when shell photographed in position suggested by Pedriali & Robba (2005, p. 111, fig. 2), as these structures disappear under the overhanging basal fasciole.

cata (Donovan, 1804). *Payraudeautia pigeonblancensis* nov. sp. can be separated from *P. intricata* by the character of its multispiral protoconch composed of 2.6 whorls; *P. intricata* has a protoconch of 1.5-1.7 whorls. *Payraudeautia fasciolata* also has a protoconch of 2.6 whorls, but the French Pliocene species differs in having a slightly stepped spire, an incised suture, a wider umbilicus, a less depressed funicle, a shorter umbilical callus and, above all, the umbilical rib is much more prominent.
Brébion (1964, p. 354) recorded *P. intricata* from the upper Miocene Tortonian Assemblage I locality of Beaulieu. In view of the close similarity between *Payraudeautia* species and the poor figure given by Brébion, we provisionally exclude it from the synonymy and distribution and will review this record when Assemblage I is reviewed.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Subfamily Sininae Woodring, 1928
Genus *Sinum* Röding, 1798

Type species (by subsequent designation, Dall, 1915) – *Helix haliotoidea* Linnaeus, 1758, present-day, Indo-Pacific.

1798 *Sinum* Röding, p. 14.
1799 *Sigaretus* Lamarck, p. 77. Type species (by monotypy): *Helix haliotoidea* Linnaeus, 1758, present-day, Indo-Pacific.
1805 *Sigaretarius* Duméril, p. 164. Type species (by subsequent designation, Kabat, 1991): *Helix haliotoidea* Linnaeus, 1758, present-day, Indo-Pacific.
1835 *Catinus* Oken, p. 416. Type species (by monotypy): *Helix haliotoidea* Linnaeus, 1758, present-day, Indo-Pacific.

***Sinum striatum* (de Serres, 1829)**
Plate 7, fig. 2

*1829 *Sigaretus striatus* de Serres, p. 127, pl. 3, figs 13, 14.
2006 *Sinum haliotoideum* (Linné, 1758) – Chirli (*partim*, *non* Linnaeus, 1758), p. 72, pl. 27, figs 7-16 (not Pleistocene to present-day records).
2009 *Sinum striatum* (de Serres, 1829) – Pedriali & Robba, p. 413, pl. 2, figs 18-20, pl. 3, fig. 20, pl. 4, fig. 24 (*cum syn*.).
2011 *Sinum striatum* (de Serres, 1829) – Landau *et al*. (*partim*), p. 16, pl. 6, fig. 7 (*cum syn*.; not Pleistocene to present-day records).
2013 *Sinum striatum* (de Serres, 1829) – Landau *et al*. (*partim*), p. 110, pl. 12, fig. 5 (*cum syn*.; not Pleistocene to present-day records).

Material and dimensions – Maximum diameter 27.3 mm x 21.6 mm, height 12.5 mm. NHMW 2015/0133/0215 (1), 2015/0133/0216 (1); FVD (1 + 1 incomplete). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was fully discussed by Pedriali & Robba (2009) and Landau *et al*. (2013). However, Landau *et al*. (2011, 2013) failed to note that Pedriali & Robba (2009) had distinguished the living Mediterranean and West African specimens as a distinct species; *S. bifasciatum* (Récluz, 1851), differing from *S. striatum* (de Serres, 1829) in having a larger 3-whorled protoconch with a rapidly expanding last whorl, a more depressed teleoconch and sculptured by more numerous spiral cords separated by shallow, narrow grooves. According to these authors *S. striatum* first appeared in the middle Miocene and became extinct towards the end of the Pliocene.
The specimens from Le Pigeon Blanc are small compared to specimens from other European Pliocene localities, but otherwise have the same shape and sculpture. The protoconch is multispiral, composed of just over 2.5 whorls.

Distribution – Lower Miocene: Paratethys (Burdigalian): Austria (Steininger, 1973). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), Loire Basin, France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1923; Bałuk, 1995), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966), Romania (Moisescu, 1955); Proto-Mediterranean Sea (Serravallian): Karaman

Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): Cacela, Portugal (Dollfus *et al*., 1903); Proto-Mediterranean (Tortonian): Tunisia (Stchepinsky, 1938). Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011), Morocco (Lecointre, 1952); north eastern Spain (Martinell, 1979; Solsona, 1998); France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1890b; Glibert 1963; Malatesta, 1974; Cavallo & Repetto, 1992; Chirli, 2006), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2013); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1970, 1976; Chirli, 1988). Pliocene (indet.): central Mediterranean, Italy (Pedriali, 1996; Lacroce, 1997; Pedriali & Robba, 2009).

Superfamily Rissooidea Gray, 1847
Family Rissoidae Gray, 1847
Subfamily Rissoinae Gray, 1847
Genus *Alvania* Risso, 1826

Type species (by subsequent designation, Nevill, 1885) – *Alvania europea* Risso, 1826 (= *Turbo cimex* Linnaeus, 1758), present-day, Mediterranean.

1826 *Alvania* Risso, p. 140.

1847a *Turbona* Leach *in* Gray, p. 271. Type species (by subsequent designation, Gray, 1847b): *Turbo reticulatus* 'Montagu' J. Adams, 1797 [= *Alvania beanii* (Hanley *in* Thorpe, 1844)], present-day, Europe.

1852 *Zocanthusa* Leach, p. 194. Type species (by subsequent designation, Coan, 1964): *Turbo reticulatus* 'Montagu' J. Adams, 1797 [= *Alvania beanii* (Hanley *in* Thorpe, 1844)], present-day, Europe.

1884a *Acinus* Monterosato, p. 161. Type species (by subsequent designation, Crosse, 1885): *Turbo cimex* Linnaeus, 1758, present-day, Mediterranean.

1884a *Acinopsis* Monterosato, p. 162. Type species (by subsequent designation, Crosse, 1885): *Turbo cancellatus* Da Costa, 1778, present-day, Europe.

1884a *Thapsia* Monterosato, p. 227. Type species (by monotypy): *Rissoa rudis* Philippi, 1844, present-day, Mediterranean. Junior homonym of *Thapsia* Albers, 1850 [Pulmonata].

1884b *Actonia* Monterosato, p. 61. Type species (by subsequent designation, Crosse, 1885): *Rissoa testae* Aradas & Maggiore, 1843, present-day, Europe.

1884 *Massotia* Bucquoy, Dautzenberg & Dollfus, p. 298. Type species (by original designation): *Rissoa lactea* Michaud, 1830, present-day, Europe.

1885 *Thapsiella* Fischer, 1885, p. 721. Type species (by monotypy): *Rissoa rudis* Philippi, 1844, present-day, Mediterranean. *Nov. nom. pro. Thapsia* Monterosato, 1884a.

1890 *Alcidia* Monterosato, p. 147. Type species (by monotypy): *Alcidia spinosa* Monterosato, 1890, Pleistocene, Italy. *Rissoa spinosa* is a replacement name for *Rissoa angulata* Seguenza, 1903, *non* Eichwald, 1830. Junior homonym of *Alcidia* Westwood, 1879 [Lepidoptera] and *Alcidia* Bourguignat, 1889 [Gastropoda Streptaxidae]

1891 *Arsenia* Monterosato, 1891. Type species (by subsequent designation, Cossmann, 1921): *Turbo punctura* Montagu, 1803, present-day, British Isles.

1895b *Alveniella* Sacco, p. 25. Type species (by original designation): *Rissoa scabra* Philippi, 1844, present-day, Mediterranean.

1895b *Galeodinopsis* Sacco, p. 28. Type species (by original designation): *Rissoa tiberiana* Coppi, 1876, Pliocene, Italy.

1903 *Acinulus* Monterosato *in* Seguenza, p. 48. Type species (by original designation): *Rissoa cimicoides* Forbes, 1844, present-day, British Isles.

1921 *Alcidiella* Cossmann, p. 26. Type species (by typification of replaced name): Type species (by monotypy): *Alcidia spinosa* Monterosato, 1890, Pleistocene, Italy. *Nom. nov. pro Alcidia* Monterosato, 1890, *non* Westwood, 1879 [Lepidoptera].

1967 *Pseudalvania* Janssen, p. 129. Type species (by original designation): *Pseudalvania dingdensis* Janssen, 1967, Miocene, Germany.

1972 *Andrewiella* Nordsieck, p. 176. Type species (by original designation): *Rissoa macandrewi* Manzoni, 1868, present-day, Madeira and Canary Islands.

1972 *Masotiella* Nordsieck, p. 182. Type species (by original designation): *Rissoa sublaevis* Boettger, 1906, Miocene, Romania.

1972 *Lanciella* Nordsieck, p. 191. Type species (by original designation): *Rissoa lanciae* Calcara, 1845, present-day, Mediterranean.

1972 *Alvanolira* Nordsieck, p. 192. Type species (by original designation): *Alvania lineata* Risso, 1826, present-day, France.

1972 *Coronalvania* Nordsieck, p. 194. Type species (by original designation): *Alvania* (*Coronalvania*) *corona* Nordsieck, 1972, present-day, Spain.

1975 *Profundialvania* Taviani, p. 207. Type species (by original designation): *Alvania heraelaciniae* Ruggieri, 1949, Pliocene, Italy.

***Alvania calasi* nov. sp.**
Plate 7, figs 3-5

Type material – Holotype NHMW 2015/0133/0148 height 2.9 mm, width 1.9 mm; paratype 1 NHMW 2015/0133/0149 height 2.8 mm, width 1.9 mm; paratype 2 NHMW 2015/0133/0150 height 2.8 mm, width 1.8 mm; paratype 3 MNHN.F.A57195, height 2.8 mm, width 1.8 mm; paratype 4 MNHN.F.A57196, height 2.8 mm, width 1.8 mm

Other material – Maximum height 3.5 mm. NHMW 2015/0133/0151 (38); LC (10); FVD (7). Type locality.

Etymology – Named after Pierre Calas, in recognition

of his work on the Redonian rissoid gastropods. *Alvania* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Alvania* species with a paucispiral protoconch bearing rows of micropustules, a squat shell with a globose last whorl bearing predominantly spiral sculpture composed of strongly sinuous and opisthocline axial ribs, which on last whorl are obsolete over base, about ten weak spiral cords, of which adapical two are slightly stronger, and a wide aperture with a flaring outer lip.

Description – Shell small, rissoiform, globose. Protoconch low dome-shaped, paucispiral, consisting of 1.75 whorls, with large nucleus (dp = 435 μm, hp = 220 μm), sculptured by spiral rows of micropustules. Teleoconch consisting of three convex whorls, with periphery at abapical suture. Suture linear, impressed. Axial sculpture consisting of very close-set, strongly opisthocline and sinuous, narrow ribs, separated by wider interspaces, rib spacing increasing abapically. Spiral sculpture consisting of about ten narrow spiral cords, visible only in interspaces between ribs; adapical two cords slighty more strongly developed. Last whorl globose, strongly convex in profile, base not delimited, bearing about 24 sinuous axial ribs, obsolete over base, and 17-19 narrow spiral cords. Aperture wide, ovate, peristome complete, outer lip not thickened by varix, flared abapically, columella short, thickened abapically, parietal callus thin, forming narrow callus rim.

Discussion – *Alvania calasi* nov. sp. is most similar to the species illustrated by Brébion (1964, pl. 4, figs 20, 21) as *Alvania* (*Massotia*) *apiniacensis* (*nomen nudum*) from the Assemblage II locality of Apigné. However, it differs from *A. calasi* in having 1) a less globose shell, 2) a higher domed protoconch of 2.2 whorls, with spiral cords instead of micropustules, 3) fewer axial ribs, 4) lacking the well-developed anal sinus forming a distinctive notch adapically on the outer lip seen in *A. calasi*. This species will be described in the subsequent paper covering the Assemblage II rissoiids.
Alvania lactanea Glibert 1949 from the middle Miocene of the Loire Basin is similar, but this species is smaller-shelled, less globose, has finer sculpture, and the axial ribs are not sinuous. There are no similar species occurring in the present-day European seas.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Alvania dissensia* nov. sp.**
Plate 7, fig. 1; plate 8, figs 1, 2

Type material – Holotype NHMW 2015/0133/0146, height 8.3 mm; paratype 1 MNHN.F.A57393, height 7.0 mm; paratype 2 NHMW 2015/0133/0262, height 5.0 mm; paratype 3 NHMW 2015/0133/0263, height 8.4 mm; paratype 4 NHMW 2015/0133/0273, height 8.5 mm.

Other material – LC (2). Type locality.

Etymology – From the Latin '*dissensio*', noun meaning dissension, disagreement, reflecting the difference of opinion amongst our malacological colleages as to the affinities of this species. *Alvania* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – An *Alvania* species with a large shell for the genus, an elevated, conical spire, sculpture composed of 9-10 narrow, elevated, ribs, spiral sculpture reduced and present only below mid-whorl on last whorl and base, and a simple outer lip.

Description – Shell small, rissoiform, with elevated conical spire. Protoconch not preserved. Teleoconch consisting of six or seven weakly convex whorls, with periphery at abapical suture. Suture undulating, impressed. Axial sculpture consisting of 9-10 narrow, elevated, rounded orthocline to slightly opisthocline ribs, roughly half as wide as their interspaces. Spiral sculpture reduced to a single narrow cord above suture on penultimate whorl and weak to subobsolete cords on last whorl below mid-whorl and on base. Last whorl moderately inflated, roundly angled at periphery; base convex, imperforate. Aperture ovate, outer lip simple, not thickened by varix, somewhat flared abapically. Columella short, slightly thickened, parietal callus thin, forming narrow callus rim.

Discussion – This species is placed in the genus *Alvania* Risso, 1826 with some hesitation. Although superficially rissoid in shape, this species is relatively large for *Alvania* (maximum height 8.5 mm), the spire is relatively tall and the outer lip is not thickened as in most *Alvania* species. Protoconch morphology may well have helped, but unfortunately is missing in all the material at hand. We wondered if a cerithiid placement was more appropriate. Photographs were sent to malacological colleagues for their suggestions. Of those that replied, opinions were split almost 50/50 as to whether this was a rissoid or not. As we can find no better placement we provisionally place it in the genus *Alvania* stressing with the choice of trivial name the discomfort we feel with this decision.
It is difficult to find any species with which to compare *Alvania dissensia* nov. sp. *Alvania lachesis* (de Basterot, 1825) [= *A. curta* (Dujardin, 1837)], widespread in the Loire Basin Miocene (Glibert, 1949; Brébion, 1964), has similar axial sculpture, but differs in being smaller shelled, lower spired and in having spiral sculpture in the interspaces between the axial ribs on all whorls.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Alvania lachesis* (de Basterot, 1825)**
Plate 8, fig. 3; Plate 9, figs 1, 2

*1825	*Turbo Lachesis* de Basterot, p. 27, pl. 1, fig. 4.
1837	*Rissoa curta* Dujardin, p. 279, pl. 19, fig. 5.
1854	*Rissoa Ovata* Millet, p. 154 (*nomen nudum*).
1865	*Rissoa ovata* Millet, p. 580.
1920	*Alvania curta* Dujardin – Harmer, p. 611, pl. 51, figs 24, 25.
1949	*Alvania* (*Alvania*) *curta* Dujardin – Calas, p. 165.
1964	*Alvania curta* Dujardin, 1837 – Brébion, p. 151.
2013	*Alvania lachesis* (de Basterot, 1825) – Landau *et al*., 2013, p. 70, pl. 6, fig. 4, pl. 57, fig. 5 (*cum syn*.).

Material and dimensions – Maximum height 5.3 mm. NHMW 2015/0133/0134 (1), NHMW 2015/0133/0135 (1), 2015/0133/0136 (40); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Alvania lachesis* (de Basterot, 1825) was discussed by Kowalke & Harzhauser (2004, p. 118) under the name *Alvania* (*Alvania*) *curta* (Dujardin, 1837). The two taxa were synonymised by Lozouet *et al*. (2001) and further discussed by Landau *et al*. (2013, p. 71).
The specimens from Le Pigeon Blanc are indistinguishable from the shell from the middle Miocene Loire Basin figured by Glibert (1949, pl. 6, fig. 3a). The protoconch is multispiral, composed of about 3.5 whorls (Pl. 9, figs 1, 2). Unfortunately the surface is too abraded to show any microsculpture (see Landau *et al*., 2013).
Its presence in the Le Pigeon Blanc assemblage is the first published record of the species in the Pliocene. Brébion (1964, p. 152) reported the species from numerous localities representing Assemblages I-IV, extending the stratigraphic record of the species to the Gelasian. Landau *et al*. (2013) questioned the presence of *A. lachesis* in the British Gelasian lower Pleistocene of St Erth (Harmer, 1920, p. 611, pl. 51, figs 24, 25), mainly due to the wide stratigraphic gap between the last known occurrence in the Tortonian and the Gelasian, but this gap seems to have been filled with its occurrence in all these NW French assemblages.

Distribution – Lower Miocene: Atlantic (Aquitanian-Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1919; Lozouet *et al*., 2001); Proto-Mediterranean Sea (late Burdigalian): Antalya Basin, Turkey (İslamoğlu & Taner, 2003). Lower-middle Miocene: North Sea Basin (upper Burdigalian-Langhian): Germany (Gürs & Weinbrecht, 2001; Moths *et al*., 2010). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1928; Bałuk, 1975), Slovakia (Hörnes, 1856; Švagrovský, 1981), Hungary (Strausz, 1954, 1966; Bohn-Havas, 1973), Czech Republic (Kowalke & Harzhauser, 2004), Bosnia (Atanacković, 1985); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (Sacco, 1895b), (lower Tortonian) Antalya Basin, Turkey (İslamoğlu & Taner, 2003). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: St Erth, British Isles (Harmer, 1920).

***Alvania merlei* nov. sp.**
Plate 8, figs 4, 5; Plate 9, fig. 3

Type material – Holotype MNHN.F.A57193, 3.9 mm; paratype 1 MNHN.F.A57194, 3.8 mm; paratype 2 NHMW 2015/0133/0143, height 4.0 mm; paratype 3 NHMW 2015/0133/0144, height 3.9 mm.

Other material – Maximum height 4.5 mm. NHMW 2015/0133/0145 (45); LC (50+); FVD (50+). Type locality.

Etymology – Named after Dr Didier Merle of the MNHN Paris for his help in finding Brébion's specimens and facilitating the loan of this material. *Alvania* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A slender *Alvania* species with a paucispiral protoconch; protoconch II bearing spiral cords separated by narrow grooves, teleoconch sculpture consisting of narrow, strongly opisthocline axial ribs, 14-15 on penultimate whorl, overrun by narrow spiral cords, nine on penultimate whorl, not forming tubercles at intersections, a short last whorl and a small aperture with a weakly thickened, somewhat expanded outer lip.

Description – Shell small, rissoiform, slender, with elevated spire. Protoconch dome-shaped, consisting of two convex whorls, with large nucleus (dp = 425 μm, hp = 435 μm, dn = 125 μm); protoconch I smooth, protoconch II bearing eight spiral cords separated by narrow irregular grooves. Junction with teleoconch sharply delimited. Teleoconch consisting of 4.5 convex whorls, with periphery just below mid-whorl. Suture linear, deeply impressed. Spiral sculpture starting at protoconch/teleoconch boundary, consisting of four narrow spiral cords on first teleoconch whorl, increasing in number abapically, nine on penultimate whorl, of subequal strength and disposition, but with ad- and abapical cords slightly more strongly developed. Axial sculpture starting one-quarter whorl after protoconch/teleoconch boundary, consisting of narrow, elevated, strongly opisthocline ribs, one-quarter the width of their interspaces, 14-15 on penultimate

whorl. Spiral cords overrun axial ribs, without forming tubercles. Last whorl 50% of total height, regularly rounded, sculptured by axial ribs that weaken at periphery, not persisting onto base; base poorly delimited, spiral sculpture on entire last whorl. Aperture small, 34% of total height, ovate. Outer lip weakly thickened by labial varix, regularly convex below, slightly expanded abapically, smooth within. Peristome complete, narrow, slightly raised abapically, bordering narrow umbilical groove.

Discussion – Despite the genus *Alvania* Risso, 1826 being speciose in the European Miocene to present-day faunas, both the protoconch and teleoconch are highly sculptured, facilitating separation at species level. *Alvania merlei* nov. sp. is easily distinguished from its congeners based on its paucispiral protoconch; protoconch II sculptured by broad cords separated by irregular grooves and its tall slender teleoconch with a short last whorl and small aperture. We can find no Pliocene to present-day European species with which we can usefully compare this species. *Alvania spiralis* Glibert, 1949 from the middle Miocene Loire Basin has similar sculpture, but differs in being smaller shelled, less slender, with a proportionately taller last whorl and aperture. The protoconch is similar to that of *A. merlei*, composed of two whorls with a large nucleus, but protoconch II bears a sculpture of spiral threads (based on Tortonian specimens from Sceaux-d'Anjou; to be reviewed).

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Alvania zetlandica* (Montagu, 1815)**
Plate 8, fig. 6; Plate 9, fig. 4

*1815	*Turbo Zetlandicus* Montagu, p. 194, pl. 13, fig. 3.
1848	*Rissoa Zetlandica* Mont. – Wood, p. 101, pl. 11, fig. 7.
non 1856	*Rissoa Zetlandica* Mont. – Hörnes, p. 566, pl. 48, fig. 11 [= *Manzonia miocrassicosta* (Sacco, 1895)].
1920	*Manzonia zetlandica* (Montagu) – Harmer, p. 622, pl. 50, figs 51, 52.
non 1932/33	*Manzonia(Taramellia) zetlandica* Montagu – Mezzerics, p. 332 [= *Manzonia miocrassicosta* (Sacco, 1895)].
1949	*Alvania (Taramellia) zetlandica* Montagu, 1914 [*sic*] – Calas, p. 167.
1964	*Alvania* (*Taramellia*) *zetlandica* Montagu, 1811 [*sic*] – Brébion, p. 167, pl. 4, figs 24, 25.
2004a	*Alvania zetlandica* (Montagu, 1815) – Landau *et al*., p. 45, pl. 9, fig. 4 (*cum syn*.).
2006	*Alvania zetlandica* (Montagu, 1815) – Marquet & Landau, p. 26, fig. 6/1a-d (*cum syn*.).
2006	*Alvania zetlandica* (Montagu, 1815) – Chirli, p. 39, pl. 19, figs 9-16.
2011	*Alvania zetlandica* (Montagu, 1815) – Tabanelli *et al*., p. 48, fig. 24.
2013	*Alvania zetlandica* (Montagu, 1815) – Raad *et al*., p. 47, figs 3, 4.

Material and dimensions – Maximum height 4.7 mm. NHMW 2015/0133/0137 (1), NHMW 2015/0133/0138 (1), 2015/0133/0139 (25); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Alvania zetlandica* (Montagu, 1815) is a very characteristic species with a coarse sculpture, in which axial and spiral sculptural elements are almost of equal strength, and with a double-rimmed inner lip. Unfortunately the protoconch sculpture in our specimens is somewhat eroded (Pl. 9, fig. 4b), but some sculpture preserved is identical to that illustrated by Giannuzzi-Savelli *et al*. (1996, fig. 480d) for the extant species. The protoconch dimensions for the Le Pigeon Blanc specimen illustrated are similar to those described by Fretter & Graham (1978) (dp = 285 μm). This species was described by Harmer (1920) under the genus *Manzonia* Brusina 1870, however, it does not have the pitted spiral microsculpture characteristic to the genus (Moolenbeek & Faber, 1987a-c).
Alvania zetlandica was discussed by Gofas (1999), with its sibling species in the Recent West African fauna; *Alvania gofasi* (Rolán & Fernandes, 1990), found from Senegal and northern Angola, which has a smaller squatter, less elongated shell, seldom larger than 2 mm, whereas Recent shells of *A. zetlandica* are usually 4-5 mm in height.
Brébion (1964, p. 169) recorded this species from Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place, Chalonnes), Assemblage III (Palluau) and Assemblage IV (Gourbesville).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Calas, 1949; Brébion, 1964); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920), Luchtbal Formation, Belgium (Marquet & Landau, 2006); central Mediterranean, Italy (Chirli, 2006). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1920); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Anfossi *et al*., 1983; Tabanelli *et al*., 2011). Pliocene (indeterminate): The Netherlands (Beets, 1946; van Regteren Altena *et al*., 1954; Raad *et al*., 2013). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: Atlantic, British Isles (Harmer, 1920); central Mediterranean, Italy (Cerulli-Irelli, 1914; Di Geronimo & La Perna, 1997). Present-day: Atlantic, Norway, southwards to Morocco, Mediterranean (Poppe & Goto, 1991).

***Alvania ziziphina* Calas, 1949**
Plate 8, figs 7, 8; Plate 9, fig. 5

*1949	*Alvania* (*Massotia*) *ziziphina* Dollfus *in* Calas, p. 165.
1964	*Alvania* (*Massotia*) *ziziphina* Dollfus in Calas, 1949 – Brébion, p. 165, pl. 4, figs 22, 23.

Material and dimensions – Maximum height 4.7 mm.

NHMW 2015/0133/0140 (1), NHMW 2015/0133/0284 (1), NHMW 2015/0133/0141 (1), 2015/0133/0142 (20); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Revised description – Shell small, rissoiform, with elevated, conical spire. Protoconch consisting of 2-2.25 smooth whorls, with medium-sized nucleus (dp = 560 μm, hp = 450 μm). Teleoconch consisting of four weakly convex whorls, with periphery at abapical suture. Suture linear, weakly impressed. Sculpture consisting of 6-7 weakly developed, broad spiral cords separated by narrow interspaces; the cords slightly more strongly developed below the suture, cords weakening abapically. Axial sculpture of 16-18 weak ribs on first two whorls giving whorls reticulated sculpture, weakening abapically, obsolete by second half of penultimate whorl. Last whorl weakly angled at periphery, base convex, not depressed, bearing subobsolete spiral cords. Aperture pyriform, peristome complete, outer lip slightly flared abapically, columella thickened forming narrow callus rim.

Discussion – Alvania ziziphina Calas, 1949 belongs to a small group of *Alvania* species with weakly reticulated sculpture on the early teleoconch whorls, which quickly weakens leaving the last and often penultimate whorls with only spiral sculpture variably developed. These species were traditionally placed in the genus/subgenus *Massotia* Bucquoy, Dautzenberg & Dollfus, 1884. The Pliocene to present-day Atlantic and Mediterranean *A. lactea* (Michaud, 1830) is larger shelled, has more numerous spiral cords and has a greater expanded last whorl and larger aperture. *Alvania sublaevigata* Boettger, 1906 from the middle Miocene Paratethys is similar in shape to *A. ziziphina*, but has finer spiral sculpture, fine subobsolete spiral ribbing persisting on the adapical half of the last whorl and the periphery is more rounded, not angled as it is in the French species. *Alvania lactanea* Glibert 1949 from the middle Miocene of the Loire Basin is much smaller, has a thinner shell and finer sculpture than any of the species discussed above.
Alvania ziziphina was recorded by Calas (1949) and Brébion (1964, p. 167) from Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place); we can add Reneauleau, Assemblage II localities (Apigné) and Assemblage III (Le Pigeon Blanc). Calas (1949) chose Apigné as the type locality, although he rightly pointed out, the specimens from Le Pigeon Blanc are twice as large as the largest from either Assemblage I or II localities.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Calas, 1949; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Calas, 1949; Brébion, 1964).

***Alvania zbyszewskii* nov. sp.**
Plate 8, figs 9, 10; Plate 9, fig. 6

Type material – Holotype MNHN.F.A57197, 3.1 mm; paratype 1 MNHN.F.A57198, 3.0 mm; paratype 2 NHMW 2015/0133/0285, height 3.5 mm; paratype 3 NHMW 2015/0133/0286, height 3.0 mm; paratype 4 NHMW 2015/0133/0287.

Other material – Maximum height 3.5 mm. NHMW 2015/0133/0288 (50+); LC (50+); FVD (50+). Type locality.

Etymology – Named after Professor Georges Zbyszewski (1909-1999) of the Direcção Geral de Minas e Serviços Geológicos (DGMSG), eminent pioneer of Portuguese geology and palaeontology. *Alvania* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Alvania* species with a paucispiral protoconch; protoconch II bearing irregular spiral cords roughly of equal width to their interspaces, a teleoconch of 3.5 angularly shouldered whorls, sculpture cancellate, axial and spiral elements narrow and of roughly equal strength, two spiral cords on first half teleoconch whorl, three on subsequent spire whorls, four on last whorl above base; about 18 axial ribs and a medium sized aperture, outer lip lirate within, and moderately thickened labial varix.

Description – Shell small, rissoiform, moderately inflated, with weakly scalate, elevated spire. Protoconch low dome-shaped, consisting of two convex whorls, with large nucleus (dp = 405 μm, hp = 120 μm, dp1 = 240 μm, dn = 130 μm); protoconch I abraded, protoconch II bearing about ten interrupted or irregular spiral lines, roughly equal in width to their interspaces. Junction with teleoconch sharply delimited. Teleoconch consisting of 3.5 convex whorls, angled at shoulder, with periphery mid-whorl. Suture linear, impressed. Sculpture openly cancellate, with axial and spiral elements of equal strength. Spiral sculpture starting at protoconch/teleoconch boundary, consisting of two narrow spiral cords on first teleoconch whorl, increasing to three on second and penultimate whorls; adapical cord delimiting relatively broad, flat subsutural ramp. Axial sculpture starting soon after protoconch/teleoconch boundary, consisting of narrow, elevated, orthocline ribs, one-quarter the width of their interspaces, about 18 on penultimate whorl. Spiral cords overrun axial ribs, forming small tubercles at intersections. Last whorl 60% of total height, rounded, sculptured by four spiral cords, base with four further cords, axial ribs weaken over base; base imperforate. Aperture 40% of total height, ovate. Outer lip moderately thickened by labial varix, regularly convex below, expanded abapically, weakly lirate within. Peristome complete, forming narrow callus rim.

Discussion – Alvania zbyszewskii nov. sp. is relatively constant in sculpture, both in the rather slender sculp-

tural elements and in their number. It does, however, show some variability in degree of inflation of the last two whorls. This type of cancellate sculpture is common amongst European fossil and present-day *Alvania* species requiring a lengthy comparison. *Alvania subcrenulata* (Bucquoy, Dautzenberg & Dollfus, 1884) differs in having a coarsely pustular protoconch microsculpture. *Alvania hispidula* (Monterosato, 1884) has a protoconch composed of 2.75 whorls, with microsculpture composed of spiral rows of fine pustules (based on fossil material; Chirli, 2006, pl. 10, figs 4-6), much finer than the lines seen in *A. zbyszewskii*. *Alvania cimicoides* (Forbes, 1844) also has a protoconch composed of 2.75 whorls with reticulate microsculpture of irregular zig-zag spiral threads. All the species compared above have a narrower subsutural platform than *A. zbyszewskii*. *Alvania beanii* (Hanley *in* Thorpe, 1844) has a protoconch of 2.5 whorls with spiral rows of fine pustules and the teleoconch has a finer reticulated sculpture. *Alvania testae* (Aradas & Maggiore, 1844) has a protoconch of 2.5 whorls with both spiral and axial sculpture. *Alvania pagodulina* Sacco, 1895 from the Italian lower Pliocene has a protoconch of 2.5 whorls covered in dense, coarse micropustules and has more numerous spiral cords on the penultimate whorl. *Alvania transiens* Sacco, 1895, also from the Italian lower Pliocene, has a protoconch of three whorls with spiral rows of fine pustules and has an extra spiral cord on the penultimate whorl. *Alvania venus* (d'Orbigny, 1852) from the lower and middle Miocene French Atlantic has a protoconch of 2.5 whorls with lines and pustules on Protoconch I, whilst Protoconch II is almost smooth bearing only a couple of granular threads above the suture (Lozouet *et al*., 2001, pl. 32, fig. 5b, c). We note that the Italian Pliocene shell identified as *A. venus* by Chirli (2006, pl. 19, figs 3-8) is not this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Alvania* sp.**
Plate 9, fig. 7; Plate 10, fig. 1

Material and dimensions – Maximum height 2.4 mm. NHMW 2015/0133/0289-0290 (1), NHMW 2015/0133/0291 (11); LC (5); FVD (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This small *Alvania* species is quite distinctive, characterised by its squat shell, broad axial ribs, strong labial varix and strongly prosocline outer lip margin when viewed laterally. It is uncommon at Le Pigeon Blanc and always abraded, but common at the upper Miocene Assemblage I locality of St-Clément-de-la-Place. We therefore wait until that assemblage is revised to formally describe this species based on the better preserved material.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (this paper).

Genus *Manzonia* Brusina, 1870

Type species (by monotypy) – *Turbo costatus* J. Adams, 1797, present-day, British Isles.

1870 *Manzonia* Brusina, p. 37.

***Manzonia crassa* (Kanmacher, 1798)**
Plate 10, fig. 2

*1798 *Turbo crassus* Kanmacher, p. 638, fig. 20.
1915 *Rissoa* (*Manzonia*) *falunica* de Morgan, p. 234, fig. 17.
1918 *Manzonia costata minuta* Cossmann, p. 380, pl. 16, fig. 22.
1949 *Alvania (Manzonia) costata* Adams, 1919 [*sic*] – Calas, p. 167.
1949 *Alvania* (*Manzonia*) *costata falunica* de Morgan, 1915 – Glibert, p. 102, pl. 5, fig. 22.
1954 *Alvania* (*Manzonia*) *crassa* (Kanmacher, 1798) – van Regteren Altena *et al*., p. 62, fig. 36.
1964 *Folinia* (*Mazonia*) *costata* Adams, 1796 – Brébion, p. 149, pl. 4, figs 9, 10.
2004a *Manzonia crassa* (Kanmacher, 1798) – Landau *et al*., p. 47, pl. 10, fig. 1 (*cum syn*.).
2011 *Manzonia crassa* (Kanmacher, 1798) – Tabanelli *et al*., p. 50, fig. 36.
2013 *Manzonia crassa* (Kanmacher, 1798) – Landau *et al*., p. 74, pl. 58, fig. 5.
2013 *Manzonia crassa* (Kanmacher, 1798) – Raad *et al*., p. 51, fig. 16.

Material and dimensions – Height 2.0 mm. NHMW 2015/0133/0153 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Manzonia crassa* (Kanmacher, 1798) seems to be extremely uncommon in the Le Pigeon Blanc assemblage, represented by a single specimen, despite having searched through over ten kilos of residue under 2.0 mm. This specimen is small compared to those found today, but with the same profile as the specimen illustrated by Giannuzzi-Savelli *et al*. (1996, fig 504). Unfortunately, the protoconch surface is worn, but it consists of just under two whorls, with a medium-sized nucleus; within the range for the Pliocene and present-day specimens (Landau *et al*., 2004a).
Manzonia costata falunica (de Morgan, 1915) from the Atlantic Middle Miocene of France (Glibert, 1949, p. 102, pl. 5, fig. 22) has the same sculpture and protoconch as *M. crassa*, but was said to differ in being smaller than usual for the Pliocene to Recent *M. crassa*, with slightly less elevated whorls, giving the shell a squatter, less elongated appearance. The size, even in present-day populations, is variable; the north Atlantic specimens being larger than the Mediterranean ones (van Aartsen, *et al*., 1984). Based on this, Landau *et al*. (2004a) accepted the middle Miocene French taxon as a valid chrono-subspecies.
However, the presence of typical *M. crassa* in the mid-

dle Miocene Proto-Mediterranean (Landau *et al*., 2004a) and Paratethys (Friedberg, 1923; Bałuk, 1975; Kowalke & Harzhauser, 2004) cast doubt on the validity of this separation. Moreover, Atlantic specimens from the Zanclean lower Pliocene of Le Pigeon Blanc discussed here and upper lower Piacenzian of the Pombal Basin, Portugal (NHMW coll.) are smaller than many of the shells from the middle Miocene of France (Ferrière-Larçon, Loire Basin; NHMW coll.). The middle Miocene shells from Ferrière-Larçon are slightly squatter than the shell figured here from Le Pigeon Blanc, but then again, so are the shells from the Pliocene of the Pombal Basin of Portugal. It seems, therefore, that there are small differences in size, whorl height and strength of the shoulder between both fossil and present-day populations of *M. crassa*, but separation at species/subspecies level is not justified.

Manzonia pontileviensis (de Morgan, 1915), also found in the Atlantic middle Miocene of France is a distinct species, much smaller, with a less scalate spire, weaker axial ribs, less numerous spiral cords and a much narrower outer lip.

Brébion (1964, p. 150) recorded this species from the Assemblage I locality of Beaulieu and the assemblage II locality of Apigné. To this we add the Assemblage III locality of Le Pigeon Blanc.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (de Morgan, 1915; Cossmann, 1918; Glibert, 1949); Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Kowalke & Harzhauser, 2004), Hungary (Strausz, 1966), Poland (Friedberg, 1923; Bałuk, 1975), Romania (Kowalke & Harzhauser, 2004); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: northeastern Atlantic (Tortonian and Messinian): NW France (Brébion, 1964; Calas, 1949); Proto-Mediterranean Sea (Tortonian and Messinian): Po Basin, Italy (Sacco, 1895b; Venzo & Pelosio, 1963). Lower Pliocene: Atlantic, NW France (this paper); central Mediterranean, Italy (Chirli, 2006); Tunisia (Fekih, 1975). Upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Sacco, 1895b; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Tabanelli *et al*., 2011). Lower upper Pleistocene: North Sea Basin, British Isles (Harmer, 1918); western Mediterranean, France (Glibert, 1962); central Mediterranean, Italy (Cerulli-Irelli, 1914; Bucchieri, 1970). Upper Pleistocene: The Netherlands (van Regteren Altena *et al.,* 1954; Raad *et al*., 2013). Present-day: northeastern Atlantic, Norway, southwards to Morocco, Mediterranean, from extreme low tide line to 50 m depth, often on sandy bottoms, but also under stones and in weeds (Poppe & Goto, 1991).

Genus *Rissoa* Desmarest, 1814

Type species (by subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1884) – *Rissoa ventricosa* Desmarest, 1814, present-day, Mediterranean.

1814 *Rissoa* Desmarest, p. 7.

1838 *Loxostoma* Bivona-Bernardi, p. 1. Type species (by subsequent designation, Verduin, 1983): *Loxostoma denticulus* Bivona-Bernardi, 1838 (=*Rissoa monodonta* Philippi, 1836), present-day, Mediterranean.

1841 *Goniostoma* A. Villa & J.B. Villa, p. 29. Type species (by subsequent designation, Coan, 1964): *Turbo auriscalpium* Linnaeus, 1758, present-day, Mediterranean.

1847a *Turboella* Leach *in* Gray, p. 271 [October]. Type species (by subsequent designation, Gray, 1847b [November]): *Turbo parvus* Da Costa, 1778, present-day, British Isles.

1848 *Rissoia* Bronn, p. 1090. Unjustified emendation of *Rissoa* Desmarest, 1814.

1852 *Zippora* Leach, p. 169. Type species (by monotypy): *Zippora drummondii* Leach, 1852 [= *Rissoa auriscalpium* (Linnaeus, 1758)], present-day, British Isles.

1852 *Persephona* Leach, p. 146. Type species (by subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1884): *Rissoa rufilabrum* Alder, 1844 (= *Rissoa lilacina* Récluz, 1843), present-day, British Isles.

1852 *Lamarckia* Leach, p. 147, 195. Leach included the single species '*Lamarckia costata*', based on '*Buccinum costatum*, Da Costa, 1778'. The latter is a recombination, by Da Costa (1778), of *Murex costatus* Pennant, 1777 [Mangeliidae]. However, Leach included in the synonym *Helix labiosa* Montagu, 1803, and from this and other references cited, it is clear that Leach was referring to the species now known as *Rissoa membranacea* (J. Adams, 1800), present-day, Mediterranean.

1884a *Apicularia* Monterosato, p. 139. Type species (by subsequent designation, Crosse, 1885): *Rissoa similis* Scacchi, 1836, present-day, Mediterranean.

1884 *Schwartzia* Bucquoy, Dautzenberg & Dollfus, p. 259, 278. Type species (by original designation): *Loxostoma monodonta* Bivona Bernardi, 1832, Pliocene, Italy.

1878 *Rissostomia* Sars, p. 448. Type species (by monotypy): *Turbo membranaceus* J. Adams, 1800, present-day, British Isles.

1972 *Auriconoba* Nordsieck, p. 170. Type species (by original designation): *Auriconoba janusi* F. Nordsieck, 1972, present-day, Madeira.

1972 *Turboella* (*Nititurboella*) Nordsieck, p. 202. Type species (by original designation): *Turboella allermonti* Nordsieck, 1972 (=*Rissoa similis* Scacchi, 1836), present-day, Mediterranean.

1972 *Apicularia* (*Sfaxiella*) Nordsieck, p. 207. Type species (by original designation): *Rissoa nina* Nordsieck, 1968, present-day, Mediterranean.

1972 *Rissostomia* (*Liavenustia*) Nordsieck, p. 208. Type species (by original designation): *Rissoa lia*

Monterosato, 1884, present-day, Mediterranean.

1972 *Gueriniana* Nordsieck, p. 212. Type species (by original designation): *Rissoa guerinii* Récluz, 1843, present-day, France.

1972 *Goniostoma* (*Elatiella*) Nordsieck, p. 216. Type species (by original designation): *Rissoa elata* Philippi, 1844 [= *Rissoa membranacea* (J. Adams, 1800)], present-day, Italy.

1972 *Rissoa* (*Lilacinia*) Nordsieck, p. 213. Type species (by typification of replaced name): *Rissoa rufilabrum* Alder, 1844 (= *Rissoa lilacina* Récluz, 1843), present-day, British Isles. *Nom. nov. pro Persephona* Leach, 1852, *non* Leach, 1817 [Crustacea].

***Rissoa pouweri* nov. sp.**
Plate 9, fig. 8; Plate 10, figs 3-5

Type material – Holotype NHMW 2015/0133/0131, height 6.4 mm; paratype 1 NHMW 2015/0133/0132, height 6.6 mm; paratype 2 NHMW 2015/0133/0133; paratype 3 NHMW 2015/0133/0209, height 6.8 mm; paratype 4 NHMW 2015/0133/0210, height 6.8 mm; paratype 5 MNHN.F.A57199, height 6.2 mm; paratype 6 MNHN.F.A57200, height 5.8 mm.

Other material – Maximum height 6.5 mm. NHMW 2015/0133/0211 (30); LC (50+); FVD (50+). Type locality.

Etymology – Named after Ronald Pouwer, collection manager Cainozoic Mollusca at the Naturalis Biodiversity Center in Leiden, in recognition of his hard work in the production of the journal Cainozoic Research. *Rissoa* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Rissoa* species, with a moderately elevated, pointed spire, a protoconch consisting of 2.5 convex whorls, a penultimate whorls only slightly swollen above the suture, predominantly axial sculpture consisting of 10-13 narrow ribs and narrow, non-pitted spiral cords, an imperforate base and a thickened, moderately flared outer lip bearing four distinct denticles within.

Description – Shell small, solid, rissoiform, with moderately elevated, pointed, slightly coeloconoid spire. Protoconch conical, consisting of about 2.5 convex whorls, with small nucleus, surface abraded. Transition to teleoconch not clearly delimited. Teleoconch consisting of five weakly convex whorls, with periphery at abapical suture. Penultimate whorl slightly inflated just above suture. Suture impressed, weakly undulating. Axial sculpture consisting of rounded, slightly opisthocline ribs, 10-13 on penultimate whorl, narrower than their interspaces. Ribs not extending to sutures, narrow adapically, widening towards lower suture. Spiral sculpture consisting of fine spiral grooves, visible only in interspaces. Last whorl evenly convex, base poorly delimited, imperforate, axial sculpture weakening over base, spiral sculpture strengthening on base towards aperture. Aperture wide, ovate, peristome complete. Outer lip thickened by broad labial varix, convex, slightly flared and everted abapically, bevelled internally, bearing four elongated denticles within, starting a short distance from lip margin and extending inwards; adapical denticle more strongly developed. Columellar callus thickened forming narrow callus rim, closing umbilicus.

Discussion – We have placed this species in the genus *Rissoa* Desmarest, 1814 rather than *Alvania* Risso, 1826, based on its predominantly axial rather than cancellate sculpture, its pointed, slightly coeloconoid spire, the slight inflation of the penultimate whorl just above the suture and the character of the abapically flared aperture. Some smaller specimens are superficially similar to *Alvania lachesis* (de Basterot, 1825), with which it co-occurs (see above), but they can be distinguished by the shape of the spire, which is regularly conical, shorter and broader in *A. lachesis*, the spiral sculpture, which is coarser in *A. lachesis*, and the shape of the aperture, which is not expanded abapically in *A. lachesis*. *Rissoa pouweri* nov. sp. can be separated from most of its present-day European congeners, such as *R. ventricosa* Desmarest, 1814, *R. variabilis* (Megerle von Mühlfeld, 1824), *R. labiosa* (Montagu, 1803), *R. guerini* Récluz, 1843 and *R. lia* (Monterosato, 1884), by having a less slender shell and narrower axial ribs. Of the living congeners, *R. violacea* Desmarest, 1814 is most similar in shape, but differs in having broader axial ribs and pitted spiral sculpture.
The most similar *Rissoa* to *R. pouweri* is the fossil species *R. basisulcata* Bell *in* Etheridge & Bell, 1898 from the Gelasian Pleistocene of St Erth (see Harmer, 1920, pl. 51, fig. 15). It has the same shape and sculpture and shows the same type of denticulation within the outer lip, but differs in its base '*with a deep sulcus below the periphery, extending from behind the pillar round the base of the shell* (Harmer, 1920, p. 635)'. The base is hardly delimited in *R. pouweri*.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Rissoa s.l.* sp.**
Plate 11, fig. 2

Material and dimensions – Maximum height 3.6 mm. NHMW 2015/0133/0194-0195 (2).

Discussion – We provisionally place this shell in *Rissoa s.l.* sp. The protoconch is somewhat bulbous, composed of two whorls, strongly convex following the nucleus and devoid of microsculpture. The teleoconch consists of four whorls, the penultimate whorl inflated below mid-whorl and also devoid of sculpture, except for fine growth lines.

The last whorl is slightly concave below the suture, convex below. Unfortunately, the outer lip is damaged in all specimens. We await better-preserved material to identify this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Genus *Crisilla* Monterosato, 1917

Type species (by monotypy) – *Turbo semistriatus* Montagu, 1808, present-day, British Isles.

1917 *Crisilla* Monterosato, p. 14.
1972 *Crissilosetia* Nordsieck, p. 163. Type species (by original designation): *Setia pseudocingulata* F. Nordsieck, 1972 [= *Crisilla galvagni* (Aradas & Maggiore, 1844)], present-day, Spain (Mediterranean).

***Crisilla ariejansseni* nov. sp.**
Plate 11, fig. 10

Type material – Holotype NHMW 2015/0133/0361, height 2.1 mm, width 1.1 mm.

Other material – Known only from holotype.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Etymology – Named in honour of Arie W. Janssen of Naturalis, Leiden, The Netherlands, in recognition of his help as editor of the journal Cainozoic Research. *Crisilla* genus feminine

Diagnosis – A *Crisilla* species with a broad, steep, smooth subsutural ramp, well-developed spiral cords below the shoulder, no axial sculpture, a moderately thickened peristome and a weakly varicose outer lip.

Description – Shell small, moderately slender, of medium thickness, ovate conic, non-umbilicate. Protoconch dome-shaped, consisting of two whorls (dp = 370 μm, hp = 220 μm), surface eroded. Teleoconch of three whorls, separated by impressed suture. First teleoconch whorl with two prominent spiral cords; adapical delimiting concave, smooth subsutural ramp, abapical placed just above suture. On second whorl a third cord appears between abapical cord and suture, followed by a fourth cord between ad- and abapical cords, all four cords rapidly becoming equal in strength. Spiral sculpture absent. Last whorl with broad, steep, smooth, concave subsutural ramp, angular at shoulder, convex below, bearing eight subequal cords below shoulder, roughly equal in width to their interspaces. Aperture ovate; peristome continuous, moderately thickened; outer lip weakly varicose.

Discussion – Although represented by a single specimen, this species is very distinctive and worthy of description. *Crisilla ariejansseni* nov. sp. is characterised by its protoconch consisting of two whorls and teleoconch consisting of three angular whorls bearing prominent spiral cords only below the shoulder. It is closely similar in shape and sculpture to *Cingula basteriae* Moolenbeek & Faber, 1986 from the present-day Canary Islands, which also has a broad, steep, smooth subsutural ramp and angular whorls, but in this species there are fewer and wider-spaced spiral cords below the shoulder. *Cingula basteriae* has pitted spiral sculpture on the protoconch and fine spiral lines on teleoconch; unfortunately the protoconch of the Le Pigeon Blanc shell is worn.
Cingula species are characterised by shells with a protoconch of about 1.5 smooth whorls, except for a few weak spiral striae and very weak spiral cords (Ponder, 1985a). The spiral cords in both *C. ariejansseni* and *C. basteriae* are much stronger than typical for the genus *Cingula*. These species are also similar to *Crisilla luquei* Templado & Rolán, 1994 from present-day Cape Verde Islands, which differs from both of the previous species in being less slender, having a larger aperture and having the spiral cords delimiting the shoulder, and base more strongly developed. *Cingula* species are characterised by shells with a protoconch bearing spiral elements and a teleoconch with sculpture of spirals and axial growth lines, the outer lip has no varix and no denticles within (Ponder, 1985a). Gofas (2015b) placed *Cingula basteriae* in the genus *Alvania*. Templado & Rolán (1994) added that *Crisilla* species differ from *Alvania* in being smaller shelled, in being less sculptured, with only the spiral element present, and in lacking a labial varix.It seems therefore that both *C. ariejansseni* and *C. basteriae* would best be placed in the genus *Crisilla*. *Crisilla graxai* Templado & Rolán, 1994, also from the Cape Verde Islands, is similar in shape to *C. ariejansseni*, but differs in having more regularly convex whorls, the cords are wide-spaced and a cord runs mid width on the subsutural ramp. The protoconch in both of these Cape Verde species is paucispiral, consisting of about 1.25 whorls, with strong spiral sculpture. The protoconch of *C. ariejansseni* seems to be smooth, but is abraded and may have had sculpture.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Crisilla* sp.**
Plate 11, fig. 1.

Material and dimensions – Height 2.1 mm. NHMW 2015/0133/0362 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species is represented in the Le Pigeon Blanc material by a single abraded, broken specimen. It seems to have a protoconch of about two whorls, possibly

with some subobsolete spiral sculpture and a teleoconch of about three convex whorls with an incised suture. The teleoconch sculpture is faint, but consists of flattened cords separated by narrow interspaces. We provisionally place it in the genus *Crisilla* Monterosato, 1917, although it has a more pupoid shape than any on the living European congeners. Although extremely uncommon at Le Pigeon Blanc, it is common at the Assemblage I locality of St-Clément-de-la-Place, and will be described based on better-preserved material in the corresponding paper.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (this paper).

Subfamily Rissoininae Stimpson, 1865
Genus *Zebinella* Mörch, 1875

Type species (by original designation) – *Helix decussata* Montagu, 1803, present-day, western Atlantic.

1875 *Zebinella* Mörch, p. 47.
1896 *Pezantia* Cossmann, p. 22. Type species (by original designation): *Rissoa dactyliosa* Deshayes, 1861, Eocene, France.
1956 *Pleneconea* Laseron, p. 402. Type species (by original designation): *Pleneconea angulata* Laseron, 1956, present-day, Queensland, Australia.
1956 *Zymalata* Laseron, p. 416. Type species (by original designation): *Zymalata concinna* Laseron, 1956, present-day, Queensland, Australia.

***Zebinella decussata sensu lato* (Montagu, 1803)**
Plate 10, fig. 6

*1803 *Helix decussata* Montagu, p. 399, pl. 15, fig. 7.
1964 *Rissoina* (*Zebinella*) *decussata* (Montagu, 1803) – Brébion, p. 185, pl. 4, fig. 39.
2004a *Rissoina* (*Zebinella*) *decussata* (Montagu, 1803) *sensu lato* – Landau *et al*., p. 53, pl. 12, fig. 2 (*cum syn*.).
2006 *Rissoina decussata* (Montagu, 1803) – Chirli, p. 52, pl. 23, figs 7-12.
2010 *Rissoina decussata* (Montagu, 1803) – Sosso & Dell'Angelo, p. 22, 32 3rd row middle.
?2013 *Rissoina* (*Zebinella*) cf. *decussata* (Montagu, 1803) – Landau *et al*., p. 77, pl. 6, fig. 13, pl. 58, fig. 8.

Material and dimensions – Maximum height 10.0 mm. NHMW 2015/0133/0269 (1); LC (4); FVD (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was fully discussed by Landau *et al*. (2004a). Unfortunately one cannot be entirely certain of the determination in the absence of the protoconch, which is missing in the Le Pigeon Blanc material, but the size, sculpture and shape fit within the broad range of variability for the species. For comparison with related species, see Landau *et al*. (2004a).
Brébion (1964, p. 186) recorded this species from Assemblage I localities (Reneauleau, Sceaux-d'Anjou, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu) and the Assemblage IV locality of Gourbesville. We add the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Miocene: (Burdigalian) Italy (Sacco, 1895b). Middle Miocene Paratethys, Poland (Bałuk, 1975), ?Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964); Proto-Mediterranean, Tortonian, Italy (Sacco, 1895b). Lower Pliocene: Atlantic, NW France (this paper); central Mediterranean, Italy (Anfossi *et al*., 1982; Chirli, 2006). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Sacco, 1895b; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914).

Family Caecidae Gray, 1850
Subfamily Caecinae Gray, 1850
Genus *Caecum* Fleming, 1813

Type species (by subsequent designation, Gray, 1847b) – *Dentalium imperforatum* Kanmacher, 1798 (= *Dentalium trachea* Montagu, 1803), present-day, temperate Europe.

1813 *Caecum* Fleming, p. 67.

Note – For this genus we follow the measurements as suggested by de Porta *et al*. (1993, p. 3, fig. 2):

L = total length;
D = diameter aperture;
d = diameter of shell at base of septum;
Ls = height of septum.

***Caecum aartseni* nov. sp.**
Plate 10, figs 7-9; Plate 11, figs 3, 4

1964 *Caecum* (*Watsonia*) *hoernesi* Brébion, p. 215, pl. 5, figs 14-16 (*nomen nudum*).

Type material – Holotype MNHN.F.A53613, height 3.0 mm; paratype 1 NHMW 2015/0133/0197, height 2.5 mm; paratype 2 NHMW 2015/0133/0198, height 2.7 mm; paratype 3 NHMW 2015/0133/0199, height 2.6 mm; paratype 4 NHMW 2015/0133/0200, height 2.6 mm.

Other material – NHMW 2015/0133/0197 (50+); FVD (50+). Type locality.

Etymology – Named after Jacobus J. ('John') van Aartsen, research associate at the Naturalis Biodiversity Center, Leiden (The Netherlands) in recognition of his enormous contribution to European malacology, especially the smaller-sized shells. *Caecum* gender neuter.

Diagnosis – A small *Caecum* species, with a pointed septum, a broad ring bordering the aperture, sculpture of 13-17 widely spaced rings at the posterior end, 5-6 closer set rings at the anterior end, with a smooth area between, without any axial sculpture.

Description – Shell small, subcylindrical, curved. Aperture circular, bordered by broad, round-edged, thickened ring. Septum subconical, flattened, with apex placed eccentrically, close to dorsal outer curved shell margin. Septum sloping shallowly from apex to anterior margin; steeply to posterior margin. Sculpture composed of concentric rings; at septal end 13-17 widely spaced (ring density 6-7/500 μm), covering posterior one-third to two-thirds of shell surface; at apertural end 5-6 slightly closer set (ring density 8-9/500 μm), covering anterior quarter of surface, with smooth, or almost smooth area between. No trace of axial sculpture.

Discussion – *Caecum aartseni* nov. sp. is quite distinctive amongst its congeners in having a pointed septum, a ringed aperture and sculpture of wide spaced rings adapically and close set rings near the aperture. The present-day European *C. subannulatum* de Folin, 1870, *C. glabrum* (Montagu, 1803), *C. armoricum* de Folin, 1869 and the fossil *C. banoni* Benoist, 1873 from the middle Miocene of the Loire Basin are immediately separated by having a hemispherical septum. *Caecum clarkii* Carpenter, 1858 is relatively more arched, with a greater difference between the circumference at the aperture and septum, and lacks sculpture. *Caecum auriculatum* de Folin 1868 has a ring around the aperture like the new French species, but differs in having a hemispherical septum with an ear-like projection on the dextral side. *Caecum multiannulatum* de Porta, Martinell & González-Delgado, 1993 from the Zanclean Mediterranean has much finer spiral rings. *Caecum gougeroti* Moroni & Ruggieri, 1985 and *C. tenuicostulatum* de Porta, Martinell & González-Delgado, 1993 from the Zanclean Mediterranean and adjacent Atlantic respectively are separated by having axial sculpture.
The species with the shell most closely similar to the French species is the Pliocene to present-day European *C. trachea* (Montagu, 1803), but this species differs in lacking a ring surrounding the aperture. In *C. trachea* the rings can cover the entire surface, or be absent in the central portion, but if so, a fine axial microsculpture is present (de Porta *et al*., 1993, p. 5, pl. 1, fig. 5), absent in *C. aartseni*. *Caecum mammillatum* Wood, 1848 a fossil species from the Pliocene North Sea Basin is quite different, lacking rings, except for one around the aperture and is sculptured by longitudinal striae. *Caecum tumidum* Carpenter, 1858, another species from the Pliocene North Sea Basin is also entirely or partially transversely rugose and has ring-shaped thickenings, but these are less well-developed than in *C. aartseni*. Moreover, this species has prominent microsculpture consisting of irregular pits, absent in *C. aartseni* (see Hoeksema & Todd, 2015 for further discussion on Pliocene North Sea Basin Caecidae).
Brébion (1964, p. 216) recorded this species from Assemblage I localities (Beaulieu, St-Michel), Assemblage II (Apigné, Vieux Chartres) and Assemblage III (Le Pigeon Blanc).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Caecum glabrum* (Montagu, 1803)**
Plate 11, fig. 5

*1803	*Dentalium glabrum* Montagu, p. 197.
1848	*Caecum glabrum* Mont. – Wood, p. 117, pl. 20, fig. 6.
1912	*Caecum glabrum* Mtg. – Cerulli-Irelli, p. 168, pl. 25, figs 28, 29.
1923	*Caecum glabrum* (Montagu) – Harmer, p. 848, pl. 64, fig. 33.
1949	*Caecum* cf. *glabrum* Montagu, 1803 – Glibert, p. 130, pl. 8, fig. 2.
1955	*Caecum glabrum* (Montagu, 1803) – van Regteren Altena *et al*., p. 29, fig. 57.
1978	*Caecum glabrum* (Montagu, 1803) – Fretter & Graham, p. 234, fig. 195.
1997a	*Caecum glabrum* (Montagu, 1803) – Marquet, p. 18, pl. 4, fig. 4.
1998	*Caecum glabrum* (Montagu, 1803) – Marquet, p. 71, fig. 46.

Specimen	L	D	d	Ls
Holotype	2946 μm	590 μm	440 μm	130 μm
Paratype 1	2678 μm	446 μm	414 μm	91 μm
Paratype 2	2670 μm	550 μm	444 μm	108 μm
Paratype 3	2635 μm	543 μm	395 μm	77 μm
Paratype 4	2623 μm	535 μm	385 μm	82 μm
Range	2946-2623 μm	590-446 μm	440-385 μm	130-77 μm
Mean	2710 μm	533 μm	416 μm	98 μm

Table 4. Dimensions of *Caecum aartseni* nov. sp., measurements based on type series, taken following de Porta *et al*. (1993).

Material and dimensions – Height 3.1 mm. NHMW 2015/0133/0196 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Caecum glabrum* (Montagu, 1803) is characterised by its dome-shaped apical septum and its lack of sculpture. Glibert (1949, p. 130) noted that in the middle Miocene of the Loire Basin, amongst all the caeciid gastropods, there was one specimen of a shell indistinguishable from *C. glabrum*. We can make exactly the same observation; in the Le Pigeon Blanc assemblage, amongst the hundreds of caeciid shells, only one can be ascribed to *C. glabrum*.
Caecum subannulatum de Folin, 1869 also has a dome-shaped apical septum, but differs in having subobsolete rings, as the name would suggest, and a strong ring surrounding the aperture (van Aartsen, 1977). *Caecum banoni* Benoist, 1873 from the middle Miocene of the Loire Basin is larger-shelled. It also has a hemispherical septum, but it is asymmetrical as opposed the regularly dome-shaped in *C. glabrum*.

Distribution – Middle Miocene: Loire Basin, France (Glibert, 1949). Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1923). Upper Pliocene: Red Crag, England (Harmer, 1923); Oorderen Sands, Belgium (Marquet, 1997a, 1998). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912). Pleistocene (indeterminate): Atlantic, British Isles (Harmer, 1923); North Sea Basin, The Netherlands (van Regteren Altena *et al*., 1955); Present-day: Atlantic coasts of Europe from British Isles (Fretter & Graham, 1978), not Mediterranean (Mediterranean records are *C. subannulatum* de Folin, 1870 or *C. auriculatum* de Folin, 1868; van Aartsen, 1977, p. 11).

Superfamily Truncatelloidea Gray, 1840
Family Elachisinidae Ponder, 1985b
Genus *Elachisina* Dall, 1918

Type species (by monotypy) – *Elachisina grippi* Dall, 1918, present-day, California.

1918 *Elachisina* Dall, p. 137.
1943 *Microdochus* Rehder, p. 193. Type species (by original designation): *Microdochus floridanus* Rehder, 1943, present-day, Florida.

***Elachisina* aff. *eritima* (Smith, 1890)**
Plate 10, fig. 10

aff. 2003 *Elachisina eritima* (Smith, 1890) – Rolán & Gofas, p. 70, figs 7-10.

Material and dimensions – Height 3.2 mm. NHMW 2015/0133/0271 (1), LC (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – A single incomplete specimens was available when this monograph was prepared, which broke further during handling for microscopy. A second complete specimen (LC coll.) was found in the last stages of preparation of this work, and too late to photograph. The shell is small and fragile. The protoconch surface is abraded, but seems to consist of 1.5-2 whorls. The teleoconch consists of three evenly convex whorls separated by an impressed suture. The entire whorl surface is covered by fine spiral threads. The aperture is wide, ovate, with a blunt angulation adapically and the outer lip is slightly everted abapically. The peristome is continuous, with a simple outer lip. The umbilicus is narrow, bordered by a sharp ridge and with fine commarginal striae within.
The present-day tropical Atlantic Elachisinidae were reviewed by Rolán & Gofas (2003). Of the species reviewed therein, the specimen from Le Pigeon Blanc is most like *Elaschisina eritima* (Smith, 1890) from the Canary Islands, which is the most globose of the tropical Atlantic species, but differs in having even more globose whorls, separated by a deeper suture and there is no obvious protruding point to the aperture where the umbilical keel meets the columella. This feature is usually well-developed in the Elachisinidae. The family is not restricted to tropical waters, as Warén (1996) transferred *Cingula globuloides* Warén, 1972 to the genus *Elachisina*. This present-day Scandinavian species is as globose as the Le Pigeon Blanc shell, but differs in having the periumbilical keel less strongly developed and lacks sculpture. We await further material to formally describe this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Iravadiidae Thiele, 1928b
Genus *Ceratia* H. Adams & A. Adams, 1852

Type species (by monotypy) – *Rissoa proxima* Forbes & Hanley, 1850, present-day, British Isles.

1852 *Ceratia* H. Adams & A. Adams, p. 359.

***Ceratia ligeriana* (Peyrot, 1938)**
Plate 10, figs 11, 12; Plate 11, fig. 6

*1938 *Cingula* (*Setia*) *ligeriana* Peyrot, p. 108, pl. 2, figs 36, 37.
1949 *Cingula* (*Ceratia*) *falunica* Glibert, p. 100, pl. 5, fig. 19.

Material and dimensions – Maximum height 3.2 mm. NHMW 2015/0133/0190-93 (3), NHMW 2015/0133/0272 (9). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Glibert (1949) was correct to separate this middle Miocene to lower Pliocene French Atlantic form as a distinct species. He named the new species *Cingula*

(*Ceratia*) *falunica*, but later realised this was a junior synonym of *Cingula* (*Setia*) *ligeriana* Peyrot, 1938 (Glibert, 1962, p. 51). In shape it resembles the present-day Atlantic and Mediterranean *Ceratia proxima* (Forbes & Hanley, 1850) in having a truncated apex, but differs in having no trace of spiral sculpture. In having a smooth teleoconch it resembles the middle Miocene to present-day Atlantic and Mediterranean *Hyala vitrea* (Montagu, 1803), but this has a taller protoconch resulting in a more tapered apex. Both Glibert (1949) and Fretter & Graham (1978) argued that the presence/absence of sculpture was insufficient reason to separate *Ceratia* H. Adams & A. Adams, 1852 and *Hyala* H. Adams & A. Adams, 1852. Ponder (1984) tentatively separated the genera based on shell features: absence of spiral sculpture and a more elevated protoconch in *Hyala*, some differences in the central radular tooth, and differences in the end foot. The intermediate shell morphology makes it difficult to assign *C. ligeriana* to one or other genus, or if indeed they should be separated. We maintain it in *Ceratia*, as originally suggested by Glibert (1949).

Distribution – Middle Miocene: Loire Basin (Glibert, 1949). Lower Pliocene: Atlantic, NW France (this paper).

Genus *Pseudonoba* Boettger, 1902

Type species (by monotypy) – *Pseudonoba peculiaris* Boettger, 1902, Miocene, Romania.

1902 *Pseudonoba* Boettger, p. 145.

***Pseudonoba* aff. *striata* (Hörnes, 1856)**
Plate 11, fig. 7

aff. *1856 *Chemnitzia striata* Hörn., Hörnes, p. 541 (*partim*, pl. 43, fig. 21 only).
aff. 2013 *Pseudonoba* aff. *striata* (Hörnes, 1856) – Landau *et al*., p. 78, pl. 7, fig. 1, pl. 58, fig. 9.

Material and dimensions – Height 4.8 mm. NHMW 2015/0133/0193 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The planorbid, depressed protoconch composed of about two whorls places this shell within the Iravadiidae Thiele, 1928. The teleoconch sculpture is similar to that of *Pseudonoba striata* (Hörnes, 1856) (see Landau *et al*., 2013, pl. 7, fig. 1, pl. 58, fig. 9), composed of numerous spiral cords, but in this species the cords are narrow, separated by wide interspaces, whilst in *P. striata* the reverse is true; wide cords separated by narrow grooves. The specimen from Le Pigeon Blanc seems to be thinner shelled than the European iravadiid genera *Pseudonoba*, *Rhombostoma* Seguenza, 1876 and from the middle Miocene of Turkey *Erentozia* Landau, Harzhauser, İslamoğlu & Silva, 2013. So much so, that the specimen crumbled when we attempted to remove it from the SEM stub. In view of the lack of further material, we cannot go further with identification.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Trucatellidae Gray, 1840
Genus *Nystia* Tournouër, 1869

Type species (by typification of replaced name) – *Paludina duchastelii* Nyst, 1836, Oligocene, Belgium. *Nom. nov. pro Forbesia* Rolle, 1859, *non* Goodsir, 1845 [Annelida].

1859 *Forbesia* Rolle, p. 515. Type species (by monotypy): *Paludina duchastelii* Nyst, 1836, Oligocene, Belgium. Junior homonym of *Forbesia* Goodsir, 1845 [Annelida] and *Forbesia* McCoy, 1846 [Trilobita].
1869 *Nystia* Tournouër, p. 91.

***Nystia guillotini* nov. sp.**
Plate 12, fig. 1

Type material – Holotype NHMW 2015/0133/0268, height 3.9 mm, width 2.3 mm.

Other material – Known only from holotype.

Etymology – Named after Dr. Joseph-Ignace Guillotin (1738-1814), French physician who proposed the device for the humane slaughter of sheep. The guillotine was later made infamous by the French Revolution. The name herein reflects the shape of the apex, which appears beheaded. *Nystia* genus feminine.

Diagnosis – A small *Nystia* species with 11 axial ribs on penultimate and last whorls and single suprasutural cord on penultimate whorl.

Description – Shell small, truncated, three whorls preserved; truncated portion closed by almost flat septum. Whorls convex, weakly angled mid-whorl, suture linear, impressed. Axial sculpture on penultimate whorl consisting of 11 low, rounded axial ribs, about one-third the width of their interspaces, orthocline to mid-whorl, weakly angled and slightly opisthocline below, ending at rounded suprasutural cord. Last whorl 70% total height, evenly convex, weakly angled at periphery; axial ribs weaken below mid-whorl, subobsolete over base. Aperture ovate, relatively wide, peristome complete, forming thin rim around aperture. Columella closely appressed, edge slightly everted, bordering small, narrow umbilical chink.

Discussion – This species resembles members of the genus *Bouryia* Cossmann, 1888 (see below) in having a truncated apex. However, we have found no species of this genus with sculpture. We therefore place it in the genus

Nystia Tournouër, 1869, many species of which are axially costate, although *Nystia* species often have a thicker peristome than has the Le Pigeon Blanc shell described herein; for example the type species, *N. duchastelii* (Nyst, 1836).
Although *Nystia guillotini* nov. sp. is represented by a single specimen, the obscure ribbing, angled at the periphery and the single suprasutural cord on the penultimate whorl give this shell quite an unusual sculpture. The closest congener we can find is *Nystia plicata* (d'Archiac & Verneuil, 1845) from the Oligocene of France. It also has a truncated apex, but differs in having more numerous axial ribs, which do not angle the whorls, and lacks any spiral sculpture.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Potamiopsidae Stimpson, 1865
Subfamily Potamiopsinae Stimpson, 1865
Genus *Bouryia* Cossmann, 1888

Type species (by original designation) – *Bouryia polygyrata* Cossmann, 1888, Eocene, France.

1888 *Bouryia* Cossmann, p. 290.
1968 *Glibertiella* Schlickum, p. 41. Type species (by original designation): *Cyclostoma microstoma* Deshayes, 1824, Eocene, France.

Note – We would agree entirely with Schlickum (1968) in separating *Glibertiella* from *Nystia* Tournouër, 1869. In his generic description the author explicitly states that there is no umbilicus, however, a narrow umbilical slit does occur in some species between the columellar callus and the venter, as in *Glibertiella cylindrica* (Cossmann & Peyrot, 1918). The type species of *Nystia*, *Paludina duchastelii* Nyst, 1836 from the Oligocene of Belgium has quite different apertural characters; *Nystia* species have a much wider aperture, with a lip flared by a varix, absent in *Glibertiella*. However, Le Renard (1997) pointed out that *Bouryia* Cossmann, 1888 was based on a juvenile shell in which the apex was not yet decollated. Therefore Cossmann's name has priority.
Three French Miocene species: *Bouryia falunica* Cossmann, 1895, *B. cylindrica* and *B. pontileviensis* (de Morgan, 1920) were all placed in *Glibertiella* by Schlickum (1968).

***Bouryia cylindrica* (Cossmann & Peyrot, 1918)**
Plate 12, fig. 2

1886 *Nystia cylindrica* Dollfus & Dautzenberg, p. 140 (*nomen nudum*).
*1918 *Nystia cylindrica* Cossmann & Peyrot, p. 422, pl. 16, figs 45, 46.
1920 *Nystia cylindrica* Dollfus et Dautzenberg – de Morgan, p. 333, fig. 28.
1949 *Nystia cylindrica* (D. et D. mss.) Cossmann et Peyrot, 1918 – Glibert, p. 95, pl. 5, fig. 15.
1968 *Glibertiella cylindrica* (Cossmann & Peyrot, 1918) – Schlickum, p. 42.

Material and dimensions – Height 6.0 mm. NHMW 2015/0133/0187 (1); LC (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Bouryia cylindrica* (Cossmann & Peyrot, 1918) is extremely uncommon at Le Pigeon Blanc. The illustrated specimen shows a shell with slightly more inflated whorls than that figured from the middle Miocene Loire Basin of France (Glibert, 1949, pl. 5, fig. 15), but otherwise shows well the characters of the species: convex whorls, deep suture, truncated apex and small aperture. *Bouryia pontileviensis* (de Morgan, 1920), also from the middle Miocene Loire Basin, differs in having fewer and less convex whorls, a less impressed suture and a smaller aperture. The older *B. falunica* Cossmann, 1895 from the Aquitanian lower Miocene of the Aquitaine Basin has a smaller, almost regularly cylindrical shell shape, with superficial sutures and weakly convex whorls.

Distribution – Middle Miocene: Loire Basin (Cossmann & Peyrot, 1918; de Morgan, 1920; Glibert, 1949). Lower Pliocene: Atlantic, NW France (this paper).

Family Tornidae Sacco, 1896 (1884) = Adeorbidae Monterosato, 1884 (based on invalid genus name)
Subfamily Torninae Sacco, 1896 (1884)
Genus *Tornus* Turton & Kingston, 1830

Type species (by monotypy) – *Helix subcarinata* Montagu, 1803, present-day, British Isles.

1830 *Tornus* Turton & Kingston, no 73, unnumbered page.
1842 *Adeorbis* Wood, p. 530. Type species (by subsequent designation, Gray, 1847): *Helix subcarinata* Montagu, 1803, present-day, British Isles. Junior objective synonym of *Tornus* Turton & Kingston, 1830, with the same type species.

***Tornus primitivus* Moroni & Ruggieri, 1985**
Plate 11, fig. 8

*1985b *Tornus pedemontanus primitivus* Moroni & Ruggieri, p. 180, fig. 2.

Material and dimensions – Maximum diameter 2.3 mm. NHMW2015/0133/0178-0179 (2), LC (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Moroni & Ruggieri (1985b) described *Tornus pedemontanus primitivus* from the upper Miocene of

Italy that was extremely similar to *Tornus pedemontanus* Pavia, 1980, at the time known only from the lower Pliocene of Italy, which differed in being smaller shelled, in having a slightly narrower umbilicus, which was bordered by a weaker carina and in lacking a mid-basal carina. This mid-basal carina is well illustrated by Chirli (2006, pl. 32, figs 3, 5) and is present in all specimens at hand from the lower Pliocene of Italy (Pietrafitta, Terre Rosse, Siena) and from a single specimen from the Atlantic Guadalquivir Basin of southern Spain (Landau *et al*. 2011, pl. 3, fig. 8). Specimens from the Tortonian upper Miocene of Cacela Velha, southern Portugal are closely similar to the Italian upper Miocene form, and consistently lack the mid-basal cord. They differ slightly from the Italian shells in being larger shelled and in having the periumbilical and peribasal cords strongly developed, we consider these Portuguese Tortonian specimens provisionally to represent *T.* cf. *primitivus*. Several shells are present in the Le Pigeon Blanc assemblage, which are indistinguishable from *T. primitivus*. The species group is represented in the northwestern French Assemblage I localities by *T. pedemontanus*, and will be discussed in the relevant paper. The density of axial ribs is somewhat variable in all these forms and they all have a protoconch of about 2-2.25 whorls. The taxonomy of the group is further complicated by the description of *T. erici* Rolán & Rubio (2002) from present-day West Africa; Ivory Coast to Angola, which also lacks a mid-basal cord and seems to differ from all of the above only in having a slightly rounder profile to the shell.
What is striking is that within a population there is little variability (apart from in the density of axial riblets). It is therefore more likely that we are dealing with a species group than a single polymorphic taxon.

Distribution –Upper Miocene: Proto-Mediterranean, Italy (Moroni & Ruggieri, 1985b). Lower Pliocene: Atlantic, NW France (this paper).

***Tornus subcarinatus* (Montagu, 1803)**
Plate 11, fig. 9; Plate 12, fig. 3

*1803	*Helix subcarinata* Montagu, p. 438, pl. 7, fig. 9.
1848	*Adeorbis subcarinatus* Mont. – Wood, p. 139, pl. 15, fig. 8.
non 1916	*Tornus subcarinatus* (Montagu, 1803) – Cerulli-Irelli, p. 489, pl. 59, fig. 13.
1923	*Adeorbis subcarinatus* (Montagu) – Harmer, p. 756, pl. 60, fig. 20.
1954	*Tornus subcarinatus* (Montagu, 1803) – van Regteren Altena *et al*., p. 64, fig 46.
1978	*Tornus subcarinatus* (Montagu, 1803) – Fretter & Graham, p. 229, figs 191, 192.
?*non* 1984	*Tornus subcarinatus* (Montagu, 1803) – van Aartsen *et al*., p. 15, fig. 054.
1996	*Tornus subcarinatus* (Montagu, 1803) – Giannuzzi-Savelli *et al*., p. 126 fig. 553 only (not figs 552, 554).
?*non* 1998	*Tornus subcarinatus* (Montagu, 1803) – van Aartsen *et al*., p. 136, figs 1, 3.
2002	*Tornus subcarinatus* (Montagu, 1803) – Rolán & Rubio (*partim*), p. 8, figs 1-6 (Atlantic specimens only; not figs 7-14).
2006	*Tornus subcarinatus* (Montagu, 1803) – Chirli, p. 79, pl. 32, figs 7-12.

Material and dimensions – Maximum diameter 3.0 mm. NHMW2015/0133/0175-0176 (2), NHMW2015/0133/0177 (50+); LC (29); FVD (15). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – There is a problem with the species concept as accepted at present; that is, paucispiral and multispiral specimens are considered conspecific. This was highlighted by van Aartsen *et al*. (1998) and Rolán & Rubio (2002), who both noted that Atlantic specimens had multispiral protoconchs of about 2.1-2.25 whorls, with a small nucleus (counting including first half whorl: Rolán & Rubio, 2002, figs 5, 6; van Aartsen *et al*. 1998, fig. 7) and Mediterranean specimens had paucispiral protoconchs of 1.25-1.4 whorls, with a larger nucleus (Rolán & Rubio, 2002, figs 13, 14; van Aartsen *et al*., 1998, fig. 7). There is also a difference in the protoconch diameter (Atlantic specimens have a diameter of 420-480 μm: Mediterranean specimens, 330-350 μm). We do not agree with van Aartsen *et al*. (1998) that the protoconch of both forms follow along the same (logarithmic) spiral and this can best be seen in the figures given by Rolán & Rubio (2002).
Whilst the number of whorls in species with multispiral protoconchs can vary by up to a whorl, the differences in the protoconch between the Atlantic and Mediterranean specimens of '*Tornus subcarinatus*' (Montagu, 1803) suggest distinct modes of development, especially taking account of the difference in the nucleus. We suspect that this is a cryptic species, which today consists of two species: a planktotrophic species in the Atlantic and a lecithotrophic one in the Mediterranean. This separation seems to be rather sharp, with specimens from Tarifa belonging to the Atlantic form and specimens from Tanger the Mediterranean form (van Aartsen *et al*., 1998, p. 136). The Atlantic form is true *T. subcarinatus*, as the type is from the British Isles. The Mediterranean form does not seem to have any applicable valid name (van Aartsen *et al*., 1998, p. 136).
The fossil record is interesting. The specimens from Le Pigeon Blanc have multispiral protoconchs, similar in number of whorls and size to those found in the Atlantic today (n=2.4, dp = 440 μm, dn = 37 μm, dp1 = 100 μm; Pl. 11, fig. 9d). However, the lower Pliocene specimens illustrated by Chirli (2006, pl. 32, figs 8, 12) clearly show the multispiral protoconch, whilst specimens at hand from Pleistocene Italian localities (Torente Stirone, Piacenza; Vallei Belice, Sicily; NHMW coll.) have paucispiral protoconchs like the present-day Mediterranean form. We would suggest that *T. subcarinatus* was widespread in the Atlantic and Mediterranean in the Pliocene, but at some stage during the upper Pliocene or lower Pleistocene was replaced in the Mediterranean by a cryptic

species with a direct mode of development. Hopefully genetic studies will test this hypothesis in the future.
Glibert (1949) separated the Langhian middle Miocene specimens from the Loire Basin of France under the subspecies *T. subcarinatus minor*, according to the author based solely on their smaller size compared to present-day specimens. We have not seen this species, nor have we found *T. subcarinatus* in the Tortonian Assemblage I localities of northwest France. Until we are able to examine this species/subspecies and its protoconch, we follow Glibert in separating the two.
Although *T. subcarinatus* has been found in the Pliocene and Pleistocene of the British Isles, it has not been found in the Belgian assemblages, where it is replaced in the upper Pliocene Oorderen and Kruisschans Sands by *T. belgicus* (Glibert, 1949). This species differs from *T. subcarinatus* in having a more depressed spire, in having weaker primary spiral sculpture, closer-set and weaker axial ribbing between the primary spirals as opposed to the strong, wide spaced axial ribs seen in *T. subcarinatus*, and in wider umbilicus, which is round instead of sharp bordered. *Tornus subcarinatus* has, however, been found in Pleistocene deposits from The Netherlands (van Regteren Altena *et al*., 1954).

Distribution –Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1923; central Mediterranean, Italy (Chirli, 2006). Upper Pliocene: Red Crag, England (Wood, 1848; Harmer, 1923). Pleistocene (indeterminate): Atlantic, British Isles (Harmer, 1923); North Sea Basin, The Netherlands (van Regteren Altena *et al*., 1954); Present-day: Atlantic coasts of Europe from British Isles to Tarifa (Fretter & Graham, 1978).

Subfamily Teinostomatinae Cossmann *in* Cossmann & Peyrot, 1917
Genus *Solariorbis* Conrad, 1865

Type species (by subsequent designation, Dall, 1892) – *Delphinula depressa* I. Lea, 1833, Eocene, Alabama, USA.

1865 *Solariorbis* Conrad, p. 30.
1958 *Vitrinella* (*Striovitrinella*) Olsson & McGinty, p. 31. Type species (by original designation): *Vitrinella elegans* Olsson & McGinty, 1958, present-day, Caribbean.

***Solariorbis woodi* (Hörnes, 1856)**
Plate 12, figs 4, 5

*1856 *Adeorbis Woodi* Hörnes, 1856, p. 440, pl. 44, fig. 4.
1918 *Tinostoma* [*sic*] (*Solariorbis*) *Dollfusi* Cossmann, p. 89, 345, pl. 2, figs 45, 46.
1964 *Solariorbis dollfusi* Cossmann, 1918 – Brébion, p. 124, pl. 3, fig. 15.
2013 *Solariorbis woodi* (Hörnes, 1856) – Landau *et al*., p. 89, pl. 7, fig. 12, pl. 61, fig. 2.

Material and dimensions – Maximum diameter 4.1 mm. NHMW 2015/0133/0172-0173 (2), NHMW 2015/0133/0174 (50+); LC (50+); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Cossmann (1918, p. 345) described the specimens from Le Pigeon Blanc as a new species: *Tinostoma* (*Solariorbis*) *dollfusi*. He compared his new species with *S. planibasis* (Cossmann & Peyrot, 1917) from the Serravallian middle Miocene of Orthez, Basses Pyrénées of France, but this species is different, with an even more depressed spire, the spire whorls having stronger spiral sculpture, the disc on the base devoid of sculpture wider than in *S. planibasis*, and the columellar callus broader and more extensive. Neither Cossmann (1918) nor Brébion (1964) compared *T.* (*S.*) *dollfusi* with *Solariorbis woodi* (Hörnes, 1856), widespread in the European Miocene and Pliocene, which we consider conspecific.
Landau *et al*. (2004a, 2011, 2013) argued that the Miocene and Pliocene forms represented a single variable species. The variability in the height of the spire and the width of the umbilicus, which can be almost closed to narrow and deep, was well illustrated in the Italian Pliocene shells figured by Chirli (2006, pl. 25, figs 8-15). This same variability is shown here in the specimens from Le Pigeon Blanc (Pl. 12, figs 4, 5).
Brébion (1964, p. 125) recorded this species (as *S. dollfusi*) only from Assemblage III localities (Le Pigeon Blanc, Le Girondor, La Gauvinière).

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896c), (late Burdigalian): Antalya Basin, Turkey (İslamoğlu & Taner, 2003). Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Friedberg, 1928; Bałuk, 1975), Hungary (Strausz, 1954, 1966), Bulgaria (Kojumdgieva & Strachimirov, 1960); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1896c). Lower Pliocene: Atlantic, NW France (Cossmann, 1918; Brébion, 1964); Guadalquivir Basin, Spain (González-Delgado, 1985; Landau *et al*., 2011); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Pavia, 1975; Chirli, 2006), Tunisia (Fekih, 1975). Lower upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); central Mediterranean (Sacco, 1896c; Cavallo & Repetto, 1992; Sosso & dell'Angelo, 2010).

Superfamily Tonnoidea Suter, 1913 (1825)
Family Tonnidae Suter, 1913 (1825)
Genus *Malea* Valenciennes, 1832

Type species (by subsequent designation, Herrmannsen,

1847) – *Cassis ringens* Swainson, 1822, Pliocene-present-day, tropical American Pacific.

1832 *Malea* Valenciennes, p. 324.
1929 *Quimalea* Iredale, p. 345. Type species (by original designation): *Buccinum pomum* Linnaeus, 1758, present-day, Indo-West Pacific.

***Malea orbiculata* (Brocchi, 1814)**
Plate 12, fig. 6

*1814 *Buccinum orbiculatum* Brocchi, p. 647, pl. 15, fig. 22.
2004b *Malea orbiculata* (Brocchi, 1814) – Landau *et al*., p. 39, pl. 1, fig. 2 (*cum syn*.).
2009 *Malea orbiculata* (Brocchi, 1814) – Landau *et al*., p. 64, pl. 1, figs 7-10 (*cum syn*.).
2011 *Malea orbiculata* (Brocchi, 1814) – Landau *et al*., p. 18, pl. 7, fig. 5 (*cum syn*.).
2013 *Malea orbiculata* (Brocchi, 1814) – Landau *et al*., p. 123, pl. 17, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 83.7 mm. FVD (1); LC (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – As discussed by Landau *et al*. (2004b, p. 40), Brocchi (1814) figured a juvenile specimen, which does not have the thickened outer lip or the strong columellar armour so characteristic of the adult shell. This led Deshayes (1833, p. 194) to describe an adult specimen under the name *Dolium denticulatum*. The Le Pigeon Blanc shells do not differ from specimens found in numerous north eastern Atlantic and Mediterranean Miocene and Pliocene localities, as discussed by Landau *et al*. (2004b).

Distribution – Lower Miocene: Paratethys (Burdigalian): Hungary (Kókay, 1967). Middle Miocene: Atlantic (Langhian): Aquitaine Basin, France (Cossmann & Peyrot, 1924); Paratethys (Langhian-Serravallian): Poland (Bałuk, 1995), Vienna Basin, Austria (Hörnes, 1852; Hoernes & Auinger, 1884; Harzhauser, 2004; Landau *et al*., 2009), Hungary (Csepreghy-Meznerics, 1954; Strausz, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian), Algarve, Cacela Basin, Portugal (Pereira Da Costa, 1867); Proto-Mediterranean Sea (Tortonian), Italy (Sacco, 1890b). Lower Pliocene: Atlantic, NW France (this paper); Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004b), north eastern Spain (Martinell, 1979; Solsona, 1998, 1999), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1890b; Cavallo & Repetto, 1992; Chirli, 2008). Upper Pliocene: central Mediterranean, Italy (Sacco, 1890b; Glibert, 1963; Caprotti, 1970; Damarco, 1992).

Family Cassidae Latreille, 1825
Subfamily Cassinae Latreille, 1825
Genus *Galeodea* Link, 1807

Type species (by monotypy) – *Galeodea echinophora* Link, 1807 (= *Buccinum echinophorum* Linnaeus, 1758), Miocene to present-day, southern Europe-Mediterranean.

1807 *Galeodea* Link, p. 113.
1810 *Morio* de Montfort, p. 479. Type species (by monotypy): *Morio echinophora* de Montfort, 1810 (= *Buccinum echinophorum* Linnaeus, 1758), Miocene to present-day, southern Europe-Mediterranean.
1816 *Cassidaria* Lamarck, p. 3. Type species (by subsequent designation, Children, 1823): *Cassidaria echinophora* Lamarck, 1816 (= *Buccinum echinophorum* Linnaeus, 1758), Miocene to present-day, southern Europe-Mediterranean.
1817 *Echinora* Schumacher, p. 75, 249. Type species (by monotypy): *Echinora tuberculosa* Schumacher, 1817 (= *Buccinum echinophorum* Linnaeus, 1758), Miocene to present-day, southern Europe-Mediterranean.
1825 *Echinophora* Latreille, p. 194 (error?; emendation of *Echinora* Schumacher, 1817?).
1937 *Taieria* Finlay & Marwick, p. 67. Type species (by original designation): *Taieria allani* Finlay & Marwick, 1937, Paleocene, New Zealand.
1939 *Mambrinia* Gardner, p. 23. Type species (by original designation): *Cassidaria planotecta* Meyer & Aldrich, 1886, middle Eocene, southeastern USA.
1939 *Gomphopages* Gardner, p. 25. Type species (by original designation): *Galeodea (Gomphopages) turneri* Gardner, 1939, Middle Eocene, Texas, USA.
1942 *Caliagaleodea* B.L. Clark, p. 118. Type species (by original designation): *Galeodea (Caliagaleodea) californica* B.L. Clark, 1942, Eocene, western USA.
1957 *Galeoocorys* Kuroda & Habe, p. 27. Type species (by original designation): *Galeodea leucodoma* Dall, 1907, present-day, north-west Pacific.

***Galeodea echinophora* (Linnaeus, 1758)**
Plate 12, figs 7, 8; Plate 13, fig. 1

*1758 *Buccinum echinophorum* Linnaeus, p. 735.
1964 *Cassidaria echinophora* (Linné, 1766 [*sic*]) – Brébion, p. 354, pl. 8, fig. 19.
2004b *Galeodea echinophora* (Linnaeus, 1758) – Landau *et al*., p. 43, pl. 2, fig. 2 (*cum syn*.).
2008 *Galeodea echinophora* (Linné, 1758) – Chirli & Richard, p. 31, pl. 5, fig. 3.
2008 *Galeodea echinophora* (Linné, 1758) – Chirli, p. 80, pl. 30, figs 9-16, pl. 31, figs 1-3.
2009 *Galeodea echinophora* (Linnaeus, 1758) – Landau *et al*., p. 66, pl. 3, figs 1, 2.
2010 *Galeodea echinophora* (Linnaeus, 1758) – Sosso

& Dell'Angelo, p. 26, 36 2nd row right.
2011 *Galeodea echinophora* (Linnaeus, 1758) – Landau *et al*., p. 18, pl. 7, fig. 7.

Material and dimensions – Maximum height 55.4 mm. NHMW 2015/0133/0248-0249 (2), NHMW 2015/0133/0306-0307 (2), 2015/0133/0250-0251 (13); LC (18 + 13 juveniles); FVD (19). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was fully discussed by Landau *et al*. (2004b, 2009). Almost every character is highly variable: the height of the spire, the position of the aperture, the character of the spiral sculpture and prominence of the nodules, the thickness of the terminal varix, the presence or absence of labial denticles and columellar folds, and the size of the umbilicus. This is also seen in the specimens from Le Pigeon Blanc, in which the number of rows of well developed tubercles covering the dorsum varies from two to five. The French Atlantic specimens do not attain the large size seen in some of the Italian Pliocene shells. This French occurrence is also the most northern record for the species in the Pliocene. Today it lives in the Mediterranean and on the Atlantic coast of West Africa, but does not occur further north than the southern coast of Portugal.
Galeodea rugosa (Linné, 1771), a Recent Eastern Atlantic and Mediterranean species, differs in that most specimens do not have any raised primary spiral cords, bearing rows of nodules as in *G. echinophora,* and therefore has more regularly convex whorls. It also reaches a much larger maximum size and has more regular, more prominent spiral cords than *G. echinophora. Galeodea bicatenata* (J. Sowerby, 1816), from the Pliocene North Sea Basin, again differs from *G. echinophora* in having spiral cords of even prominence. This species is more similar to the modern *G. rugosa*, but differs in having a broader shell, with more angular whorls. The spiral sculpture on the spire whorls and the shoulder of the last whorl is somewhat undulating in most specimens, whereas the cords are totally smooth in *G. rugosa*. Harmer (1914, p. 58) recorded *G. rugosa* from the North Sea Basin, however, these records are doubtful, as are records of *G. echinophora* in the Danish and German Miocene (Marquet, 1997b, p. 80).
Brébion (1964, p. 355) recoded *G. echinophora* from almost all Assemblage III localities (Le Pigeon Blanc, Palluau, Le Girondor, La Dixmerie, Les Cléons, Corcoué-sur-Logne). Interestingly, according to Brébion, it is replaced by *G. bicatenata* in Assemblage IV localities (Gourbesville, Le Bosq d'Aubigny).

Distribution – Lower Miocene: Paratethys (Eggenburgian), Germany (Hölzl, 1958). Middle Miocene: Proto-Mediterranean, Italy (Sacco, 1890a); Paratethys, Austria (Hörnes, 1852; Hoernes & Auinger, 1884; Glibert, 1963), Bulgaria (Kojumdgieva & Strachimirov, 1960), Romania (Hoernes & Auinger, 1884; Boettger, 1902). Upper Miocene: Atlantic (Tortonian), Algarve, Cacela Basin, Portugal (Pereira Da Costa, 1867); Proto-Mediterranean, Italy (Sacco, 1890a). Lower Pliocene: Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, NE Spain (Glibert, 1963; Martinell, 1979; Solsona, 1998, 1999), France (Fontannes, 1879), Morocco (Lecointre, 1952); central Mediterranean, Italy (Sacco, 1890a; Pelosio, 1967; Chirli, 2008; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004b), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1890a; Glibert, 1963; Caprotti, 1970, 1974; Malatesta, 1974; Cavallo & Repetto, 1992). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911), Sicily (Glibert, 1963). Recent: Mediterranean, infralittoral to bathyal (Bouchet & Warén, 1993).

Subfamily Phaliinae Beu, 1981
Genus *Semicassis* Mörch, 1852

Type species (by subsequent designation, Harris, 1897) – *Cassis japonica* Reeve, 1848 (= *C. bisulcata* Schubert & Wagner, 1829), present-day, Indo-West Pacific.

1852 *Semicassis* Mörch, p. 112.
1888 *Faurotis* Jousseaume, p. 188. Type species (by original designation): *F. faurotis* Jousseaume, 1888, present-day, western Indian Ocean and Red Sea.
1928 *Tylocassis* Woodring, p. 306. Type species (by original designation): *Buccinum inflatum* Shaw, 1811 (= *B. granulatum* Born, 1778), present-day, western Atlantic.
1927 *Xenophalium* Iredale, p. 333. Type species (by original designation): *X. hedleyi* Iredale, 1927 (= *Cassidea royana* Iredale, 1914), present-day, northern New Zealand and southeastern Australia.
1927 *Xenogalea* Iredale, p. 339. Type species (by original designation): *Cassis pyrum* Lamarck, 1822, present-day, New Zealand and southeastern Australia.

***Semicassis laevigata* (Defrance, 1817)**
Plate 13, fig. 2

*1817 *Cassis laevigata* Defrance, *in* Cuvier, p. 210.
2004b *Semicassis laevigata* (Defrance, 1817) – Landau *et al*., pl. 3, figs 1, 2 (*cum syn*.).
2009 *Semicassis laevigata* (Defrance, 1817) – Landau *et al*., p. 67, pl. 4, figs 1, 2 (*cum syn*.).
2011 *Semicassis laevigata* (Defrance, 1817) – Landau *et al*., p. 18, pl. 7, fig. 8 (*cum syn*.).
2013 *Semicassis laevigata* (Defrance, 1817) – Landau *et al*., p. 125, pl. 17, fig. 6 (*cum syn*.).

Material and dimensions – Height 45.2 mm. LC (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Semicassis laevigata* (Defrance, 1817) is

extremely uncommon at Le Pigeon Blanc, known from a single incomplete specimen. As expected from lower Pliocene specimens, it is typical of the more slender, thinner-shelled and narrower-lipped Pliocene *S. laevigata* morphotype rather than the more inflated and more solid Miocene *S. miolaevigata* Sacco, 1890 morphotype. Landau *et al*. (2004b, 2009) considered all these forms to be conspecific. For further discussion see Landau *et al*. (2004b, 2009).

Distribution – Lower Miocene: Paratethys (Burdigalian): Hungary (Harzhauser, 2004); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1890b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (Janssen, 1984), Germany (Moths, 1989; Wienrich, 2001). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1924; Glibert, 1963); Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Hörnes, 1852; Schultz, 1998; Harzhauser, 2002, 2004; Landau *et al*., 2009), Czech Republic (Hörnes, 1852; Harzhauser, 2004), Poland (Friedberg, 1912; Bogsch, 1936; Bałuk, 1995; Bałuk & Radwański, 1996; Ceranka & Złotnik, 2003), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Bogsch, 1936; Strausz, 1966; Csepreghy-Meznerics, 1956, 1969), Bosnia (Atanackovíc, 1963, 1985), Romania (Boettger, 1902; Moisescu, 1955; Hinculov, 1968; Ionesi & Nicorici, 1994; Landau *et al*., 2009), Ukraine (Zelinskaya *et al*., 1968); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al*., 2013). Upper Miocene: North Sea Basin (Tortonian), Denmark (Rasmussen, 1956; Schnetler, 2005); north-eastern Atlantic (Tortonian), Cacela Basin, Portugal (Pereira Da Costa, 1867), southern Spain (Wenz, 1942); Proto-Mediterranean Sea (Tortonian), Italy (Sacco, 1890b). Lower Pliocene: North Sea Basin, England (Wood, 1872), Belgium (Marquet, 1997b); Atlantic, NW France (this paper); Mondego Basin, Portugal (Zbyszewski, 1959, Silva, 2001), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al*., 2011), Morocco (Lecointre, 1952); western Mediterranean, north eastern Spain (Martinell, 1979; Solsona, 1998, 1999), Roussillon Basin, France (Fontannes, 1882); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1974; Cavallo & Repetto, 1992; Chirli, 2008), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004b), central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1970; Malatesta, 1974; Damarco, 1993). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911).

Family Ranellidae Gray, 1854
Subfamily Cymatiinae Iredale, 1913
Genus *Monoplex* Perry, 1810

Type species (by subsequent designation, Dall, 1904) – *Monoplex australasiae* Perry, 1811 (= *Murex parthenopeus* von Salis Marschlins, 1793), present-day, cosmopolitan.

1810 *Monoplex* Perry, M7.
1817 *Lampusia* Schumacher, p. 350. Type species (by subsequent designation, Herrmannsen, 1847): *Murex pilearis* Linnaeus, 1758, present-day, Indo-West Pacific.
1936 *Cabestanimorpha* Iredale, p. 307 (unavailable, no definition, published after 1931). Type species (by monotypy): *Triton exaratus* Reeve, 1844, present-day, Pacific.
1957 *Cymatriton* Clench & Turner, p. 210. Type species (by original designation): *Tritonium nicobaricum* Röding, 1798, present-day, Indo-West Pacific and eastern and western Atlantic.

***Monoplex corrugatus* (Lamarck, 1816)**
Plate 13, fig. 3

*1816 *Triton corrugatum* Lamarck, p. 181.
1964 *Cymatium* (*Lampusia*) *subcorrugatum* d'Orbigny, 1852 – Brébion, p. 357, pl. 8 figs 20, 21.
2013 *Monoplex corrugatus* (Lamarck, 1816) – Landau *et al*., p. 127, pl. 18, figs 5-7 (*cum syn.*).

Material and dimensions – Height 20.7 mm. NHMW 2015/0133/0359 (1); FVD (fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Brébion (1964, p. 358) recorded two specimens from Le Pigeon Blanc he identified as *Cymatium* (*Lampusia*) *subcorrugatum* d'Orbigny, 1852. *Monoplex subcorrugatus* (d'Orbigny, 1852) is an early Miocene Atlantic species from the Aquitanian and Burdigalian of the Aquitaine Basin, France (Lozouet *et al.,* 2001, p. 46, pl. 19, fig. 1a, b) and is likely to have been ancestral to *M. corrugatus* (Lamarck, 1816). It is similar to *M. corrugatus* in most characters, but differs in its smaller maximum size, wider shape, more prominent spiral cords, and much heavier, thicker varices. Lozouet *et al.* (2001a, p. 46) pointed out that nearly all the species proposed in *Eutritonium* and *Ranularia* by Cossmann & Peyrot (1924) are synonyms of *M. subcorrugatus* (*E. aquitanicum, E. doliaroides, R. multicostata, R. duvergieri*). The shells from Le Pigeon Blanc are certainly small (maximum height 39 mm; Brébion, 1964), but this is a poor defining character. *Monoplex corrugatus* is common in the middle Miocene Serravallian of the Karaman Basin of Turkey, where fully adult specimens can vary threefold in size. They are also variable in breadth and in the strength of the varices. Whether specimens of the two species can be consistently separated remains to be seen.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Bellardi, 1873). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (Janssen, 1984). Middle Miocene: Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Hörnes, 1853; Hoernes & Auinger, 1884; Schultz, 1998; Landau *et al*., 2009), Poland (Friedberg,

1912; Bałuk, 1995; Bałuk & Radwański, 1996), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Hörnes, 1853; Strausz, 1966; Csepreghy-Meznerics, 1950, 1969), Czech Republic (Hörnes, 1853), Romania (Boettger, 1902), Ukraine (Zelinskaya *et al*., 1968); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.,* 2013). Upper Miocene: north eastern Atlantic (Tortonian): Cacela Basin, Portugal (Pereira Da Costa, 1867); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Bellardi, 1873; Montanaro, 1935). Lower Pliocene: Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (Landau *et al*., 2011), Morocco (Lecointre, 1952); western Mediterranean, north eastern Spain (Martinell, 1979; Solsona, 1998), Roussillon Basin, France (Fontannes, 1880; Glibert, 1963; Chirli & Richard, 2008); central Mediterranean, Italy (Bellardi, 1873; Malatesta, 1974; Cavallo & Repetto, 1992; Chirli, 2008), Tunisia (Fekih, 1975). Upper Pliocene: Estepona Basin, Spain (Landau *et al*., 2004b), central Mediterranean, Italy (Bellardi, 1873; Glibert, 1963a; Caprotti, 1970; Malatesta, 1974; Inzani, 1988; Damarco, 1992; Spadini, 1994; Inzani & Bertarelli, 1995). Pleistocene: Atlantic, Morocco (Lecointre, 1952; Brébion, 1979); Balearic Islands (Cuerda Barceló, 1987). Present-day: Atlantic, Bay of Biscay to Angola, Canaries and Madeira, Mediterranean, commoner in the western part. All types of bottoms at depths 15-22 m (Poppe & Goto, 1991).

***Monoplex heptagonus* (Brocchi, 1814)**
Plate 13, fig. 4

*1814	*Murex heptagonus* Brocchi, p. 404, pl. 9, fig. 2.
2013	*Monoplex heptagonus* (Brocchi, 1814) – Landau *et al*., p. 128, pl. 18, figs 8-10 (*cum syn.*).

Material and dimensions – Height 27.9 mm. NHMW 2015/0133/0360 (1); FVD (1); LC (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Monoplex heptagonus* (Brocchi, 1814) is distinguished from its congeners by its rather squat shape, its depressed scalate spire, its fewer axial ribs and by having only two varices. The denticles within the outer lip are bifid in most specimens, as opposed to simple in most other species, and the siphonal canal is straight and very narrow (Landau *et al*., 2004b, 2009). This species is widespread in the European Miocene and Pliocene.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Glibert, 1963). Middle Miocene: Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Hörnes, 1853; Hoernes & Auinger, 1884), Poland (Friedberg, 1912; Bałuk, 1995), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Hörnes, 1853; Strausz, 1966; Csepreghy-Meznerics, 1950, 1969), Romania (Hörnes, 1853; Landau *et al*., 2009); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Bellardi, 1873; Glibert, 1963). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848, 1872, 1879; ?Harmer, 1914); Atlantic, NW France (this paper), Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, Morocco (Lecointre, 1952), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Bellardi, 1873; Sacco, 1904; Cavallo & Repetto, 1992; Chirli, 2008). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Cox, 1936); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004b), central Mediterranean, Italy (Bellardi, 1873; Sacco, 1904; Glibert, 1963; Inzani, 1988; Spadini, 1994).

Superfamily Ficoidea Meek, 1864 (1840)
Family Ficidae Meek, 1864
Genus *Ficus* Röding, 1798

Type species (by subsequent designation, Dall, 1906) – *Ficus variegata* Röding, 1798, present-day, Indo-West Pacific.

1798	*Ficus* Röding, p. 148.
1799	*Pyrula* Lamarck, p. 73. Type species (by monotypy): '*Bulla ficus*. Linné.', *i.e.*, *Murex ficus* Linnaeus, 1758, present-day, Indo-West Pacific.
1810	*Pirula* de Montfort, p. 486. Type species (by monotypy): *Murex ficus* Linnaeus, 1758, present-day, Indo-West Pacific.
1835	*Ficula* Swainson, p. 21. No included species. Two species subsequently included by Swainson (1840). Type species (by subsequent designation, Gray, 1847): *Murex ficus* Linnaeus, 1758, present-day, Indo-West Pacific.
1847	*Sycotypus* Gray, p. 135. Type species (by original designation): *Murex ficus* Linnaeus, 1758, present-day, Indo-West Pacific.
1983	*Diconoficus* Covacevich & Frassinetti, p. 106. Type species (by original designation): *Ficus gayana* Covacevich & Frassinetti, 1983, Oligocene/Miocene, Chile.

***Ficus geometra* (Borson, 1825)**
Plate 13, figs 5, 6

*1825	*Pyrula geometra* Borson, p. 311.
1964	*Ficus geometra* var. *bifida* Brébion, p. 360, pl. 8, fig. 25 (*nomen nudum*).
2004b	*Ficus geometra* (Borson, 1825) – Landau *et al*., p. 79, pl. 8, fig. 3 (*cum syn*.).
2008	*Ficus geometra* (Borson, 1825) – Chirli & Richard, p. 30, pl. 5, fig. 2.
2008	*Ficus geometra* (Borson, 1825) – Chirli, p. 78, pl. 29, figs 7-12.
2010	*Ficus geometra* (Borson, 1825) – Sosso & Dell'-Angelo, p. 27, 37 fig. top left.

Material and dimensions – Maximum height 56.8 mm.

NHMW 2015/0133/0243-0244 (2), 2015/0133/0245 (8); FVD (6). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Landau *et al*. (2004b) discussed the Mediterranean Pliocene species of *Ficus*, drawing attention to the importance of the protoconch characters, and concluded that three species occurred: *Ficus subintermedia* (d'Orbigny, 1852), *F. geometra* (Borson, 1825) and *F. ficoides* (Brocchi, 1814). The numerous Pliocene records for F. *condita* (Brongniart, 1823) are incorrect and refer to *F. subintermedia*.
Ficus geometra differs from *F. subintermedia* in having the squares formed by the reticulate pattern flat and without secondary spiral ornament, or at most one secondary spiral thread, whereas in *F. subintermedia* they are concave, with 1-3 spiral threads in the interspaces. The number of primary spiral cords in *F. subintermedia* is always greater than in *F. geometra* (20-25 *vs*. 30+). According to Caprotti (1973) the number of spiral cords on the first two teleoconch whorls is the most reliable distinguishing character; three spiral cords are present in *F. subintermedia*, 5-6 in *F. geometra*. The specimens from Le Pigeon Blanc usually have a single thread running along the centre of the squares and six spiral cords on the early teleoconch whorls; typical for *F. geometra*. *Ficus ficoides* is easily distinguished from the other two Pliocene species by the character of the spiral sculpture, which forms 15-18 prominent, subacute carinae with strongly concave interspaces.
Ficus subintermedia can easily be distinguished from the two other Pliocene species, based on their protoconch type. Both *Ficus ficoides* and *F. geometra* have relatively large protoconchs with a small nucleus, whereas *F. subintermedia* has a protoconch of only 1.5 whorls with a smaller diameter, but a larger nucleus than in *F. geometra* and *F. ficoides*.
Brébion (1964, p. 361) considered the specimens from Le Pigeon Blanc and other Assemblage III localities (Les Cléons, La Dixmerie) to represent a distinct subspecies of *F. geometra* he called '*bifida*' *nomen nudum* (Brébion's material is here illustrated Pl. 13, fig. 6). It is not clear what made him separate these forms, although in the species description he wrote; '*Coquille d'assez grande taille ornée de nombreux cordons spiraux serrées, larges et bifides*…. (Brébion, 1964, p. 360)'. As illustrated here (Pl. 13, fig. 5d), the spiral cords are not bifid. The author also recorded this species from Assemblage IV (Gourbesville), but said it was a little different. We have not seen these specimens, and provisionally exclude them from the distribution.

Distribution – Middle Miocene: ?North Sea Basin, Jutland, Denmark (Sorgenfrei, 1958); Proto-Mediterranean, Italy (Sacco, 1890b); Paratethys Austria, (Hörnes, 1856; Hoernes & Auinger, 1890), Poland (Friedberg, 1912; Bałuk, 1995), Hungary (Csepreghy-Meznerics, 1969; Strausz, 1966). Upper Miocene: Proto-Mediterranean, Italy (Sacco, 1890b). Lower Pliocene: Atlantic, NW France (Brébion, 1964); western Mediterranean, north eastern Spain, (Martinell, 1979; Solsona, 1998, 1999); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1973, 1974; Pavia, 1975; Cavallo & Repetto, 1992; Chirli, 2008; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004b), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1973).

Superfamily Vermetoidea Rafinesque, 1815
Family Vermetidae Rafinesque, 1815
Subfamily Vermetinae Rafinesque, 1815
Genus *Petaloconchus* H.C. Lea, 1843

Type species (by monotypy) – *Petaloconchus sculpturatus* H.C. Lea, 1845, Miocene, Virginia.

1843 *Petaloconchus* H.C. Lea, p. 162.
1857 *Macrophragma* Carpenter, p. 308. Type species (by tautonomy): *Petaloconchus macrophragma* Carpenter, 1857, present-day, Mexico (Pacific).
1860 *Thylacodus* Mörch, 1860, p. 77. Type species (by monotypy): *Vermetus subcancellatus* Bivona-Bernardi, 1832 [= *Petaloconchus glomeratus* (Linnaeus, 1758)], present-day, Mediterranean.
1868 *Petalocrechas* Hall, p. 48. Error for *Petaloconchus*.
1912 *Petaloconcha* Cossmann, p. 135. Unjustified emendation of *Petaloconchus* H.C. Lea, 1843.
1936 *Petalochonchus* Prat, p. 7. Error for *Petaloconchus*.
1955 *Petaloconhus* Korobkov, p. 225. Error for *Petaloconchus*.

***Petaloconchus intortus* (Lamarck, 1818)**
Plate 13, fig. 7

*1818 *Serpula intortus* Lamarck, p. 365.
1964 *Petaloconchus intortus var. woodi* Mörch, 1861 – Brébion, p. 209.
2004a *Petaloconchus glomeratus* (Linnaeus, 1758) – Landau *et al*., p. 27, pl. 3, figs 15, 16 (*cum syn.*; fossil references only) [*non Petaloconchus glomeratus* (Linnaeus, 1758)].
2011 *Petaloconchus glomeratus* (Linnaeus, 1758) – Landau *et al*., p. 13, pl. 4, fig. 1 [*non Petaloconchus glomeratus* Linnaeus, 1758)].
2013 *Petaloconchus intortus* (Lamarck, 1818) – Landau *et al*., p. 65, pl. 5, fig. 15.

Material and dimensions – Maximum diameter 11.5 mm. NHMW 2015/0133/0275 (1); LC (5); FVD (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – As discussed by Landau *et al*. (2013, p. 65), Scuderi (2012) considered the fossil European Neogene species *Petaloconchus intortus* (Lamarck, 1818) to be distinct from the present-day species *P. glomeratus* (Lin-

naeus, 1758). The fossil species differing from the extant one in details of the protoconch. Whilst both have a protoconch consisting of about 2.5 whorls, that of the fossil species is smaller (0.65 × 0.4, vs. 1.1 × 0.7 mm), and there is a basal cord on the protoconch in the fossil species that is absent in *P. glomeratus*. Again, we accept this distinction, although we do not have a specimen with a protoconch from Le Pigeon Blanc. This species is uncommon in the NW French lower Pliocene and all the specimens are small compared with those of other Neogene deposits. For further discussion see Landau *et al*. (2013).
Brébion (1964, p. 210) recorded this species from Assemblage I (Reneauleau, Sceaux-d'Anjou, Thorigné, St. Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu), Assemblage II (Apigné) and Assemblage III (Le Pigeon Blanc, Le Girondor, La Gauvinière, Palluau) and Assemblage IV (St-Jean-la-Poterie).

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964; Moths, 1989), The Netherlands (Janssen, 1984). Middle Miocene: Atlantic (Aquitanian-Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1924; Lozouet *et al*., 2001), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1914; Bałuk, 1970, 1975), Vienna Basin, Austria (Hörnes, 1856; Tejkal *et al*., 1967; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966), Romania (Moisescu, 1955; Stancu & Andreescu, 1968); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentoz, 1958). Upper Miocene: northeastern Atlantic (Tortonian and Messinian): NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1896b), Tunisia (Stchepinsky, 1938). Lower Pliocene: North Sea Basin, England (Wood, 1848; Harmer, 1918), Belgium (Glibert, 1958; Marquet, 1997b); Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (González-Delgado, 1986; Landau *et al*., 2011), Morocco (Lecointre, 1952); western Mediterranean, northeastern Spain, (Martinell & Domènech, 1984; Solsona, 1998), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974; Anfossi *et al*., 1983; Baroncelli, 2001); Tunisia (Fekih, 1975). Lower-upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912; Taviani *et al*., 1998).

Genus *Thylacodes* Guettard, 1770

Type species (by subsequent designation, Keen, 1961) – *Serpulorbis polyphragma* Sassi, 1827, present-day, Mediterranean.

1770 *Thylacodes* Guettard, p. 143.
1770 *Tulaxodus* Guettard, p. 143. Type species (by subsequent designation, Keen, 1961): *Serpulorbis polyphragma* Sassi, 1827, present-day, Mediterranean. Considered unavailable by Keen (1961, p. 191), but is available following ICZN (1999) Art. 11.4.1, 11.5, and 12.1., see Bieler & Petit (2010, p. 183).
1826 *Lemintina* Risso, p. 114.Type species (by monotypy): *Lemintina cuvieri* Risso, 1826 [= *Thylacodes polyphragma* (Sassi, 1827)], present-day, Mediterranean.
1826 *Lementina* Risso, p. 432 [= captions to pl. 2]. Variant original spelling of *Lemintina*.
1827 *Serpulorbis* Sassi, p. 483. Type species (by monotypy): *Serpulorbis polyphragma* Sassi, 1827, present-day, Mediterranean (see Bieler & Petit, 2010).
1849 *Tulaxodes* Herrmannsen, p. 636. Incorrect subsequent spelling; see Bieler & Petit (2010, p. 183–184).
1884 *Lememtima* Bucquoy *et al*., p. 236. Error for *Lemintina*.
1973 *Lemitina* Higo, p. 58; Higo & Goto, 1993, p. 110. Error for *Lemintina*.

***Thylacodes arenarius* (Linnaeus, 1758)**
Plate 13, fig. 8

*1758 *Serpula arenaria* Linnaeus, p. 1266.
1964 *Lemintina arenaria* Linné, 1766 [*sic*] – Brébion, p. 211.
2013 *Tylacodes* [*sic*] *arenarius* (Linnaeus, 1758) – Landau *et al*., p. 65, pl. 5, fig. 16 (*cum syn*.).

Material and dimensions – Maximum diameter 30.4 mm. NHMW 2015/0133/0172-0173 (2), NHMW 2015/0133/0174 (12); FVD (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was fully discussed by Landau *et al*. (2013, p. 65). The material from Le Pigeon Blanc is relatively small compared to that found in other localities. We have not found any protoconch material belonging to this species and therefore cannot add any new information to the discussion given earlier. The junior author notes, with embarrassment, that the genus name was misspelled in that paper; the correct spelling being *Thylacodes*.
Brébion (1964, p. 211) recorded this species from Assemblage I (Reneauleau, Sceaux-d'Anjou, Thorigné, St. Michel, St-Clément-de-la-Place, Les Cléons, Beaulieu), Assemblage II (Apigné) and Assemblage III (Le Pigeon Blanc, Le Girondor) and Assemblage IV (Gourbesville).

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), The Netherlands

(Janssen, 1984). Middle Miocene: Atlantic (Aquitanian-Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1924), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1914, 1938; Bałuk, 1975), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Csepreghy-Meznerics, 1954; Strausz, 1966), Romania (Moisescu, 1955; Stancu & Andreescu, 1968), Bosnia (Atanacković, 1969; Eremija, 1971), Ukraine (Zelinskaya *et al*., 1968); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, Spain (González-Delgado, 1986; Landau *et al*., 2011), Morocco (Lecointre, 1952); western Mediterranean, northeastern Spain, (Solsona, 1998), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974; Anfossi *et al*., 1983); Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2004a); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1912). Present-day: northeastern Atlantic, Iberian Peninsula, Morocco, Mediterranean (Poppe & Goto, 1991).

Superfamily Vanikoroidea Gray, 1840

Note – Based on nuclear and mitochondrial DNA, Takano & Kato (2014) suggested the Vanikoridae as the sister group to Eulimidae. The two families were collectively placed by the authors in a redefined superfamily Vanikoroidea, with Truncatelloidea and (potentially paraphyletic) Rissooidea as closest relatives.

Superfamily Vanikoroidea Gray, 1840
Family Aclididae Sars, 1878
Genus *Aclis* Lovén, 1846

Type species (by monotypy) – *Alvania supranitida* Wood, 1842 [= *Aclis minor* (Brown, 1827)], Pliocene, British Isles.

1846 *Aclis* Lovén, p. 148.
1867 *Menippe* Jeffreys, p. 106. Type species (by monotypy): *Chemnitzia gulsonae* W. Clark, 1850, present-day, British Isles. Junior homonym of *Menippe* de Haan, 1833 [Crustacea]
1869 *Pherusa* Jeffreys, p. 210. Type species (by monotypy): *Chemnitzia gulsonae* W. Clark, 1850, present-day, British Isles. Junior homonym of *Pherusa* Oken, 1807 [Annelida], *Pherusa* Leach, 1814 [Crustacea].
1888 *Pherusina* Norman, p. 18. Type species (by typification of replaced name): *Chemnitzia gulsonae* W. Clark, 1850, present-day, British Isles. *Nom. nov. pro Pherusa* Jeffreys, 1869, *non* Oken, 1807 [Annelida].
1912 *Phaerusa* Cossmann, p. 103. Incorrect subsequent spelling.
1914 *Marteliella* Dautzenberg & Durouchoux, p. 34. Type species (by typification of replaced name): *Chemnitzia gulsonae* W. Clark, 1850, present-day, British Isles. *Nom. nov. pro Pherusa* Jeffreys, 1869, *non* Oken, 1807 [Annelida].
1947 *Schwengelia* Bartsch, p. 10. Type species (by original designation): *Aclis hendersoni* Dall, 1927, present-day, Florida.

***Aclis pacaudi* nov. sp.**
Plate 13, fig. 9

Type material – Holotype NHMW 2015/0133/0217, height 2.8 mm; paratype 1 NHMW 2015/0133/0218, height 2.7 mm.

Other material – Known from type series only.

Etymology – Named after Jean-Michel Pacaud of the MNHN Paris for his help in finding Brébion's material and facilitating the loan of this material. *Aclis* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Aclis* species with a tall, very slender spire, a paucispiral protoconch, the first four teleoconch whorls smooth, abapically crowded spirals appear on lower half of later whorls, increasing in number progressively, last whorl with six cords, a small aperture, and a smooth imperforate base.

Description – Shell minute, turriculate, with tall, very slender spire. Protoconch somewhat abraded, but paucispiral, consisting of 1.5-2 convex whorls. Teleoconch consisting of eight regularly convex whorls, with periphery just below mid-whorl. Suture linear, impressed. First four teleoconch whorls smooth. A single abapical cord appears on fifth whorl, a short distance above suture. Abapically, further cords appear, each time developed just above suture on lower half of whorl, so that sixth whorl bears 3-4 cords, all placed below mid-whorl; seventh whorl bearing five cords on lower two-thirds of whorl. Last whorl regularly convex, with smooth, steep subsutural ramp to shoulder cord; six cords between shoulder cord and peribasal cord; base rounded, smooth, imperforate. Aperture small, ovate. Outer lip convex, not thickened. Columella straight, smooth; columellar callus slightly thickened and erect abapically.

Discussion – *Aclis pacaudi* nov. sp. differs from its spi-

rally sculptured European congeners such as *A. ascaris* (Turton, 1819), *A. minor* (Brown, 1827) and *A. verduini* van Aartsen, Menkhorst & Gittenberger, 1984 in having a more slender shell and in having more numerous but less elevated cords, which only appear on the late teleoconch whorl. All the other congeners have the cords appearing at the protoconch/teleoconch boundary. Bartsch (1947) reviewed the Western Atlantic Aclididae, but again none of the species described has the combination of very slender shell and spiral sculpture on the late teleoconch whorls.
The fossil record for the genus is poor, although recent revisions show it occurs fairly extensively in the European Neogene (Landau *et al*., 2006; Landau *et al*., 2013). We draw special attention to Chirli (2009) who figured five species for the lower Pliocene of Italy. Again, all the spirally sculptured species from Italy differ in having stronger, elevated cords on all teleoconch whorls.
We have only found *Aclis pacaudi* at Le Pigeon Blanc, where it is very uncommon.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Eulimidae H. Adams & A. Adams, 1853
Genus *Eulima* Risso, 1826

Type species (by subsequent designation, Herrmannsen, 1847) – *Turbo subulatus* Donovan, 1804 [= *Eulima glabra* (Da Costa, 1778)], present-day, British Isles.

1778 *Strombiformis* Da Costa, p. 107. Type species (by subsequent designation, Iredale, 1915): *Strombiformis glaber* Da Costa, 1778, present-day, British Isles. Suppressed, and placed on the Official Index (Opinion 1718, ICZN 1993a).
1826 *Eulima* Risso, p. 123.
1853 *Leiostraca* H. Adams & A. Adams, p. 237. Type species (by subsequent designation, Bucquoy *et al*., 1883): *Turbo subulatus* Donovan, 1804 [= *Eulima glabra* (Da Costa, 1778)], present-day, British Isles.
1884b *Subularia* Monterosato, p. 103. Type species (by subsequent designation, Crosse, 1885): *Turbo subulatus* Donovan, 1804 [= *Eulima glabra* (Da Costa, 1778)], present-day, British Isles. Unnecessary substitute name for *Leiostraca* H. Adams & A. Adams, 1853, by Monterosato assumed to be preoccupied by *Leiostracus* Albers, 1850.
1955 *Cuspeulima* Laseron, p. 91. Type species (by original designation): *Leiostraca acutissima* G.B. Sowerby II, 1866, present-day, New South Wales, Australia.

***Eulima* sp.**
Plate 13, fig. 10

1964 *Leiostraca glabra* var. *gigantea* Doderlein, 1862 – Brébion, p. 272, pl. 7, fig. 2.

Material and dimensions – Maximum height 20.6 mm. NHMW 2015/0133/0252 (1), 2015/0133/0253 (50+); LC (30); FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Warén (1984) illustrated the importance of protoconch type and the shape and position of incremental growth scars, marking the position of early lip margins, in the classification of this superfamily. Despite photographing the Le Pigeon Blanc shells with SEM, we have not found a well-preserved protoconch.
This species is characterised by its unusually large size (up to 20.6 mm), very slender shape, with an apical angle of about 17-18º, almost flat-sided spire whorls and elongated aperture. The last whorl is 43% of total height; shell width/height 19%; aperture 26% of total height; aperture width/height 41%. The outer lip is slightly projecting abapically, just below the insertion, below which it is straight to weakly concave. The surface is smooth and glossy, devoid of sculpture, apart from the incremental growth scars placed irregularly, which are almost straight and slightly prosocline. A colour pattern of broad spiral bands is preserved in some specimens, similar to that seen in the present-day *Eulima glabra* (Da Costa, 1778). The Le Pigeon Blanc shells are similar to *E. glabra* in colour pattern, but differ in having twice the maximum size (maximum size for *E. glabra* is 10 mm; Fretter & Graham, 1982, p. 412). The specimens from Le Pigeon Blanc are quite variable in size, but that is normal in *Eulima*, and some are fully grown but smaller and more slender, presumably males (Fretter & Graham, 1982, p. 412; Warén, 1984, p. 24). If one compares the shell morphometrics to those of *E. glabra* given by Fretter & Graham (1982), apart from being larger, the French Pliocene shells are at the lower end of the range for apical angle and the width/height less, *i.e*. more slender, the last whorl and aperture are shorter in relation to to total height, and the aperture is narrower.
Landau *et al*. (2006, p. 60) pointed out that the Italian Pliocene shells usually ascribed to *E. glabra* are not in fact that species, but *Helix subulata* Brocchi, 1814 *non* Donovan, 1804. They differed from the living species in having a protoconch with a more horizontal suture and a more depressed first whorl, and erected the name *E. boucheti* Landau, La Perna & Marquet, 2006 for this Pliocene species. Although the protoconch is not well-preserved in the French material, it does not seem to be the same species. The specimens from Le Pigeon Blanc are still larger than *E. boucheti* (maximum height 15.5 mm), the apical angle is smaller (17-18º vs. 19-21º), the spire whorls are flatter sided and the aperture is slightly longer (26% vs. 21-24%).
Brébion (1964, p. 272) identified this large eulimid as *Leiostraca glabra* var. *gigantea* Doderlein, 1862, but it is difficult to be certain based on the shell illustrated by Sacco (1904, pl. 24, fig. 4). In the absence of a well preserved protoconch, we leave this species in open taxonomy, although it is probably undescribed. This large eulimid was recorded by Brébion (1964) from most Assemblage III localities (Le Pigeon Blanc, Le Girondor, La

Gauvinière, La Dixmerie).

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Genus *Melanella* Bowdich, 1822

Type species (by monotypy) – *Melanella dufresnei* Bowdich, 1822, present-day, Indo-Pacific.

1822 *Melanella* Bowdich, p. 27.
1847a *Balcis* Gray, p. 271. Type species (by monotypy): *Balcis montagui* Leach *in* Gray, 1847 [= *Melanella alba* (Da Costa, 1778)], present-day, British Isles. Placed on the Official List (Opinion 1739, ICZN 1993b).

***Melanella alba* (Da Costa, 1778)**
Plate 14, fig. 1

*1778 *Strombiformis albus* Da Costa, p. 116.
2006 *Melanella alba* (Da Costa, 1778) – Landau *et al*., p. 62, pl. 19, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 18.8 mm (incomplete). NHMW 2015/0133/0292 (1); LC (7); FVD (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Warén (1988) discussed the confusion surrounding *Strombiformis albus* Da Costa, 1778 and *Turbo politus* Linnaeus, 1758, with which it has often been confused. *Melanella alba* is characterised by its very fine reticulate mesh sculpture, visible only under magnification and reflected light. We have only included in the synonymy and distribution localities from which we have confirmed the presence of this microsculpture. Due to surface abrasion, the surface sculpture is not as obvious as it is in specimens from other fossil assemblages, in which the shells are better preserved (*i.e*. Estepona; see Landau *et al*., 2006, pl. 19, fig 1c).
Today this is primarily an Atlantic species, rare in the Mediterranean, where it does not reach as large as size as in the Atlantic (Warén, 1988). The shells from Le Pigeon Blanc are similar in size to the present-day Atlantic population described by Fretter & Graham (1982, p. 416). Brébion (1964, p. 274) reported *Melanella polita* from many Assemblage I localities. These records may well refer to *M. alba*, but will be reviewed in the relevant paper. He did not record any *Melanella* species from Assemblage III localities.

Distribution – Middle Miocene: North Sea Basin, The Netherlands (Janssen, 1984). Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Harmer, 1920), Kattendijk Formation, Belgium (Marquet, 1998). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1920), Atlantic, Mondego Basin, Portugal (Landau *et al*., 2006); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2006). Pliocene (unspecified): North Sea Basin, The Netherlands (van Regteren Altena *et al*., 1955). Pleistocene: Atlantic, St Erth, England (Harmer, 1920). Present-day: Atlantic, from Norway and into the Mediterranean (Fretter & Graham, 1982). Ectoparasite on the holothurian *Neopentadactyla mixta* (Cabioch *et al*., 1978).

***Melanella spiridioni* (Dautzenberg & Fischer, 1896)**
Plate 13, fig. 11; Plate 14, fig. 2

*1896 *Eulima spiridioni* Dautzenberg & Fischer, p. 464, pl. 19, fig. 25.
1927 *Eulima spiridioni* Dautzenberg & Fischer – Dautzenberg, p. 167, pl. 5, fig. 3.
1986 *Melanella spiridioni* (Dautzenberg & Fischer, 1896) – Bouchet & Warén, p. 354, figs 835-838, 923.
1999 *Melanella spiridioni* (Dautzenberg & Fischer, 1896) – Giannuzzi-Savelli *et al*., p. 104, figs 292, 293.

Material and dimensions – Maximum height 7.9 mm. NHMW 2015/0133/0254-0255 (2), 2015/0133/0256 (9). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This melanellid is characterised by its relatively small size, its paucispiral protoconch, its prominent incremental growth scars on the left hand side of the shell, placed above and behind each other on preceding whorls, its small aperture and curved outer lip. As commented by Bouchet & Warén (1986, p. 354), some eulimids with curved shells may be confused with *M. spiridioni*, but there is no species described that has a blunt larval shell, as seen in *M. spiridioni*.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Present-day: eastern Atlantic, Azores, Bay of Biscay, Mediterranean (Bouchet & Warén, 1986).

Genus *Niso* Risso, 1826

Type species (by monotypy) – *Niso eburnea* Risso, 1826, Pleistocene, France.

1826 *Niso* Risso, p. 218.
1838 *Bonellia* Deshayes *in* Deshayes & Milne-Edwards, p. 286. Type species (by original designation): *Bulimus terebellatus* Lamarck, 1804, Eocene, France. Junior homonym of *Bonellia* Rolando, 1822 [Echiurida].
1861 *Volusia* A. Adams, p. 306. Type species (by monotypy): *Eulima imbricata* G.B. Sowerby I, 1834b, present-day, Ecuador. Junior homonym of *Volusia* Robineau-Desvoidy, 1830 [Diptera].
1965 *Neovolusia* Emerson, p. 8. Type species (by typi-

fication of replaced name): *Eulima imbricata* G.B. Sowerby I, 1834b, present-day, Ecuador. *Nom. nov. pro Volusia* A. Adams, 1861, *non* Robineau-Desvoidy, 1830 [Diptera].

***Niso dollfusi* nov. sp.**
Plate 14, figs 3, 4

1964 *Niso baudouinae* Brébion, p. 280, pl. 7, fig. 6 (*nomen nudum*).

Type material – Holotype MNHN.F.A57394, height 13.9 mm (incomplete), paratype 1 NHMW 2015/0133/0258, height 7.4 mm (incomplete); paratype 2 NHMW 2015/0133/0257, height 13.6 mm (incomplete).

Other material –NHMW 2015/0133/0259 (3 fragments); LC (1). Type locality.

Etymology – Named after Gustave Frédéric Dollfus (1850-1931), French geologist and malacologist, who first coined the term 'Redonien' in 1902. *Niso* gender feminine.

Locus typicus – Le Pigeon Blanc, Le Landreau, Loire-Atlantique department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Niso* species, with a tall, conical, slender spire, a deep suture lying in a V-shaped groove, sculpture of collabral axial lines and very fine spiral threads, a weakly angled base and a narrow, round-edged umbilicus.

Description – Shell solid, slender, with tall conical spire. Protoconch not preserved. Teleoconch consisting of about 15 low, straight sided whorls, apical angle 19.5-26º. Suture linear, V-shaped, deeply impressed. Sculpture consisting of fine irregular collabral axial lines and even finer spiral threads, visible only under magnification. Last whorl weakly angled at base; base convex, bearing deep, relatively narrow, round edged umbilicus. Aperture short, ovate. Outer lip simple, weakly sinusoid in profile. Columella straight, smooth, edge sharp, erect. No parietal callus.

Discussion – *Niso dollfusi* nov. sp. is separated from its European Pliocene to present-day congeners by its tall slender spire, low whorls and very deep suture. *Niso eburnea* Risso, 1826, widespread in the Mediterranean Pliocene, is a much larger shelled species with a wider apical angle and a linear impressed suture that does not lie in a V-shaped groove. *Niso foresti* Bouchet & Warén, 1986 originally described from the Azores, but also present in the lower upper Pliocene of Estepona, southern Spain (Landau *et al*., 2006), is smaller shelled than *N. dollfusi* and again differs in not having a V-shaped suture and more convex spire whorls. The umbilicus is narrower than in either *N. dollfusi* or *N. eburnea*. *Niso turoniensis* Glibert, 1949 from the middle Miocene Loire Basin of France is more closely similar to *N. eburnea* and is separated from *N. dollfusi* by the same characters. *Niso degrangei* Cossmann & Peyrot, 1917 from the middle Miocene Aquitaine Basin is the most similar, also with a tall spire and slender shell, but has taller whorls than *N. dollfusi* and the suture is less deeply V-shaped.
Brébion (1964, p. 280) recorded this species only from the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Family Vanikoridae Gray, 1840
Genus *Macromphalus* Wood, 1842

Type species (by monotypy) – *Macromphalus reticulatus* Wood, 1842, Pliocene, England.

1842 *Macromphalus* Wood, p. 537.
1860 *Couthouyia* A. Adams, p. 410. Type species (by monotypy): *Couthouyia decussata* A. Adams, 1860, present-day, Japan.
1888 *Dialytostoma* Cossmann, p. 185. Type species (by original designation): *Fossarus fischeri* de Laubrière, 1881, Eocene, France.
1888 *Escharella* Cossmann, p. 183. Type species (by original designation): *Escharella citharella* Cossmann, 1888, Eocene, France.

***Macromphalus reticulatus* Wood, 1842**
Plate 14, fig. 5

*1842 *Macromphalus reticulatus* Wood, p. 537.
1848 *Lacuna reticulata* S. Wood – Wood, p. 122, pl. 12, fig. 10; pl. 15, fig. 12.
1988 *Macromphalus reticulatus* (S.V. Wood) – Warén & Bouchet, p. 73, fig. 26.

Material and dimensions – Maximum height 3.8 mm. NHMW 2015/0133/0180 (1), 2015/0133/0181 (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The specimens found at Le Pigeon Blanc agree with the description of *Macromphalus reticulatus* Wood, 1842, and figure (Wood, 1848, pl. 12, fig. 10; pl. 15, fig. 12). Warén & Bouchet (1988, fig. 26) illustrated a syntype in which the surface sculpture is much abraded, but the shape, protoconch type, reticulated sculpture, size of aperture and elongated umbilical slit are consistent with the specimens from Le Pigeon Blanc. Similar to other members of the genus, the protoconch in the French shells is elevated, paucispiral, consisting of about 1-1.25 globose whorls, with a large nucleus, suggestive of non-planktotrophic development. Unfortunately, the proto-

conch surface is somewhat abraded, which might have removed any surface microsculpture described in other members of the genus (Warén & Bouchet, 1988).
The present-day *M. abylensis* Warén & Bouchet, 1988 from Spanish Morocco differs in having predominantly spiral sculpture. Several superficially similar shells were described from the middle Miocene Loire Basin of France: *Macromphalus roberti* (de Morgan, 1915) has similar sculpture to *M. reticulatus*, but differs in having a wider umbilical slit and a multispiral protoconch and *Macromphalus bourgeoisi* (de Morgan, 1915) is similar to *M. roberti* but has more disjunct whorls, finer spiral sculpture and a paucispiral ribbed protoconch. *Macromphalus bourgeoisi* differs from *M. reticulatus* by its disjunct whorls and fine spiral sculpture, and although they both have a paucispiral protoconch, there is no sculpture visible in *M. reticulatus* (although it might be abraded).

Distribution – Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1842, 1848).

Genus *Macromphalina* Cossmann, 1888

Type species (by original designation) – *Sigaretus problematicus* Deshayes, 1864, Middle Eocene, France.

1888 *Macromphalina* Cossmann, p. 184.
1888 *Micromphalina* Cossmann, p. 187. Type species (by original designation): *Lacuna elegans* Deshayes, 1861, Eocene, France.
1945 *Chonebasis* Pilsbry & Olsson, p. 285. Type species (by original designation): *Chonebasis peruviana* Pilsbry & Olsson, 1945, present-day, Peru.

***Macromphalina* sp.**
Plate 14, fig. 6

Material and dimensions – Maximum diameter 1.5 mm (incomplete), height 800 μm. NHMW 2015/0133/0409 (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – A single incomplete shell at hand belongs to the genus *Macromphalina* Cossmann, 1888. The shell has a paucispiral protoconch composed of 1.3 whorls with a bulbous nucleus, the surface of which appears smooth, but any surface sculpture is probably abraded. The teleoconch is composed of 1.25 rapidly expanding, flattened whorls separated by a deeply impressed suture. Surface sculpture on the dorsum consists of conspicuous axial growth lines, sometimes forming small, irregular folds and subobsolete axial sculpture most clearly seen at the broken abapertural edge. The base is strongly depressed, with a wide, poorly delimited, deep umbilicus, delimited by an obsoletely angular edge. On the base the growth lines are stronger, lamellar and elevated.

Three *Macromphalina* species are known from the middle Miocene Loire Basin of north western France. *Macromphalina cossmanni* (Dollfus & Dautzenberg, 1899) has a less depressed shell, an even deeper suture and the axial lamellae on the base are most strongly developed within the umbilicus. *Macromphalina pontileviensis* (de Morgan, 1915) is similar in shape and axial sculpture, but lacks any trace of spiral sculpture. The original description discusses four whorls; the teleoconch seems to consist of 2-2.5 whorls, whereas in the Le Pigeon Blanc shell the teleoconch is composed of just over 1.25 whorls. The third, *Macromphalina bouryi* (de Morgan, 1915) (Syntypes, 2 ex., MNHN.F.R64366) can easily be separated by its carinate shoulder. We note that this species is a secondary homonym of *Macromphalina bouryi* (Dautzenberg, 1912) and requires a new name. We would suggest ***Macromphalina massicardi nom. nov.*** for de Morgan's taxon in honour of Mr. Peter Massicard who took the excellent photographs of the syntype of the French middle Miocene species posted on the MNHN website (https://science.mnhn.fr/institution/mnhn/collection/f/item/r64366?listIndex=455&listCount=250948). The sculpture of the Le Pigeon Blanc specimen is reminiscent of some of the present-day West African species such as *M. dautzenbergi* Adam & Knudsen, 1969 and *M. gofasi* Rubio & Rolán, 1994, but in both of these the spiral cords are stronger and the protoconch has more numerous whorls. We await better preserved material to further characterise this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

'Group' Ptenoglossa
Superfamily Triphoroidea Gray, 1847

Note – As discussed by Landau *et al*. (2006, p. 10), many triphoroidean species cannot be identified with certainty without the protoconch and many genera and subgenera within both the Triphoridae Gray, 1847, and the Cerithiopsidae Forbes & Hanley, 1850 cannot be distinguished on teleoconch characters alone. With the Le Pigeon Blanc material at hand we are frustrated by the poor state of preservation of the protoconch. We therefore leave all species in open nomenclature. A 'most likely' species approximation is given, but the distribution is restricted to the Zanclean of NW France, despite many of these species being known to occur in the North Sea Basin (Marquet, 1996) and Mediterranean Pliocene (Landau *et al*., 2006; Chirli, 2008).

Family Triphoridae Gray, 1847
Genus *Marshallora* Bouchet, 1985

Type species (by original designation) – *Murex adversus* Montagu, 1803, present-day, France.

1985 *Marshallora* Bouchet, p. 44.

***Mashallora* cf. *adversa* (Montagu, 1803)**
Plate 14, figs 7, 8

cf. *1803	*Murex adversus* Montagu, p. 271.
cf. 1985	*Marshallora adversa* (Montagu, 1803) – Bouchet, p. 45, figs 4, 12, 31-32, 36 (*cum syn*.).
cf. 1996	*Marshallora adversa* (Montagu, 1803) – Marquet, p. 138, pl. 1, fig. 1. (*cum syn*.).
cf. 1999	*Marshallora adversa* (Montagu, 1803) – Giannuzzi-Savelli *et al.*, p. 22, figs 3-4.
cf. 2006	*Marshallora* cf. *adversa* (Montagu, 1803) – Landau *et al*., p. 5, pl. 1, fig. 1.
cf. 2008	*Marshallora adversa* (Montagu, 1803) – Chirli, p. 17, pl. 8, figs 4-11.

Material and dimensions – Maximum height 4.3 mm. NHMW 2015/0133/0225-0226 (2), 2015/0133/0227 (18); LC (50+); FVD (23). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Both the preserved protoconch sculpture and teleoconch sculpture are highly suggestive of *Marshallora adversa* (Montagu, 1803), although as noted by Marquet (1996), this species, *Cheirodonta pallescens* (Jeffreys, 1867) and *Similiphora similior* (Bouchet & Guillemot, 1978) are almost indistinguishable based on shell characters alone.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Genus *Obesula* Jousseaume, 1897

Type species (by original designation) – *Mastonia obesula* Jousseaume, 1884a, present-day, New Caledonia.

1897 *Obesula* Jousseaume, p. 75.

***Obesula* sp.**
Plate 14, figs 9, 10

Material and dimensions – Maximum height 2.0 mm (incomplete). NHMW 2015/0133/0228-0229 (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell minute, turriculate. Protoconch abraded, but consisting of about three whorls; protoconch II bearing a strong central carina; no surface sculpture seen. Three teleoconch whorls preserved. First whorl bearing two cords; cord 1 placed immediately below suture, cord 3 placed just below mid-whorl. Cord 2 appears between cords 1 and 3 on third teleoconch whorl. Axial sculpture of prosocline ribs, roughly equal in strength to cords, with tubercles formed at sculptural intersections.

Discussion – The genus *Obesula* Jousseaume, 1897 is characterised by species having narrowly cyrtoconoid shells, with a moderately high spire and teleoconch spiral cord 2 commencing later than cords 1 and 3. Marshall (1983) discussed two groups within *Obesula*; a) shells having multispiral protoconchs sculptured by granules on the embryonic shell and axial riblets on the larval shell, and b) shells with a paucispiral protoconchs, with a smooth first whorl, followed by a sculpture of axial riblets and a submedian spiral thread on the last whorl. This species from France belongs within the second group.
Few congeners belonging to this second group have been described from the Neogene of Europe. *Obesula scaldensis* Marquet, 1996 from the Luchtbal Sand Member of the Lillo Formation, upper Pliocene of Belgium also has a keeled protoconch, but differs in having only two protoconch whorls and cord 2 appears later, on the fourth to sixth teleoconch whorl. *Obesula protopaucispirata* Landau, La Perna & Marquet, 2006 from the lower upper Pliocene of Estepona, southern Spain is similar in having cord 2 appearing on the third teleoconch whorl, but differs in having a completely smooth, paucispiral protoconch, lacking the median carina. We await better preserved material to characterise the late teleoconch whorls and possibly describe this species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Family Cerithiopsidae Forbes & Hanley, 1850
Genus *Cerithiopsis* (*s. lat*.) Forbes & Hanley, 1850

Type species (by monotypy) – *Murex tubercularis* Montagu, 1803, present-day, British Isles.

1850 *Cerithiopsis* Forbes & Hanley, pl. OO.

***Cerithiopsis* cf. *tubercularis* (Montagu, 1803)**
Plate 14, fig. 11

cf. *1803	*Murex tubercularis* Montagu, p. 270.
cf. 1999	*Cerithiopsis tubercularis* (Montagu, 1803) – Gianuzzi-Savelli *et al*., p. 38, figs 50-56.
cf. 2006	*Cerithiopsis* (*s. l.*) cf. *tubercularis* (Montagu, 1803) – Landau *et al*., p. 13, pl. 3, figs 4, 5.
cf. 2009	*Cerithiopsis tubercularis* (Montagu, 1803) – Chirli, p. 11, pl. 5, figs 8-15, pl. 6, figs 1-11.
cf. 2010	*Cerithiopsis tubercularis* (Montagu, 1803) – Cecalupo & Robba, p. 50, figs 1A-D, G-J, 2D-G.
cf. 2013	*Cerithiopsis* (*s. lat.*) cf. *tubercularis* (Montagu, 1803) – Landau *et al*., p. 137, pl. 63, fig. 6.

Material and dimensions – Maximum height 6.7 mm. NHMW 2015/0133/0221 (1), 2015/0133/0222 (40), LC (32); FVD (17). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Despite the relatively plentiful material from Le Pigeon Blanc, not one protoconch is preserved. In the absence of this, definitive identification is not pos-

sible, although the teleoconch concurs with *Cerithiopsis tubercularis* (Montagu, 1803).

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Genus *Dizoniopsis* Sacco, 1895

Type species (by original designation) – *Cerithium bilineatum* Hörnes, 1848, middle Miocene, Vienna Basin.

1895a *Dizoniopsis* Sacco, p. 67.

Note – Landau *et al*. (2006, p. 10) discussed the difficulties associated with ascribing cerithiopsids to certain genera, especially *Dizoniopsis* Sacco, 1895, which is used by most authors for cerithiopsids with two rows of tubercles. They concluded that in the absence of soft parts, species could not be reliably separated into genera based on either protoconch or teleoconch morphology alone.
Bouchet *et al*. (2010) reviewed the extant Mediterranean cerithiopsids with two rows of tubercles on the teleoconch shell and considered the species with two rows of tubercles until at least the penultimate whorl a monophyletic group: *Dizoniopsis*. We therefore use this genus for all fossil forms with this type of teleoconch sculpture, regardless of protoconch type.

***Dizoniopsis* cf. *bilineata* (Hörnes, 1848)**
Plate 14, fig. 12

cf. *1848 *Cerithium bilineatum* Hörnes, p. 21.
cf. 1964 *Cerithiopsis (Dizoniopsis) bilineata* Hörnes, 1856 [*sic*] – Brébion, p. 247.
cf. 2006 *Cerithiopsis* (*s. lat.*) cf. *bilineata* (Hörnes, 1848) – Landau *et al*. p. 14, text-fig. 1, figs 1-3, pl. 4, fig. 2 (*cum syn*.).
cf. 2009 *Dizoniopsis bilineata* (Hörnes, 1848) – Chirli, p. 14, pl. 7, figs 1-12.
cf. 2013 *Cerithiopsis* (*s. lat.*) cf. *bilineata* (Hörnes, 1848) – Landau *et al*. p. 136, pl. 63, figs 1, 2.

Material and dimensions – Maximum height 5.4 mm. NHMW 2015/0133/0219 (1), 2015/0133/0220 (3); LC (7); FVD (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The identification is based on the teleoconch having two rows of tubercles per whorl. The problems associated with identifying this group of cerithiopsids was discussed at length by Landau *et al*. (2006, p. 10, 14). Without the protoconch, which is missing in the Le Pigeon Blanc material, specific assignment is impossible. Brébion (1964, p. 248) recorded this species (or species-group) from Assemblage I localities (Reneauleau, St-Clément-de-la-Place, St-Michel), Assemblage II (Apigné, Le Temple du Cerisier), Assemblage III (Palluau, Le Girondor) to which we add Le Pigeon Blanc. Only the Assemblage III records are placed in the distribution in the hope that the other French fossil material may have its protoconch preserved.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

Subfamily Seilinae Golikov & Starobogatov, 1975
Genus *Seila* A. Adams, 1861

Type species (by subsequent designation, Dall, 1889) – *Triphoris dextroversus* A. Adams & Reeve, 1850, present-day, China Sea.

1861 *Seila* A. Adams, p. 131.
1884b *Cinctella* Monterosato, p. 123. Type species (by original designation): *Cerithium trilineatum* Philippi, 1836, present-day, Mediterranean.

***Seila suttonensis* Marquet, 2001**
Plate 15, fig. 1

1848 *Cerithium trilineatum* Phil. – Wood, p. 70, pl. 8, fig. 4 [*non Seila trilineata* (Philippi, 1836)].
1918 *Newtoniella* (*Seila*) *trilineata* (Philippi) – Harmer, p. 424, pl. 41, fig. 24 [*non Seila trilineata* (Philippi, 1836)].
1946 *Seila* (*Seila*) *turritissima* Sacco, 1895 – Beets, p. 46, pl. 3, fig. 2 (*non* Sacco, 1895a).
1955 *Seila trilineata* (Philippi, 1836) – van Regteren Altena *et al*., p. 30, pl. 6, fig. 65 [*non Seila trilineata* (Philippi, 1836)].
1964 *Seila trilineata* Philippi, 1836 – Brébion (*partim*), p. 250 [*non Seila trilineata* (Philippi, 1836)].
1997b *Seila trilineata* (Philippi, 1836) – Marquet, p. 83, pl. 5, fig. 3 [*non Seila trilineata* (Philippi, 1836)].
1998 *Seila trilineata* auct. non Philippi, 1836 – Marquet, p. 110, fig. 84.
*2001 *Seila (Hebeseila) suttonensis* Marquet, p. 201, pl. 1, fig. 6.

Material and dimensions – Maximum height 7.2 mm. NHMW 2015/0133/0223 (1), 2015/0133/0224 (21); LC (50+); FVD (30). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Marquet (2001) placed this species and the closely similar *S. sancticlementi* Marquet, 2001 from the Tortonian Assemblage I locality St-Clément-de-la-Place in the subgenus *Hebeseila* Finlay, 1926 based on the flat-sided whorls, cords of roughly equal strength, absence of additional spirals before the last whorl and highly sculptured protoconch. These two species do indeed share these conchological characters with the type species; *Seila bulbosa* Suter, 1908 from the extant fauna of New Zealand. However, the only other species attributed to this subgenus is also neozelandic. It is difficult to imagine these two groups of species, so distantly separated

both stratigraphically and geographically, forming a single phylogenetic group.
As discussed above, *Seila suttonensis* Marquet, 2001 and *S. sancticlementi* differ from all their European fossil and Neogene congeners in having a highly ornate paucispiral protoconch. *S. sancticlementi* differs from *S. suttonensis* in having a carinate protoconch and in lacking teleoconch axial sculpture.

Distribution – Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1918), Kattendijk Formation, Belgium (Marquet, 1997b, 1998); Atlantic, NW France (Brébion, 1964). ?Upper Pliocene: Red Crag, England (Harmer, 1918). Pliocene (unspecified): The Netherlands (Beets, 1946; van Regteren Altena *et al*., 1955).

Superfamily Epitonoidea Berry, 1910 (1812)
Family Epitoniidae Berry, 1910 (1812)

Note – Robertson (1983) recommended that rib counts should be based on larger samples of shells and, in order to take into account ontogenic changes, the ribs on each teleoconch whorl (or on the last whorl at each shell length) be analysed separately. Unfortunately epitonids are not only uncommon in the Le Pigeon Blanc assemblage, but almost always fragmentary. In the discussion we have counted the axial ribs or lamellae on the first teleoconch whorl (or first preserved whorl), on the mid teleoconch whorl and on the last whorl, giving ranges where available. The number of ribs is recorded thus: 'Axial sculpture consists of (16-18: 14-15: 12-13) narrow….ribs/lamellae.'

Genus *Epitonium* Röding, 1798

Type species (by subsequent designation, Suter, 1913) – *Turbo scalaris* Linnaeus, 1758, present-day, Mediterranean.

1798 *Epitonium* Röding, p. 91.
1909 *Lamelliscala* de Boury, p. 258. Type species (by original designation): *Scalaria fasciata* G.B. Sowerby II, 1844, present-day, Philippines.

***Epitonium* aff. *candidissimum* (Monterosato, 1877)**
Plate 15, fig. 2

aff. *1877 *Scalaria candidissima* Monterosato, p. 37, pl. 5, fig. 5.
aff. 2006 *Epitonium candidissimum* (Monterosato, 1877) – Landau *et al*., p. 22, pl. 6, figs 5, 6.

Material and dimensions – Height 10.2 mm (incomplete). NHMW 2015/0133/0296 (1); LC (11 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell small, of medium thickness, turriculate, with prominent axial sculpture, which is continuous along teleoconch. Protoconch not preserved. Teleoconch consisting of eight strongly convex whorls, separated by very deep, linear suture. Axial sculpture consisting of (12: 12: 12) thin, elevated, erect, prosocline lamellae, fused and continuous on each preceding whorl, winding around shell in clockwise direction when seen from base. Lamellae slightly more developed at shoulder, but do not produce spine or auricle. Whorl surface between lamellae smooth, devoid of spiral sculpture. Varices absent. Basal cord and disc absent. Aperture subcircular, peristome continuous, although narrowed on parietal wall. Outer lip damaged. Funicle well developed, narrow. Shell white, glossy.

Discussion – The species from Le Pigeon Blanc is characterised by its small shell, with 12 erect, continuous axial lamellae, the shell surface smooth between the axial sculpture. Other species with fused lamellae, continuous on each preceding whorl, winding around shell in a clockwise direction are: *Epitonium septemcostatum* (Conti, 1871) from the Mediterranean Pliocene, which differs in having fewer (7-9: 7-9: 7-9) axial lamellae, which are more robust and reflected as opposed to erect; *E. foliaceum* (J.D.C. Sowerby, 1825) from the Pliocene North Sea Basin has delicate, erect axial lamellae like the French Pliocene shell, but fewer in number (7-8: 7-8: 7-8) and attains quite a large size (upto 25 mm); *E. candidissimum* (Monterosato, 1877) from the Pliocene to present-day Mediterranean and adjacent Atlantic is broadly turriculate with a greater number of less elevated axial lamellae (15: 15: 15). In this species the lamellae are more or less vertically aligned, whereas in the previous two they wind around the shell clockwise from base to apex. *E. clathratulum* (Kanmacher, 1798) is similar in shape to the French Pliocene species, but has far more numerous and less elevated lamellae (20-21: 19-21: 17-21). The North Sea Basin Pliocene specimens were described as a separate species *Scalaria minuta* J.D.C. Sowerby, 1823, considered a synonym of *E. clathratulum* by subsequent authors, until Cossmann (1912, p. 40) again separated them. *Epitonium minutum* has slightly higher, less convex whorls, less arched but more erect lamellae and above all differs in the character of the funicle, far more strongly developed in *E. minutum* (see Landau *et al*., 2006, pl. 6, figs 10-11). In the middle Miocene Loire Basin *E. falunicum* (de Boury *in* Ivolas & Peyrot, 1900) is similar in shape and size but most specimens have fewer axial lamellae (9-10: 9-10: 9-10), although the occasional specimen can have 11 or 12 (Glibert, 1949, p. 171). The lamellae seem to be less elevated than in the French Pliocene shell.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

***Epitonium frondiculum* (Wood, 1848)**
Plate 15, figs 3, 4

1842 *Scalaria frondicula* Wood, p. 535 (*nomen nudum*).

1845 *Scalaria frondosa* Nyst, p. 393, pl. 38, fig. 7.
*1848 *Scalaria frondicula* Wood –Wood, p. 92, pl. 8, figs 16.
1878 *Scalaria frondicula* S. Wood – Nyst, pl. 6, fig. 15.
1882 *Scalaria frondicula* S. Wood – Nyst, p. 87.
1912 *Scala* (*Spiniscala*) *frondicula* Wood – Cossmann, p. 31, pl. 1, figs 28, 29.
?*non* 1914 *Scala* (*Spiniscala*) *frondicula* Wood – Cerulli-Irelli, p. 221, pl. 20, figs 21-25 [? = *Epitonium spiniferum* (Seguenza, 1876)].
1920 *Scala* (*Linctoscala*) *frondicula* (S.V. Wood) – Harmer, p. 531, pl. 48, figs 19, 20.
1955 *Epitonium* (*Epitonium*) *frondiculum* (S.V. Wood, 1848) – van Regteren Altena *et al*., p. 32, pl. 7, fig. 74.
1964 *Scala* (*Spiniscala*) *frondicula* Wood 1842 [*sic*] – Brébion, p. 263, pl. 6, fig. 34.
1997b *Epitonium frondiculum frondiculum* (Wood, 1842) [*sic*] – Marquet, p. 86, pl. 4, fig. 7.
1998 *Epitonium frondiculum frondiculum* (Wood, 1842 [*sic*]) – Marquet, p. 117, fig. 92.
2006 *Epitonium frondiculum* (Wood, 1848) – Landau *et al*., p. 29, pl. 12, fig. 4.
2013 *Epitonium frondiculum* (Wood, 1842 [*sic*]) – Wesselingh *et al*., p. 172, fig. 10.

Material and dimensions – Maximum height 24.4 mm. NHMW 2015/0133/0293-0294 (2 incomplete), 2015/0133/0295 (3 fragments); LC (10 fragments); FVD (2 + 3 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The shells probably represent *Epitonium frondiculum* (Wood, 1848), which is characterised by its spinous lamellae and by the absence of spiral sculpture and basal disc. The lamellae are not as well-developed as they are in the Pliocene North Sea Basin specimens. Brébion (1964, p. 264) recorded this species only from Assemblage III (Le Pigeon Blanc).

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964); North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1842, 1848; Harmer, 1920); Oorderen Sands, Belgium (Marquet, 1997b, 1998). Pliocene (indeterminate): The Netherlands (van Regteren Altena *et al*., 1955; Wesselingh *et al*., 2013).

***Epitonium* aff. *subulatum* (J.D.C. Sowerby, 1823)**
Plate 15, figs 5, 6

aff. *1823 *Scalaria subulata* J.D.C. Sowerby, p. 125, pl. 390, fig. 1.
aff. 1998 *Epitonium subulatum* (J. de C. Sowerby, 1823) – Marquet, p. 118, fig. 93.

Material and dimensions – Maximum height 14.4 mm. NHMW 2015/0133/0297-0298 (2 incomplete); LC (20 fragments); FVD (2 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – As with most of the epitoniids in Le Pigeon Blanc, only fragments are preserved. This species is characterised by its relatively narrow apical angle, deep suture, 14-15 flattened lamellae with a small auricle developed at the adapical suture, and absence of spiral sculpture and basal disc. It is closely similar to the North Sea Basin *Epitonium subulatum* (J.D.C. Sowerby, 1823), but this species has fewer (8-10) and broader axial ribs.

Distribution – Lower Pliocene: Atlantic, NW France (this paper).

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

Type species (by subsequent designation, de Boury, 1909) – *Scalaria magnifica* G.B. Sowerby II, 1844, present-day, tropical south-east Asia.

1853 *Amaea* H. Adams & A. Adams, p. 223.

Subgenus *Acrilla* H. Adams, 1860

Type species (by original designation) – *Scalaria acuminata* G.B. Sowerby II, 1844, present-day, Strait of Malacca.

1860 *Acrilla* H. Adams, p. 241.
1890c *Adiscoscala* Sacco, p. 321. Type species (by monotypy): *Acrilla coppii* de Boury, 1890, Pliocene, Italy.

***Amaea* (*Acrilla*) *stefanii* (de Boury, 1890)**
Plate 15, fig. 7

*1890 *Scalaria Stefanii* de Boury, p. 152.
2006 *Amaea* (*Acrilla*) *stefanii* (de Boury, 1890) – Landau *et al*., p. 43, pl. 10, figs 7, 8 (*cum syn*.).
2009 *Amaea coppii* (de Boury, 1890) – Chirli (*partim*), pl. 18, figs 10-15 [not figs 8, 9 = *Amaea* (*Acrilla*) *coppii* (de Boury, 1890)].

Material and dimensions – Maximum height 18.3 mm. NHMW 2015/0133/0260 (1 incomplete), 2015/0133/0261 (4 fragments); LC (10 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Two closely similar species occur in the Mediterranean Pliocene: *Amaea* (*Acrilla*) *coppii* (de Boury, 1890) and *Amaea* (*Acrilla*) *stefanii* (de Boury, 1890). The main difference between the two is in the rib count; (12-13: 13-14: 15-17) and (20-22: 22-28: 32-36) respectively (Landau *et al*., 2006). *Amaea* (*Acrilla*) *coppii* is also a squatter shell, with fewer teleoconch whorls and more prominent spiral sculpture. Chirli (2009) repeated

the original description of *A.* (*A.*) *coppii* giving the same rib count as that recorded by Landau *et al*. (2006), and yet figured shells that represent two different species. In our opinion Chirli (pl. 18, figs 8, 9) is *A.* (*A.*) *coppii*, whereas figs 10-15 show shells with a far greater number of ribs and weaker spiral sculpture; *i.e. A.* (*A.*) *stefanii*. It is possible that Chirli considered these extreme forms of a single species, but this is unlikely as the name *A.* (*A.*) *stefanii* is not included in his extensive synonymy.
The shells from Le Pigeon Blanc have about ten teleoconch whorls, sculptured by very close-set axial lamellae (32: 30: 23), fine and close-set spiral threads in the interspaces and a weakly delimited basal disc. The shape and sculpture correspond to that of *A.* (*A.*) *stefanii*. The rib formula is slightly higher, but as discussed by Landau *et al*. (2006), some Italian Pliocene forms such as *Acrilla stefanii* var. *leptoglyptobronni* Sacco, 1891 also have a greater number of ribs at the 11 mm stage (35 vs. 22-28), but probably fit within the range of variability of *A.* (*A.*) *stefanii*. Therefore, based on the scant and fragmentary material available, we consider these Le Pigeon Blanc shells conspecific with *A.* (*A.*) *stefanii*.

Distribution – Upper Miocene: Proto-Mediterranean, Italy (de Boury, 1890; Sacco, 1891). Lower Pliocene: Atlantic, NW France (this paper); central Mediterranean, Italy (Chirli, 2009). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2006); central Mediterranean, Italy (Sacco, 1891). Pliocene (unspecified): central Mediterranean, Italy (de Boury, 1890).

Genus *Clathroscala* de Boury, 1890

Type species (by original designation) – *Turbo cancellatus* Brocchi, 1814, Pliocene, Italy.

1890 *Clathroscala* de Boury, p. 215.

***Clathroscala bureaui* de Boury *in* Cossmann, 1912**
Plate 15, fig. 8

*1912 *Clathroscala Bureaui* de Boury *in* Cossmann, p. 71, pl. 5, figs 16, 17.
1964 *Amaea* (*Clathroscala*) *cancellata* var. *bureaui* de Boury *in* Cossmann, 1912 – Brébion, p. 260, pl. 6, figs 31, 32.

Material and dimensions – Maximum height 29.1 mm. NHMW 2015/0133/0299 (1), 2015/0133/0300 (4 fragments); LC (30 fragments); FVD (6 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Cossmann (1912) illustrated *Clathroscala bureaui* from the French Redonian, without specifying the locality of his specimen, and included it in the genus *Clathroscala* de Boury, 1890. Although no discussion was provided, the species differs from *C. cancellata* (Brocchi, 1814) in having weaker axial sculpture; on the last two whorls the spiral sculpture predominates. The sculpture is also finer, forming a denser and rather irregular reticulated surface sculpture. In contrast, *C. cancellata* has a very regular, more open reticulation, with the axial component predominant. This last character is well illustrated in both the shell figured by Cossmann (1912, pl. 5, figs 16, 17) and the shell figured herein (Pl. 15, fig. 8). Brébion (1964, p. 261) recorded the species from only Assemblage III (Le Pigeon Blanc, La Dixmerie).

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Clathroscala cancellata* (Brocchi, 1814)**
Plate 15, fig. 9

*1814 *Turbo cancellatus* Brocchi, p. 377, pl. 7, fig. 8.
1848 *Scalaria cancellata* Broc. – Wood, p. 95, pl. 8, fig. 22.
1864 *Scalaria Woodi* Deshayes, p. 339.
1872 *Scalaria cancellata* Broc. – Wood, p. 59, pl. 4, fig. 2.
1920 *Scala* (*Clathroscala*) *Woodi* Deshayes – Harmer, p. 552, pl. 48, figs 10, 11.
2006 *Clathroscala cancellata* (Brocchi, 1814) – Landau *et al*., p. 41, pl. 13, figs 3, 4 (*cum syn.*).
2009 *Amaea cancellata* (Brocchi, 1814) – Chirli, p. 45, pl. 18, figs 2-7.
2010 *Clathroscala cancellata* (Brocchi, 1814) – Sosso & Dell'Angelo, p. 28, 37 middle row left.
2013 *Clathroscala* cf. *cancellata* (Brocchi, 1814) – Wesselingh *et al*., p. 175, fig. 20-22.

Material and dimensions – Maximum height 14.8 mm. NHMW 2015/0133/0301 (1), 2015/0133/0302 (2 fragments); LC (3 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Wesselingh *et al*. (2013) correctly pointed out that the northern forms tend to be smaller with slightly more numerous axial ribs than is usual seen in the Mediterrean Pliocene populations. However, *Clathroscala cancellata* (Brocchi, 1814) is a somewhat variable species, and despite the slightly denser sculpture, the regular reticulation with the axial component predominant is typical for *C. cancellata*. If one insisted in separating the northern forms, the name *C. woodi* (Deshayes, 1864) could be used for them.
Brébion (1964, p. 261, pl. 6, fig. 33) illustrated a shell fragment from Le Pigeon Blanc as *Amaea* (*Clathroscala*) *redoniensis* de Boury ms. (*nomen nudum*). It was said to differ from *C. bureaui* de Boury *in* Cossmann, 1912 in having fewer an thicker spiral cords separated by narrow interspaces, fewer and thicker cords, the reticulated pit elongated. This description could also apply to *C. cancellata*. We have been unable to trace the shell illustrated by Brébion, but suspect it fits within the range of variability of *C. cancellata*.

Distribution – Lower Miocene: Proto-Mediterranean, Italy (de Boury, 1890). Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Wood, 1848, 1872; Harmer, 1920); western Mediterranean, northern Spain (Martinell, 1979), central Mediterranean, Italy (Chirli, 2009). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2006); central Mediterranean, Italy (de Gregorio, 1889; de Boury, 1890; Sacco, 1891, 1904; Pavia, 1975; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Pliocene (indeterminate): The Netherlands (Wesselingh *et al*., 2013).

Genus *Acirsa* Mörch, 1857

Type species (by subsequent designation, Bouchet & Warén, 1986) – *Scalaria eschrichti* Holböll *in* Möller, 1842, present-day, Greenland.

1857 *Acirsa* Mörch, p. 77.
1890 *Hemiacirsa* de Boury, p. 268. Type species (by original designation): *Turbo lanceolatus* Brocchi, 1814, Pliocene, Italy.
1909 *Pseudoacirsa* de Boury, p. 256. Type species (by original designation): *Acirsa bezanconi* de Boury, 1883, Eocene, France.
1926a *Notacirsa* Finlay, p. 231. Type species (by original designation): *Turbonilla oamarutica* Suter, 1917, Miocene, New Zealand.

***Acirsa semicorrugata* Chirli, 2009**
Plate 15, fig. 11

1964 *Acirsa* (*Hemiacirsa*) *couffoni* Brébion, p. 255, pl. 6, fig. 28 (*nomen nudum*).
*2009 *Acirsa semicorrugata* d'Ancona ms., Chirli, p. 43, pl. 17, figs 1-8.

Material and dimensions – Maximum height 12.7 mm. NHMW 2015/0133/0303 (1), 2015/0133/0304 (1 fragment); LC (6 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Chirli (2009) figured a shell from the lower Pliocene of Italy, almost identical to the one illustrated here from Le Pigeon Blanc, as a new species *Acirsa semicorrugata*, the name written on a label by d'Ancona accompanying a specimen in the Pecchioli collection in the department of Geologia e Paleontologia del Museo si Storia Naturale dell'Università di Firenze. In the fossil record, the author only compared his new species with *Acirsa corrugata* (Brocchi, 1814) also from the Italian Pliocene, which differs in having more convex whorls bearing narrow axial ribs developed on all the teleoconch whorls and persisting strongly upto the outer lip. *Acirsa semicorrugata* Chirli, 2009 was said to have less convex whorls and the ribs obsolete on the last whorl. We note that some of the specimens of the new species figured by Chirli (*i.e*., 2009, fig. 8) approximates in its sculpture to *A. corrugata*. This makes us wonder about *Acirsa lanceolata* (Brocchi, 1814), also from the Pliocene Mediterranean. Typical specimens have ribs persisting on all whorls (see Chirli, 2009, pl. 16, figs 13-18). However, the specimen from the lower upper Pliocene Estepona Basin illustrated by Landau *et al*. (2006, pl. 14, fig. 6) loses its axial rib after the first few teleoconch whorls. Nevertheless, Chirli (2009, p. 42) included the Estepona record in his synonymy of *A. lanceolata*. The shell illustrated by Sacco (1904, pl. 23, fig. 30) as *Hemiacirsa lanceolata* from Astigiana, Italy is not unlike some of the shells illustrated by Chirli as *A. semicorrugata*. Brébion (1964, p. 255) described *Acirsa* (*Hemiacirsa*) *couffoni* (*nomen nudum*) from the Assemblage I locality of St-Michel. This small species differs in having stronger sculpture that persists onto the last teleoconch whorls and more numerous axial ribs. It will be formally described in a subsequent paper.
We wonder if a little over-enthusiatic splitting is involved, but in view of the larger amount of Italian material available to Chirli, we provisionally accept his new species.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); central Mediterranean, Italy (Chirli, 2009).

Genus *Nodiscala* de Boury, 1890

Type species (by original designation) – *Scalaria bicarinata* G.B. Sowerby II, 1844, present-day, Philippines.

1890 *Nodiscala* de Boury, p. 168.

***Nodiscala scacchii* (Hörnes, 1856)**
Plate 15, fig. 10

*1856 *Scalaria Scacchii* Hörnes, p. 479, pl. 46, fig. 12.
2006 *Nodiscala scacchii* (Hörnes, 1856) – Landau *et al*., p. 50, pl. 15, figs 4-8, pl. 16, figs 1-4 (*cum syn*).

Material and dimensions – Apertural fragment, height 4.4 mm. (LC 1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Numerous *Nodiscala* species have been described in the European Neogene. Based on the wide variability in the shells seen in the Pliocene assemblages in Estepona, Spain, many of these were considered by Landau *et al*. (2006, p. 51) to represent a single species: *Nodiscala scacchii* (Hörnes, 1856). Despite being represented by a single apertural fragment, the two rows of nodules on the last whorl place it within this species, as defined by Landau *et al*. (2006). *Nodiscala scacchii* seems therefore to have had a wide European distribution in the Miocene and Pliocene, although it is always uncommon.

Distribution – Lower Miocene: Atlantic (Aquitanian),

France (Lozouet *et al*., 2001), North Sea Basin, Belgium (Glibert, 1949). Middle Miocene: North Sea Basin, The Netherlands (Nordsieck, 1972; A.W. Janssen, 1984), Germany (A.W. Janssen, 1967; Wienrich, 2001); ? Touraine Basin, France (Glibert, 1949); Paratethys, Austria (Hörnes, 1856); Romania (Boettger, 1902; Cossmann, 1912), Hungary (Cossmann, 1912; Csepreghy-Meznerics, 1956; Strausz, 1966), Poland (Bałuk, 1975); central Mediterranean, Italy (Sacco, 1891). Lower Pliocene: Atlantic, NW France (this paper). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2006); central Mediterranean, Italy (Cavallo & Repetto, 1992; Brunetti, 2000).

Genus *Cirsotrema* Mörch, 1852

Type species (by monotypy) – *Scalaria varicosa* Lamarck, 1822, present-day, Indo-Pacific.

1852 *Cirsotrema* Mörch, p. 49.
1892 *Cyrsotrema* Sacco, p. 66. Incorrect subsequent spelling.
1909 *Coroniscala* de Boury, p. 255. Type species (by original designation): *Scalaria coronalis* Deshayes, 1861, Eocene, France.
1911 *Elegantiscala* de Boury, p. 216. Type species (by original designation): *Scalaria elegantissima* Deshayes, 1861, Eocene, France.
1928a *Cirsotremopsis* Thiele, p. 92. Type species (by monotypy): *Scalaria cochlea* G.B. Sowerby II, 1844, present-day, Angola.

***Cirsotrema fimbriosum* (Wood, 1848)**
Plate 15, fig. 12

1842 *Scalaria fimbriosa* Wood, p. 535 (*nomen nudum*).
*1848 *Scalaria fimbriosa* S. Wood – Wood, p. 91, pl. 8, fig. 12.
1878 *Scalaria fimbriosa* S. Wood – Nyst (*partim*), pl. 6, fig. 18a only [18b = *Cirsotrema fimbriosum exfimbriosum* (Sacco, 1891)].
1882 *Scalaria fimbriosa* S. Wood – Nyst (*partim*), p. 89.
1879 *Scalaria fimbriosa* S. Wood – Wood, p. 25, pl. 3, fig. 17.
1920 *Scala* (*Cirsotrema*) *fimbriosa* (S.V. Wood) – Harmer, p. 542, pl. 48, figs 1, 2, 6.
1955 *Cirsotrema fimbriosum* (S.V. Wood, 1848) – van Regteren Altena *et al*., p. 31, pl. 7, fig. 70.
1964 *Cirsotrema fimbriosa* Wood, 1842 [*sic*] – Brébion, p. 259, pl. 6, fig. 30.
1997b *Cirsotrema* (*C.*) *fimbriosum fimbriosum* (Wood, 1842 [*sic*]) – Marquet, p. 84, pl. 4, fig. 4.
1998 *Cirsotrema* (*C.*) *fimbriosum fimbriosum* (Wood, 1842 [*sic*]) – Marquet, p. 114, fig. 88a, b.
2006 *Cirsotrema* (*C.*) *fimbriosum fimbriosum* (Wood, 1842 [*sic*]) – Landau *et al*., pl. 13, fig. 1.
2013 *Cirsotrema fimbriosum* (Wood, 1842 [*sic*]) – Wesselingh *et al*., p. 177, fig. 27.

Material and dimensions – Maximum height approx. 32.0 mm (reconstructed). NHMW 2015/0133/0264 (1), 2015/0133/0265 (7 fragments); LC (16); FVD (10 incomplete). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Two similar *Cirsotrema* species have been recognised in the North Sea Basin Pliocene: *C. fimbriosum* (Wood, 1848) and *C. funiculus* (Wood, 1872). They are said to differ in that *C. funiculus* has more numerous weaker axial ribs (11-14 in *C. fimbriosum* vs. 20+ in *C. funiculus*). In typical specimens, as the ones illustrated here, the difference is apparent. However, some specimens are difficult to ascribe to one or other species and seem to have an intermediate number of ribs. Wesselingh *et al*. (2013, p. 177) commented on this variability in the Pliocene fossil specimens washed up on Dutch beaches and wondered if they did not represent a single species, with a rather variable number of axial ribs.
At Le Pigeon Blanc *Cirsotrema* specimens are seldom found complete. The *C. funiculus* morphotype is commoner than the *C. fimbriosum* one, and here also some specimens are difficult to convincingly ascribe to one or other species. However, we hesitate to synonymise the two, as typical *C. funiculus* with very close set ribs (about 27) occur in the Assemblage I locality of St-Clément-de-la-Place, but not *C. fimbriosum*. Brébion (1964, p. 260) also reported *C. fimbriosum* from Assemblage III localities (Le Girondor, La Gauvinière, Le Pigeon Blanc, La Dixmérie) and Assemblage IV (Gourbesville), but not from the upper Miocene assemblages. It seems, therefore, that *C. funiculus* appeared earlier, in the Atlantic upper Miocene, was coeval with *C. fimbriosum* during the Pliocene, but disappeared before *C. fimbriosum*, which survived into the Pleistocene. It is also possible that the two nominal taxa represent extremes in sculpture of a single species, with the finely ribbed morphotype appearing earlier and the coarser ribbed form predominating, until finally becoming extinct in the Pleistocene. We provisionally prefer to keep the two forms separate.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Harmer, 1920); Kattendijk Formation, Belgium (Marquet, 1997b, 1998). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1842, 1848, 1879; Harmer, 1920); Oorderen Sands, Belgium (Landau *et al*., 2006). Pliocene (indeterminate): The Netherlands (van Regteren Altena *et al*., 1955; Wesselingh *et al*., 2013). Upper Pliocene-Pleistocene: NW France (Brébion, 1964).

***Cirsotrema funiculus* (Wood, 1872)**
Plate 15, fig. 13

1842 *Scalaria fimbriata* Wood, p. 535 (*nomen nudum*).
1848 *Scalaria varicosa* Lam. – Wood, p. 90, pl. 8, fig. 14 [*non Cirsotrema varicosum* (Lamarck, 1822)].
1854 *Scalaria Crenulata* Millet, p. 155 (*nomen nudum*).

1865 *Scalaria crenulata* Millet, p. 580 (*non* Kiener, 1838).
1872 *Scalaria varicosa* Lamarck – Wood, p. 98.
*1872 *Scalaria funiculus* Wood, p. 98.
1920 *Scala* (*Cirsotrema*) *funiculus* (S.V. Wood) – Harmer, p. 544, pl. 48, fig. 8.
1955 *Cirsotrema funiculus* (S.V. Wood, 1872) – van Regteren Altena *et al*., p. 31, pl. 7, fig. 69.
1958 *Cirsotrema funiculus* Wood, 1872 – Glibert, p. 12, pl. 2, fig. 8.
1964 *Cirsotrema funiculus* Wood, 1872 – Brébion, p. 257, pl. 6, fig. 29.
1997b *Cirsotrema* (*C.*) *funiculus* (Wood, 1872) – Marquet, p. 85, pl. 4, fig. 5.
1998 *Cirsotrema* (*C.*) *funiculus* (Wood, 1872) – Marquet, p. 115, fig. 88d.

Material and dimensions – Maximum height 31.4 mm. NHMW 2015/0133/0266 (1), 2015/0133/0267 (16 fragments); LC (23); FVD (16 incomplete). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – See above. Brébion (1964, p. 258) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, Les Pierres Blanches), Assemblage II (Apigné, Carcé), Assemblage III (Le Pigeon Blanc, Le Girondor, La Gauvinière) and Assemblage IV (Gourbesville).

Distribution – Upper Miocene (Tortonian and Messinian): NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (this paper); North Sea Basin, Coralline Crag, England (Harmer, 1920); Kattendijk Formation, Belgium (Glibert, 1958; Marquet, 1997b, 1998). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848, 1872; Harmer, 1920). Pliocene (indeterminate): The Netherlands (van Regteren Altena *et al*., 1955). Upper Pliocene-Plesitocene: NW France (Brébion, 1964).

Discussion

In this paper we record 91 caenogastropod species, of which 15 are left in open nomenclature, representing 58 genera. This is more than double the number of species reported by Brébion (1964) from the Assemblage III localities of NW France. Seventeen species are described as new: *Bittium lozoueti* nov. sp., *Bittium gliberti* nov. sp., *Tympanotonos redoniensis* nov. sp., *Oligodia palumbina* nov. sp., *Cochlis robbai* nov. sp., *Cochlis pedrialii* nov. sp., *Payraudeautia pigeonblancensis* nov. sp., *Alvania calasi* nov. sp., *Alvania dissensia* nov. sp., *Alvania merlei* nov. sp., *Alvania zbyszewskii* nov. sp., *Crisilla ariejansseni* nov. sp., *Rissoa pouweri* nov. sp., *Caecum aartseni* nov. sp., *Nystia guillotini* nov. sp., *Aclis pacaudi* nov. sp. and *Niso dollfusi* nov. sp. Of the 91 caenogastropod species here recorded, 24 (26%) occur exclusively in north western French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. Stratigraphically (see Fig. 1), 22 (24%) of the species found at Le Pigeon Blanc are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1949). 32 (36%) are also present in the Assemblage I (sensu Van Dingenen *et al*., 2015) of north western France. Twenty-nine species (32%) are also found in the North Sea Basin Pliocene and 29 species (32%) are relatively cosmopolitan in the European Pliocene, found in the Atlantic and Mediterranean.

At genus level, many of the taxa are still found today off the coast of north western France. However, an important number of genera such *as Tympanotonos*, *Macromphalus*, *Thylacodes*, *Schilderia*, *Neosimnia*, *Cochlis*, *Payraudeautia*, *Sinum*, and the Tonnoidea and Ficoidea, are still found in European waters, but with a more southern distribution.

The finding of this paper echo those discussed in the first part of this series (Ceulemans *et al*., 2016). Based on the gastropods, we find a relatively endemic assemblage in the Zanclean lower Pliocene of north western France, with small and equal influences from both northern and southern seas. The faunal composition suggests that average Sea Surface Temperatures were higher than they are at these latitudes today, possibly similar to those found off the southern Portuguese coasts at present time.

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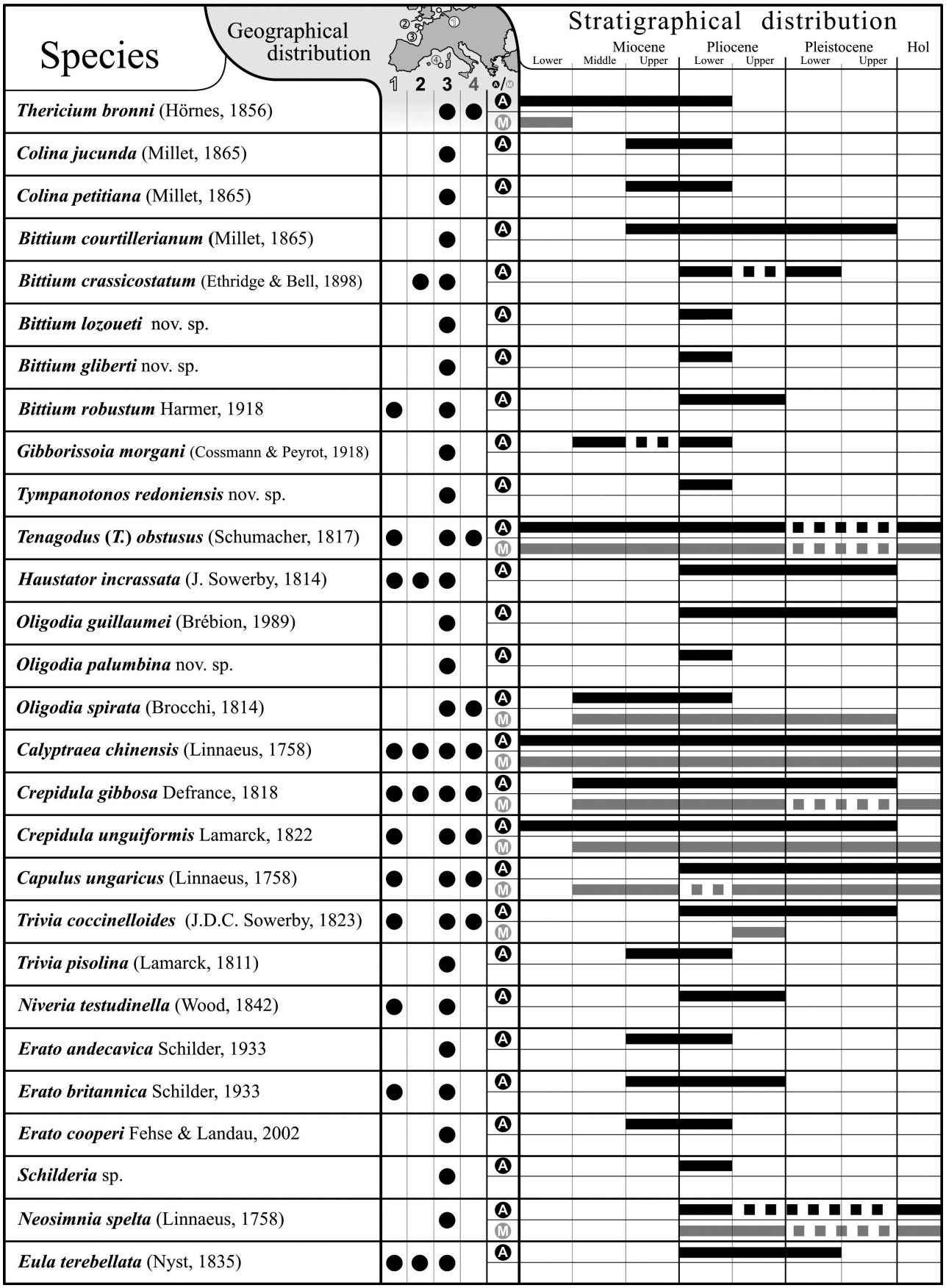
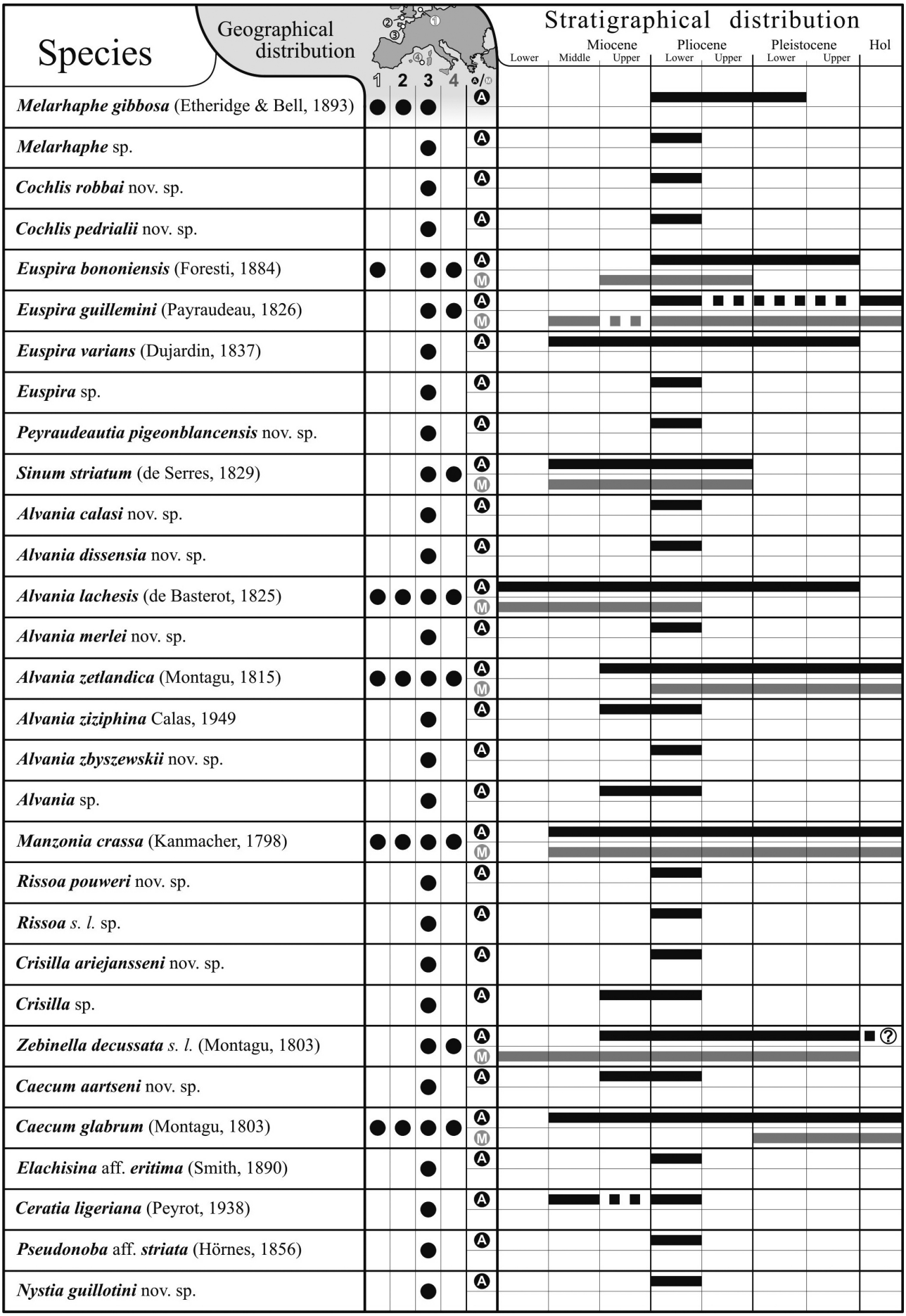
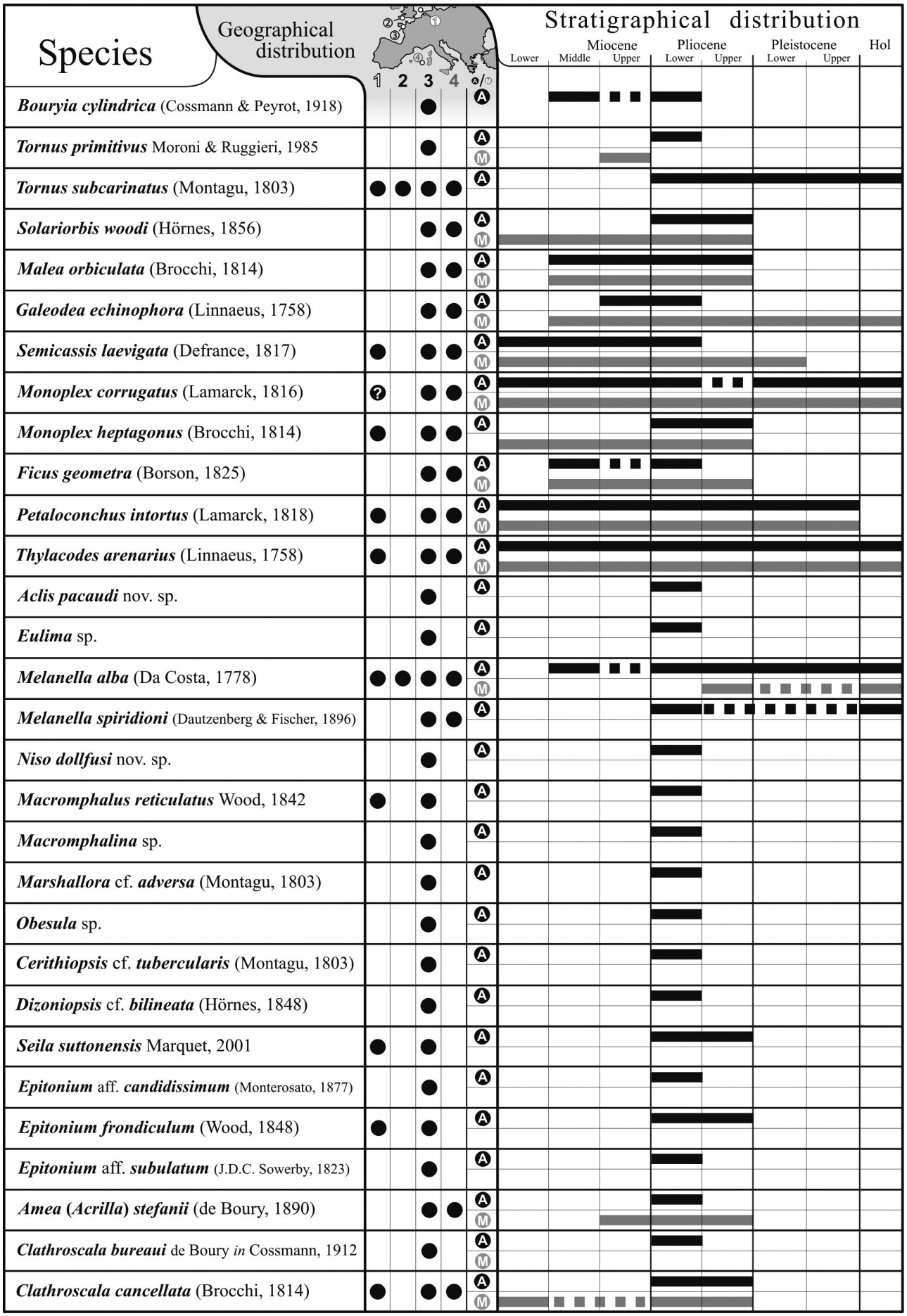


Figure 1. Geography, stratigraphy and distribution of species found in the Pliocene of Le Pigeon Blanc. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black signified Atlantic distribution (A), grey Mediterranean distribution (M).


Species
Geographical distribution
1
2
3
4
A/M
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower
Middle
Upper
Lower
Upper
Lower
Upper
Melarhaphe gibbosa (Etheridge & Bell, 1893)
Melarhaphe sp.
Cochlis robbai nov. sp.
Cochlis pedrialii nov. sp.
Euspira bononiensis (Foresti, 1884)
Euspira guillemini (Payraudeau, 1826)
Euspira varians (Dujardin, 1837)
Euspira sp.
Peyraudeautia pigeonblancensis nov. sp.
Sinum striatum (de Serres, 1829)
Alvania calasi nov. sp.
Alvania dissensia nov. sp.
Alvania lachesis (de Basterot, 1825)
Alvania merlei nov. sp.
Alvania zetlandica (Montagu, 1815)
Alvania ziziphina Calas, 1949
Alvania zbyszewskii nov. sp.
Alvania sp.
Manzonia crassa (Kanmacher, 1798)
Rissoa pouweri nov. sp.
Rissoa *s. l.* sp.
Crisilla ariejansseni nov. sp.
Crisilla sp.
Zebinella decussata *s. l.* (Montagu, 1803)
Caecum aartseni nov. sp.
Caecum glabrum (Montagu, 1803)
Elachisina aff. ***eritima*** (Smith, 1890)
Ceratia ligeriana (Peyrot, 1938)
Pseudonoba aff. ***striata*** (Hörnes, 1856)
Nystia guillotini nov. sp.


Species
Geographical distribution
1 2 3 4
A/M
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower
Middle
Upper
Lower
Upper
Lower
Upper
Bouryia cylindrica (Cossmann & Peyrot, 1918)
Tornus primitivus Moroni & Ruggieri, 1985
Tornus subcarinatus (Montagu, 1803)
Solariorbis woodi (Hörnes, 1856)
Malea orbiculata (Brocchi, 1814)
Galeodea echinophora (Linnaeus, 1758)
Semicassis laevigata (Defrance, 1817)
Monoplex corrugatus (Lamarck, 1816)
Monoplex heptagonus (Brocchi, 1814)
Ficus geometra (Borson, 1825)
Petaloconchus intortus (Lamarck, 1818)
Thylacodes arenarius (Linnaeus, 1758)
Aclis pacaudi nov. sp.
Eulima sp.
Melanella alba (Da Costa, 1778)
Melanella spiridioni (Dautzenberg & Fischer, 1896)
Niso dollfusi nov. sp.
Macromphalus reticulatus Wood, 1842
Macromphalina sp.
Marshallora cf. adversa (Montagu, 1803)
Obesula sp.
Cerithiopsis cf. tubercularis (Montagu, 1803)
Dizoniopsis cf. bilineata (Hörnes, 1848)
Seila suttonensis Marquet, 2001
Epitonium aff. candidissimum (Monterosato, 1877)
Epitonium frondiculum (Wood, 1848)
Epitonium aff. subulatum (J.D.C. Sowerby, 1823)
Amea (Acrilla) stefanii (de Boury, 1890)
Clathroscala bureaui de Boury in Cossmann, 1912
Clathroscala cancellata (Brocchi, 1814)

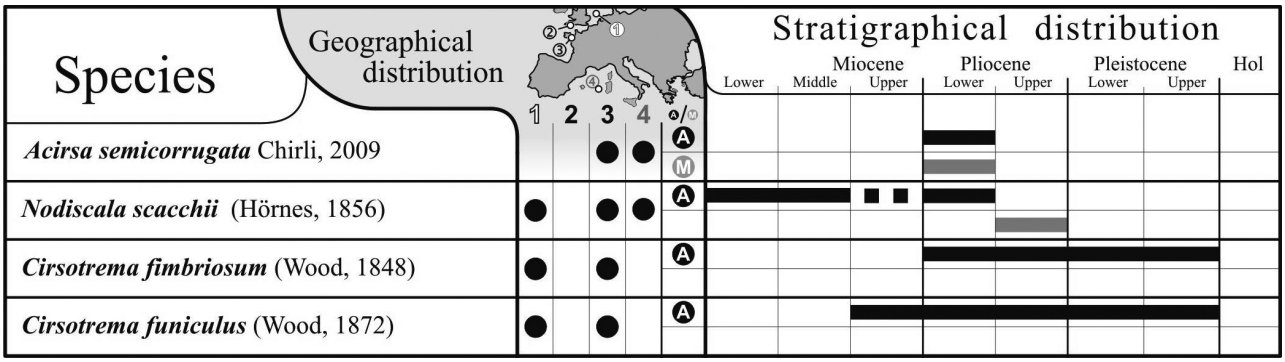


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Plate 1

1. *Thericium bronni* (Hörnes, 1845), NHMW 2015/0133/0203, height 29.8 mm.
2. *Thericium bronni* (Hörnes, 1845), NHMW 2015/0133/0204, height 23.3 mm.
3. *Thericium bronni* (Hörnes, 1845), NHMW 2015/0133/0205, height 25.5 mm.
4. *Colina jucunda* (Millet, 1865), NHMW 2015/0133/0277, height 11.3 mm.
5. *Colina jucunda* (Millet, 1865), NHMW 2015/0133/0278, height 13.3 mm.
6. *Colina jucunda* (Millet, 1865), NHMW 2015/0133/0279, height 5.3 mm.
7. *Colina jucunda* (Millet, 1865), LC coll., height 9.0 mm.
8. *Colina petitiana* (Millet, 1865), NHMW 2015/0133/0280, height 13.0 mm.
9. *Bittium courtillerianum* (Millet, 1865), NHMW 2015/0133/0104, height 9.5 mm.
10. *Bittium crassicostatum* (Etheridge & Bell, 1898), NHMW 2015/0133/0106, height 9.3 mm.
11. *Bittium lozoueti* nov. sp., holotype MNHN.F.A53621, height 11.0 mm, figured in Brébion (1964, pl. 5, fig. 27, as *Bittium reticulatum* var. *lecointrei nomen nudum*) (photo MNHN).
12. *Bittium lozoueti* nov. sp., paratype 1 MNHN.F.A53622, height 9.1 mm, figured in Brébion (1964, pl. 5, fig. 28, as *Bittium reticulatum* var. *lecointrei nomen nudum*) (photo MNHN).
13. *Bittium lozoueti* nov. sp., paratype 2 NHMW 2015/0133/0108, height 9.7 mm.
14. *Bittium lozoueti* nov. sp., paratype 3 NHMW 2015/0133/0115, height 10.6 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

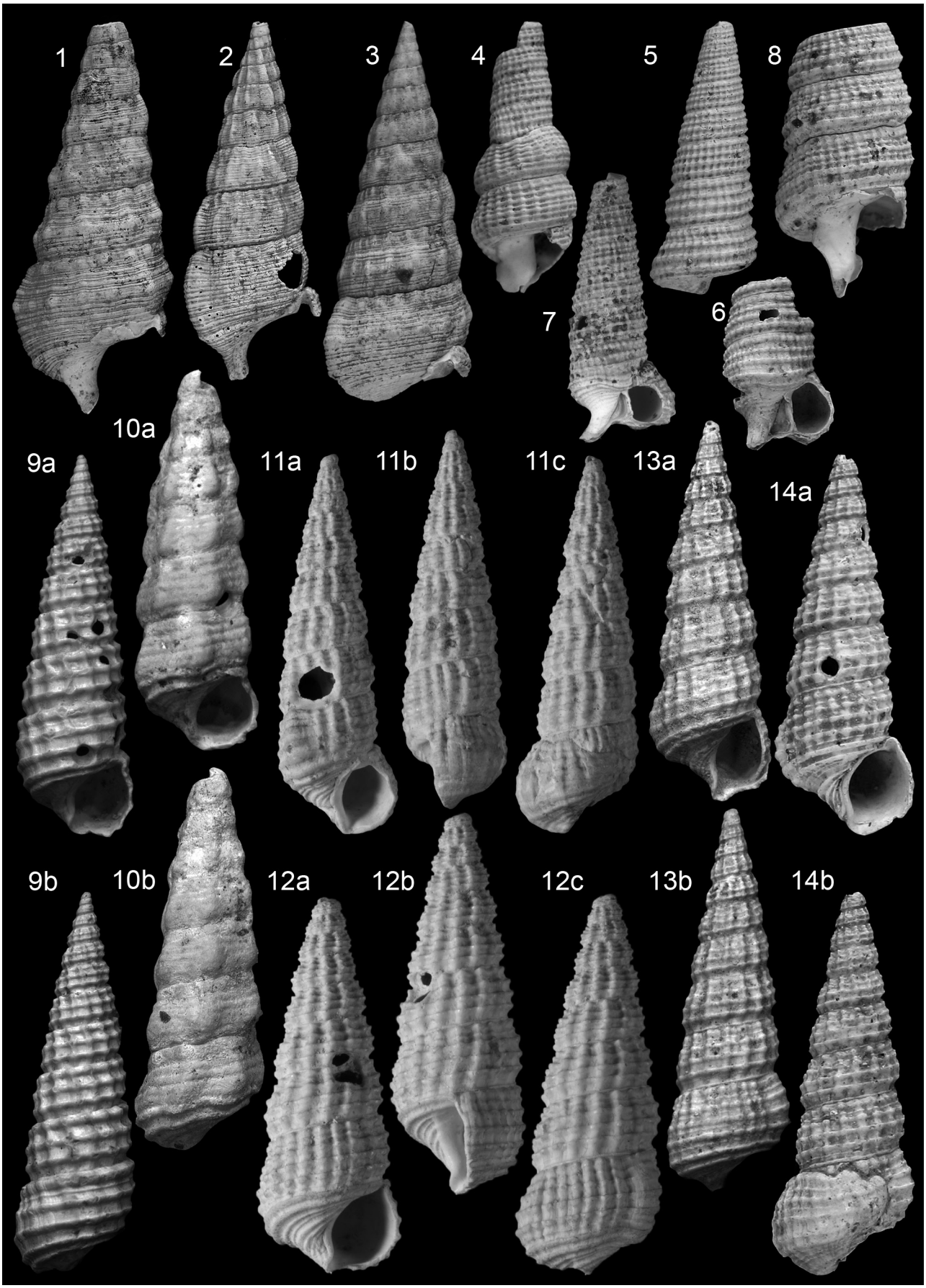

Plate 1

Plate 2

1. *Bittium gliberti* nov. sp., holotype MNHN.F.A53623, height 10.5 mm, figured in Brébion (1964, pl. 6, fig. 1, as *Bittium turritelloides* Dollfus mss. *nomen nudum*) (photo MNHN).
2. *Bittium gliberti* nov. sp., paratype 1 MNHN.F.A53624, height 10.7 mm, figured in Brébion (1964, pl. 6, fig. 2, as *Bittium turritelloides* Dollfus mss. *nomen nudum*) (photo MNHN).
3. *Bittium gliberti* nov. sp., paratype 7 NHMW 2015/0133/0112, height 12.8 mm.
4. *Bittium courtillerianum* (Millet, 1865), NHMW 2015/0133/0111 (SEM).
5. *Bittium lozoueti* nov. sp., paratype 8 NHMW 2015/0133/0109 (SEM).
6. *Bittium gliberti* nov. sp., paratype 2 NHMW 2015/0133/0113 (SEM).
7. *Bittium robustum* Harmer, 1918, NHMW 2015/0133/0119, height 13.1 mm.
8. *Bittium robustum* Harmer, 1918, NHMW 2015/0133/0281, height 15.7 mm.
9. *Gibborissoia morgani* (Cossmann & Peyrot, 1918), NHMW 2015/0133/0188, height 6.2 mm.
10. *Tympanotonos redoniensis* nov. sp., paratype 1 NHMW 2015/0133/0206, height 17.5 mm.
11. *Tympanotonos redoniensis* nov. sp., paratype 2 NHMW 2015/0133/0207, height 29.4 mm.
12. *Tympanotonos redoniensis* nov. sp., holotype MNHN.F.A57392, height 24.2 mm.
13. *Tympanotonos redoniensis* nov. sp., paratype 3 NHMW 2015/0133/0208, height 21.2 mm.
14. *Tenagodus* (*Tenagodus*) *obtusus* (Schumacher, 1817), NHMW 2015/0133/0121, height 15.8 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

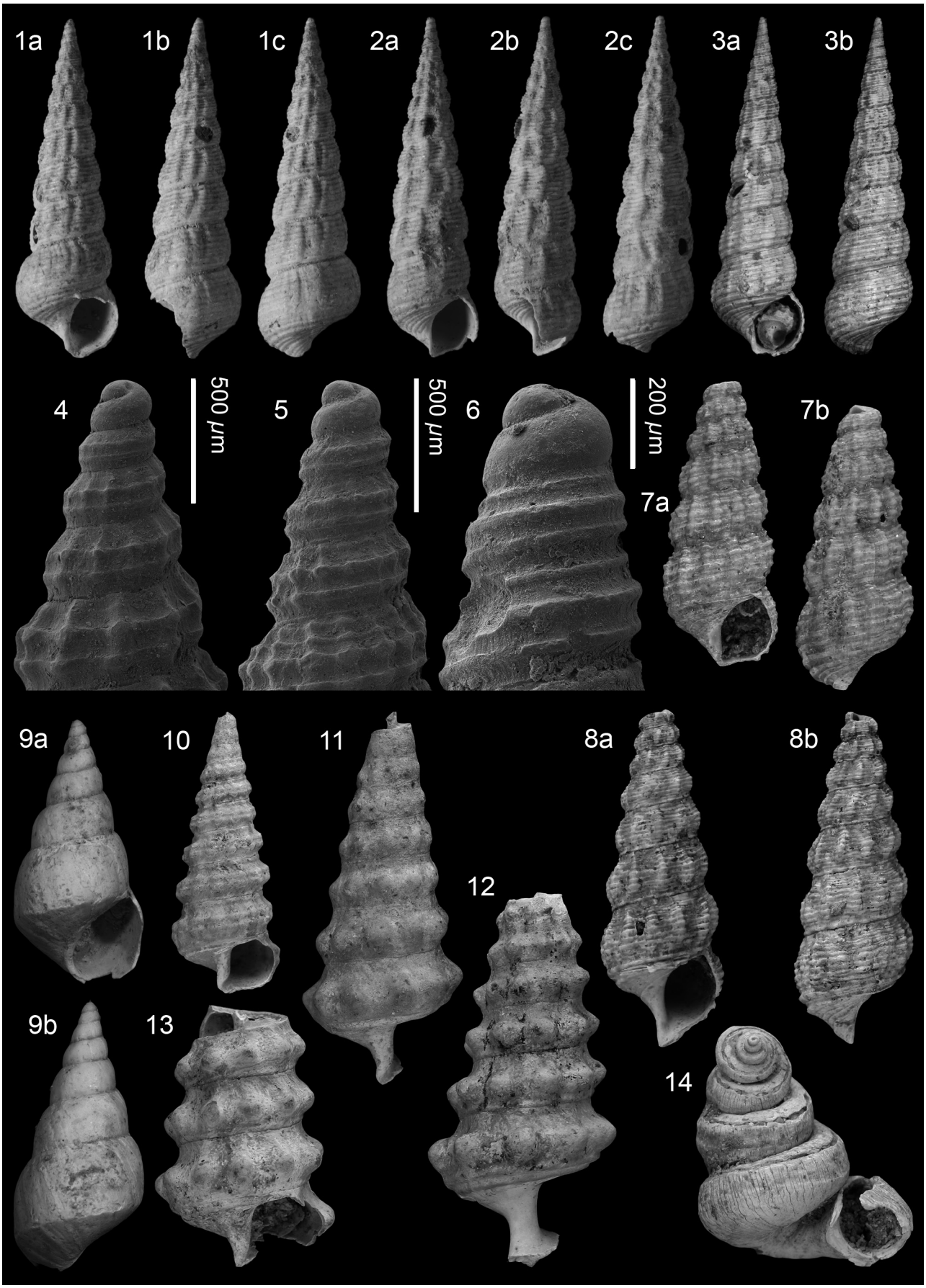
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Plate 2

Plate 3

1. *Haustator incrassata* (J. Sowerby, 1814), NHMW 2015/0133/0282, height 20.5 mm.
2. *Haustator incrassata* (J. Sowerby, 1814), MNHN.F.A53617, height 9.5 mm, Palluau.
3. *Oligodia guillaumei* (Brébion, 1989), MNHN.F.A53619, height 37.2 mm.
4. *Oligodia guillaumei* (Brébion, 1989), NHMW 2015/0133/0123, height 44.0 mm.
5. *Oligodia guillaumei* (Brébion, 1989), NHMW 2015/0133/0124, height 42.8 mm.
6. *Oligodia palumbina* nov. sp., holotype NHMW 2015/0133/0129, height 70.2 mm.
7. *Oligodia palumbina* nov. sp., paratype 1 NHMW 2015/0133/0130, height 54.1 mm.
8. *Turritella spirata* (Brocchi, 1814), NHMW 2015/0133/0126, height 18.5 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

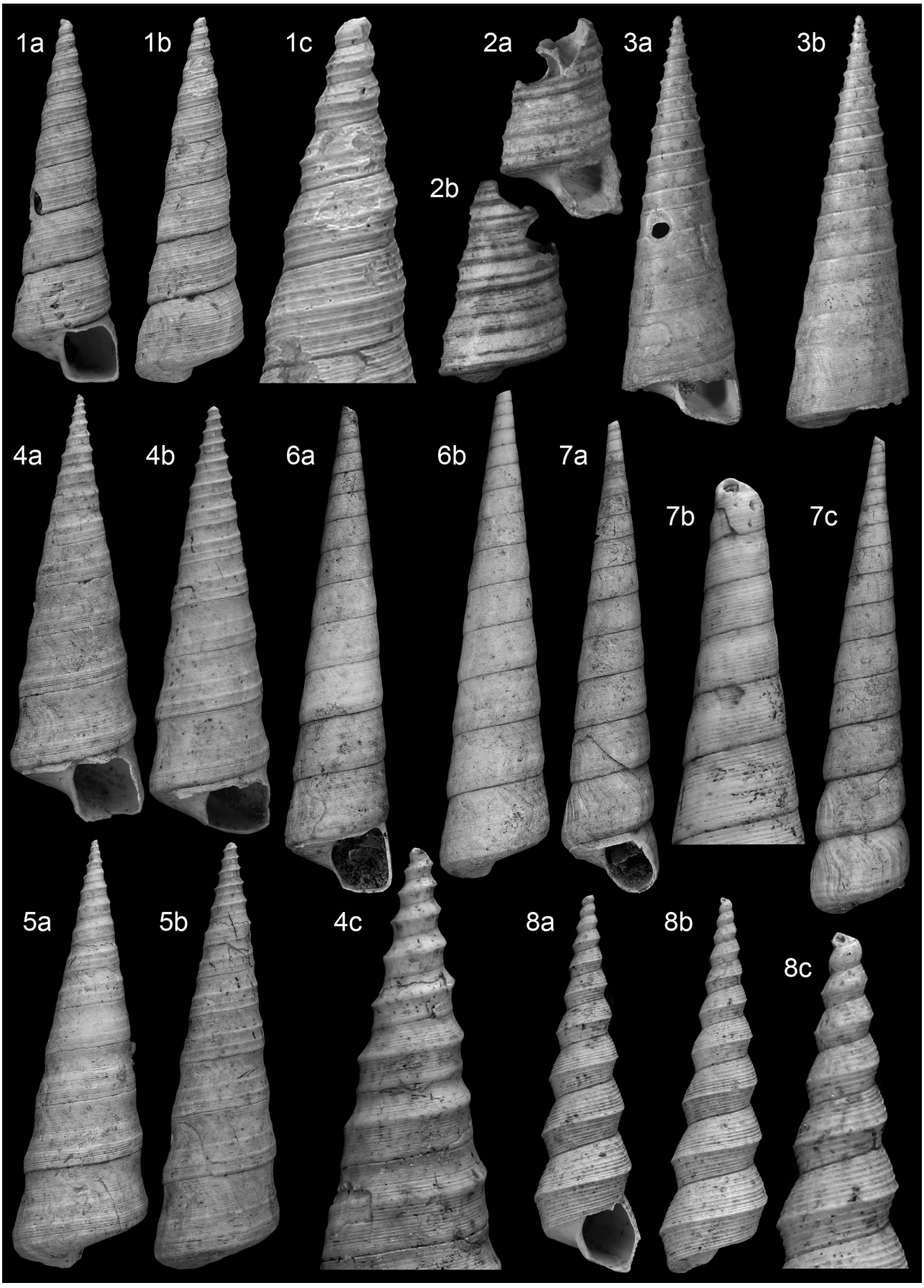

Plate 3

Plate 4

1. *Calyptraea chinensis* (Linnaeus, 1758), NHMW 2015/0133/0213, maximum diameter 19.3 mm.
2. *Crepidula gibbosa* Defrance, 1818, NHMW 2015/0133/0152, maximum diameter 23.8 mm.
3. *Crepidula unguiformis* Lamarck, 1822, NHMW 2015/0133/0274, maximum diameter 17.8 mm.
4. *Capulus ungaricus* (Linnaeus, 1758), NHMW 2015/0133/0212, maximum diameter 20.5 mm.
5. *Trivia coccinelloides* (J.D.C. Sowerby, 1823), NHMW 2015/0133/0236, length 7.9 mm.
6. *Trivia pisolina* (Lamarck, 1811), NHMW 2015/0133/0305, length 9.3 mm.
7. *Niveria testudinella* (Wood, 1842), NHMW 2015/0133/0238, length 12.6 mm.
8. *Erato andecavica* Schilder, 1933, NHMW 2015/0133/0232, height 8.8 mm.
9. *Erato britannica* Schilder, 1933, NHMW 2015/0133/0234, height 7.7 mm.
10. *Erato cooperi* Fehse & Landau, 2002, NHMW 2015/0133/0230, height 5.4 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

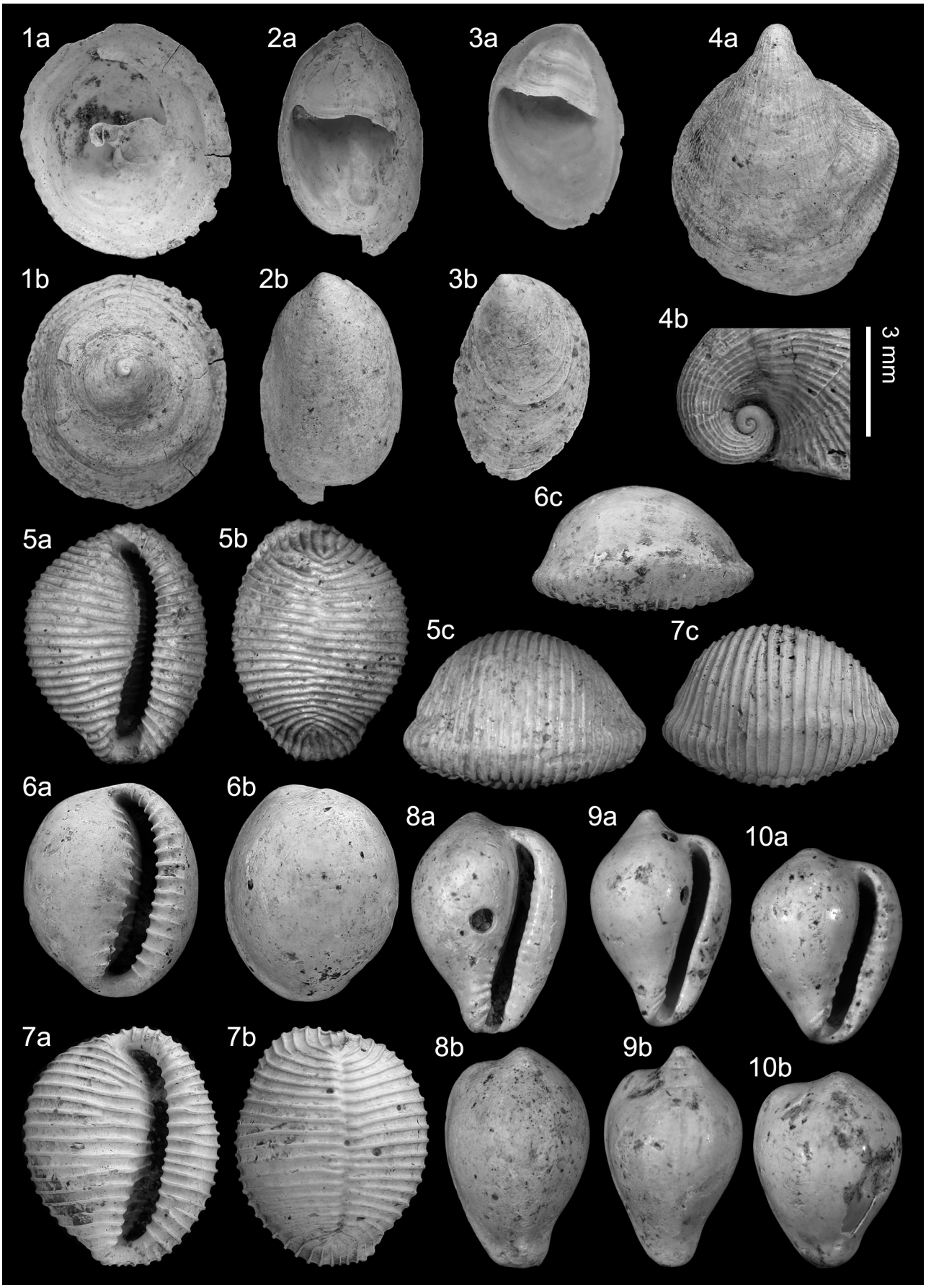
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Plate 4

Plate 5

1. *Schilderia* sp., FVD coll., length 41.7 mm (photo FVD).
2. *Neosimnia spelta* Linnaeus, 1758, NHMW 2015/0133/0408 height 10.7 mm.
3. *Eula terebellata* (Nyst, 1835), NHMW 2015/0133/0270, height 5.4 mm.
4. *Melarhaphe gibbosa* (Etheridge & Bell, 1893), NHMW 2015/0133/0131, height 3.8 mm.
5. *Melarhaphe* sp., NHMW 2015/0133/0276, height 3.9 mm.
6. *Cochlis robbai* nov. sp., holotype, MNHN.F.A53620, 21.0 mm.
7. *Cochlis robbai* nov. sp., paratype 1 NHMW 2015/0133/0333, height 21.8 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

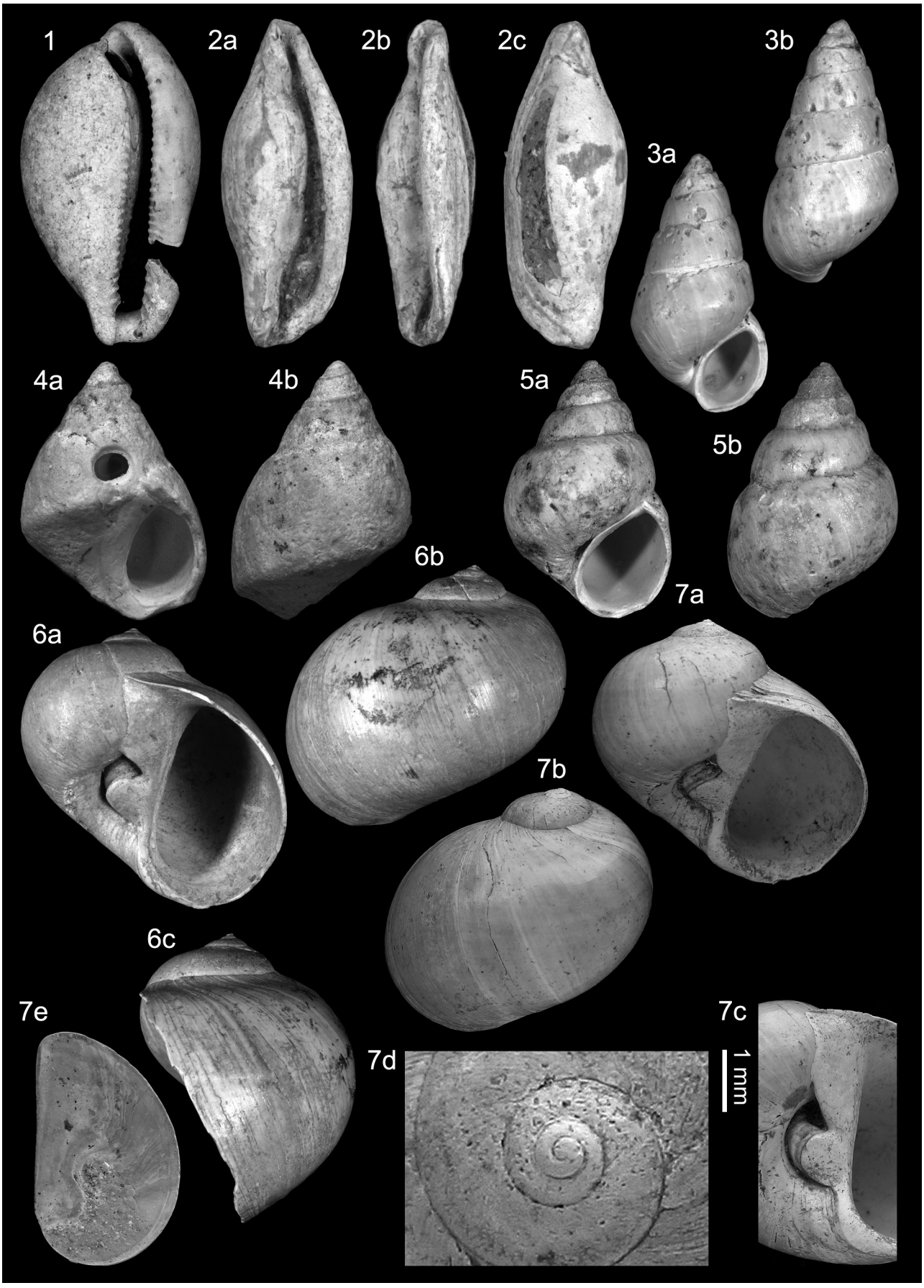

Plate 5

Plate 6

1. *Cochlis pedrialii* nov. sp., holotype NHMW 2015/0133/0339, height 21.8 mm.
2. *Cochlis pedrialii* nov. sp., paratype 1 NHMW 2015/0133/0340, height 30.0 mm.
3. *Euspira bononensis* (Foresti, 1884), NHMW 2015/0133/0346, height 26.1 mm.
4. *Euspira guillemini* (Payraudeau, 1826), NHMW 2015/0133/0348, height 3.0 mm.
5. *Euspira varians* (Dujardin, 1837). NHMW 2015/0133/0349, height 13.9 mm.
6. *Payraudeautia pigeonblancensis* nov. sp., holotype NHMW 2015/0133/0351, height 8.9 mm.
7. *Payraudeautia pigeonblancensis* nov. sp., paratype 1 NHMW 2015/0133/0352, height 7.7 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

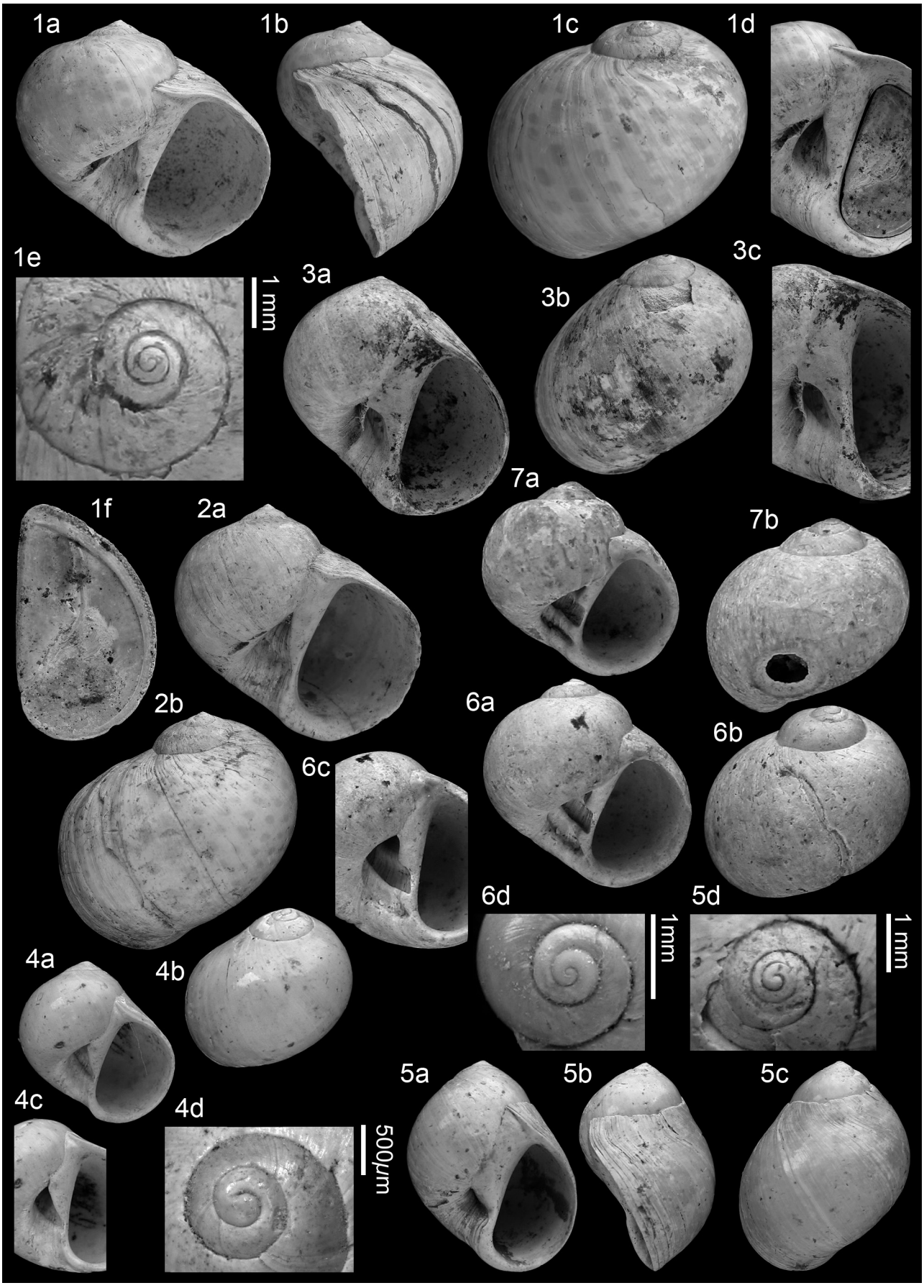
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Plate 6

Plate 7

1. *Euspira* sp., NHMW 2015/0133/0358, height 7.4 mm.
2. *Sinum striatum* (de Serres, 1829), NHMW 2015/0133/0215, diameter 23.2 mm x 18.9 mm.
3. *Alvania calasi* nov. sp., holotype NHMW 2015/0133/0148, height 2.9 mm (SEM).
4. *Alvania calasi* nov. sp., paratype 1 NHMW 2015/0133/0149, height 2.8 mm.
5. *Alvania calasi* nov. sp., paratype 2 NHMW 2015/0133/0150, height 2.8 mm.
6. *Alvania dissensia* nov. sp., holotype NHMW 2015/0133/0146, height 8.3 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

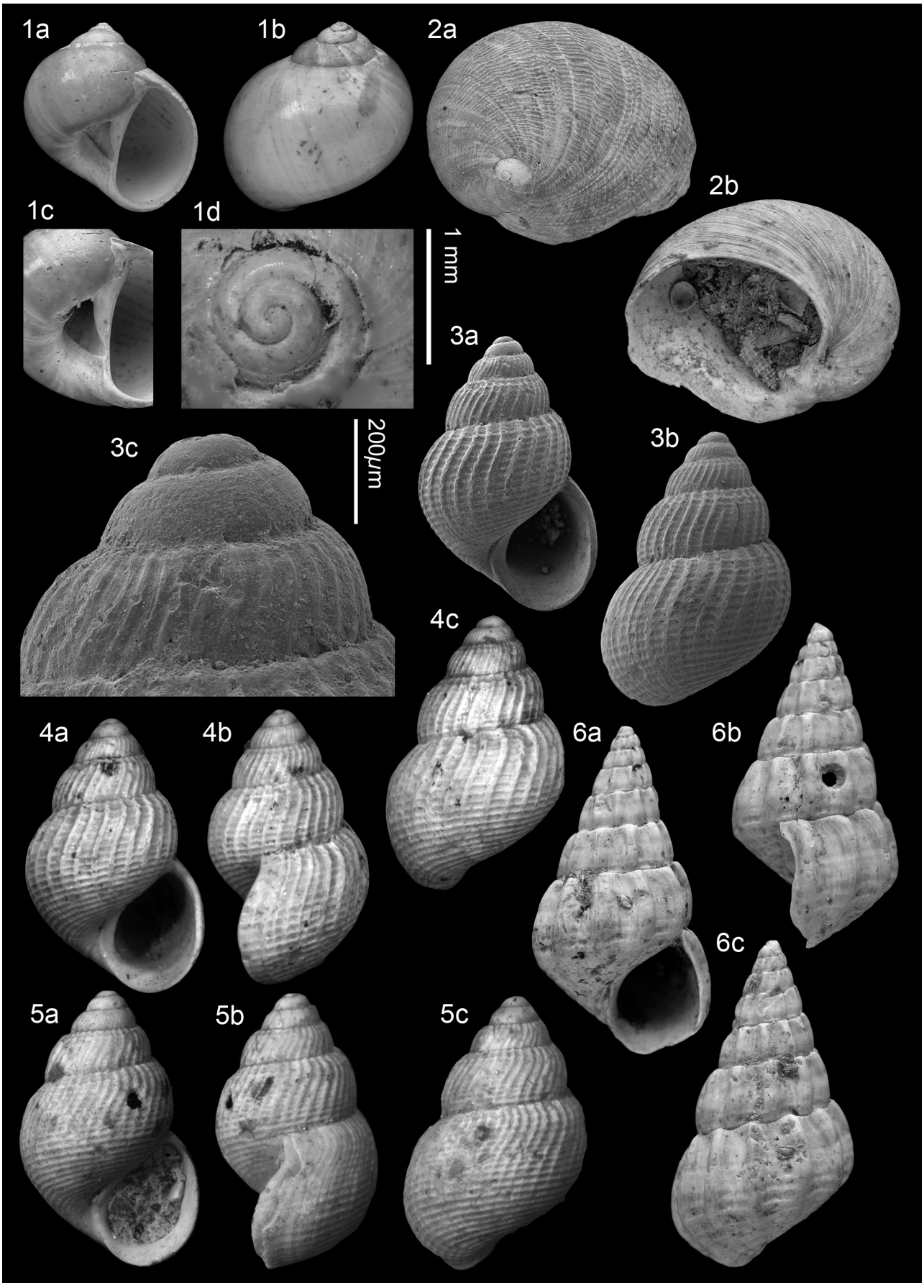

Plate 7

Plate 8

1. *Alvania dissensia* nov. sp., paratype 2 NHMW 2015/0133/0262, height 5.0 mm.
2. *Alvania dissensia* nov. sp., paratype 1 MNHN.F.A57393, height 7.0 mm.
3. *Alvania lachesis* (de Basterot, 1825), NHMW 2015/0133/0134, height 5.3 mm.
4. *Alvania merlei* nov. sp., holotype MNHN.F.A57193, height 3.9 mm.
5. *Alvania merlei* nov. sp., paratype 1 MNHN.F.A57194, height 3.8 mm.
6. *Alvania zetlandica* (Montagu, 1815), NHMW 2015/0133/0137, height 4.6 mm.
7. *Alvania ziziphina* Dollfus in Calas, 1949, NHMW 2015/0133/0140, height 4.3 mm.
8. *Alvania ziziphina* Dollfus in Calas, 1949, NHMW 2015/0133/0140, height 4.7 mm.
9. *Alvania zbyszewskii* nov. sp., holotype MNHN.F.A57197, height 3.1 mm.
10. *Alvania zbyszewskii* nov. sp., paratype 2 NHMW 2015/0133/0285, height 3.5 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

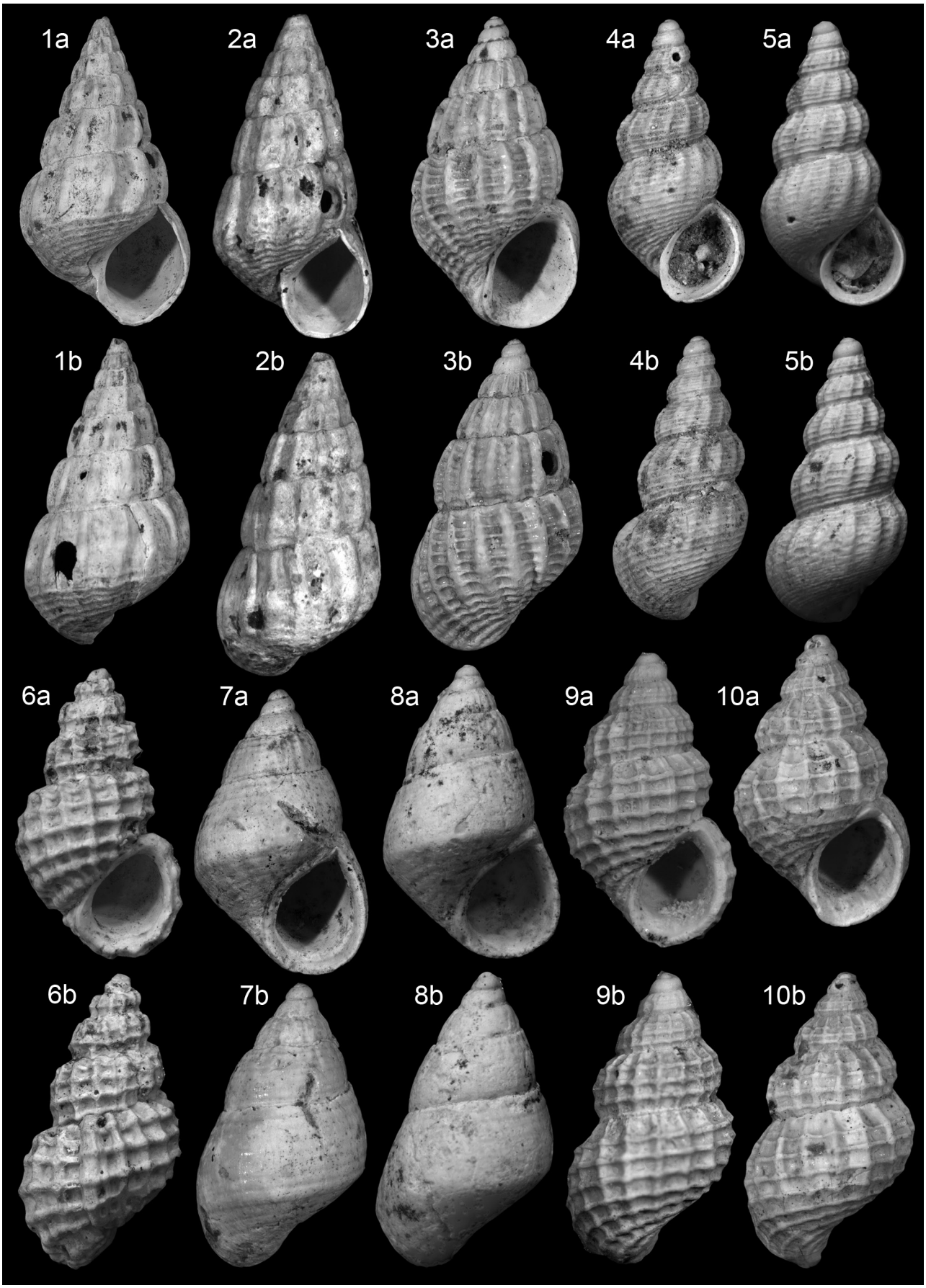

Plate 8

Plate 9

1. *Alvania lachesis* (de Basterot, 1825), NHMW 2015/0133/0135.
2. *Alvania lachesis* (de Basterot, 1825), NHMW 2015/0133/0135.
3. *Alvania merlei* nov. sp., paratype 3 NHMW 2015/0133/0144.
4. *Alvania zetlandica* (Montagu, 1815), NHMW 2015/0133/0138, height 4.1 mm.
5. *Alvania ziziphina* Dollfus in Calas, 1949, NHMW 2015/0133/0141, height 3.9 mm.
6. *Alvania zbyszewskii* nov. sp., paratype 1 MNHN.F.A57198, height 3.0 mm.
7. *Alvania* sp., NHMW 2015/0133/0290, height 2.3 mm.
8. *Rissoa pouweri* nov. sp., paratype 2 NHMW 2015/0133/0133, height 6.4 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

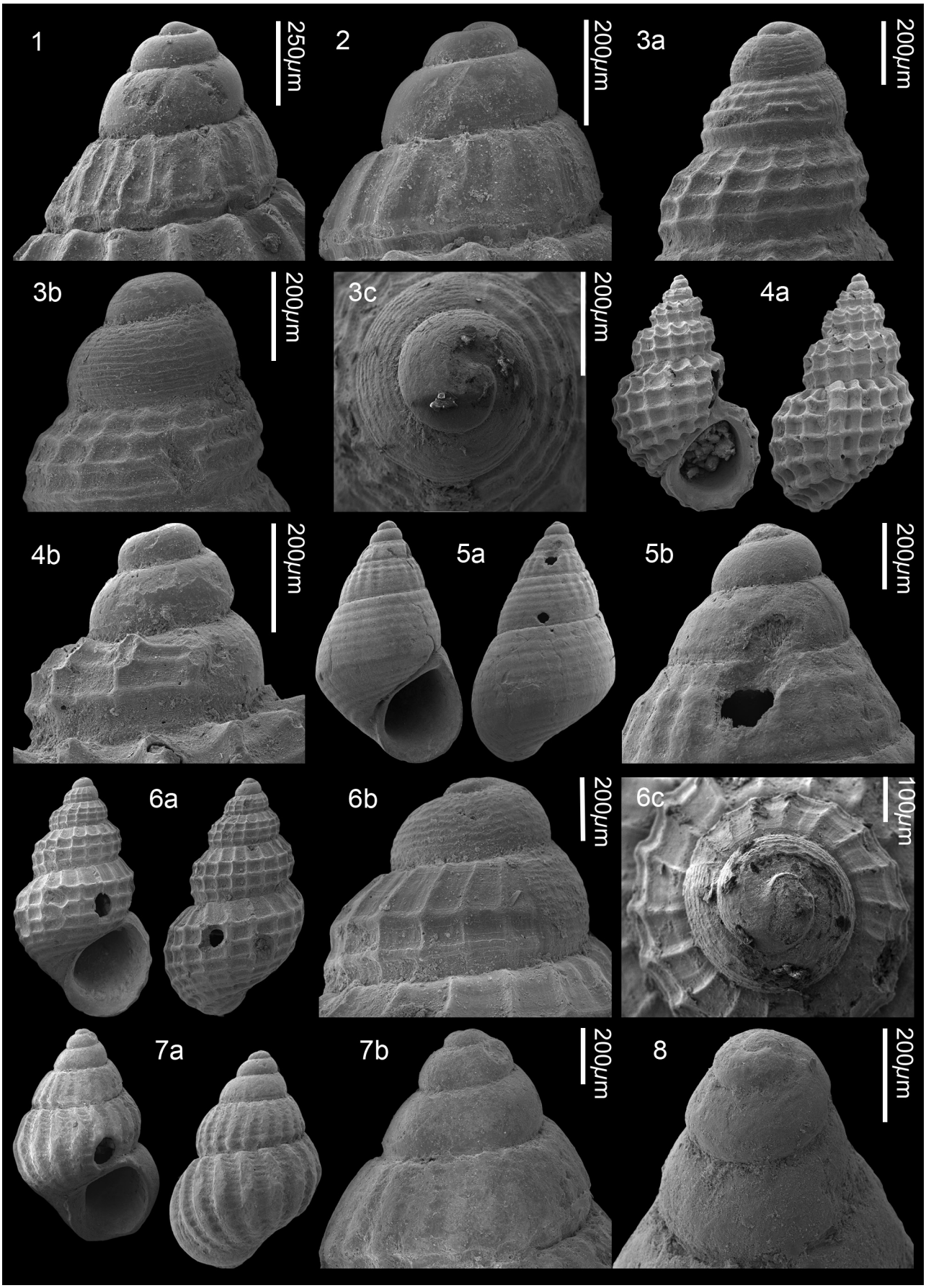
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Plate 9

Plate 10

1. *Alvania* sp., NHMW 2015/0133/0289, height 2.4 mm.
2. *Manzonia crassa* (Kanmacher, 1798), NHMW 2015/0133/0153, height 7.1 mm, height 2.0 mm.
3. *Rissoa pouweri* nov. sp., holotype NHMW 2015/0133/0131, height 6.4 mm.
4. *Rissoa pouweri* nov. sp., paratype 1 NHMW 2015/0133/0132, height 6.6 mm.
5. *Rissoa pouweri* nov. sp., paratype 3 NHMW 2015/0133/0209, height 6.8 mm.
6. *Zebinella decussata* (Montagu, 1803) *sensu lato*, NHMW 2015/0133/0269, height 10.0 mm.
7. *Caecum aartseni* nov. sp., holotype MNHN.F.A53613, height 3.0 mm (photo MNHN).
8. *Caecum aartseni* nov. sp., paratype 3 NHMW 2015/0133/0199, height 2.6 mm.
9. *Caecum aartseni* nov. sp., paratype 4 NHMW 2015/0133/0200, height 2.6 mm.
10. *Elachisina* aff. *eritima* (Smith, 1890), NHMW 2015/0133/0271, height 3.2 mm.
11. *Ceratia ligeriana* (Peyrot, 1938), NHMW 2015/0133/0190, height 3.2 mm.
12. *Ceratia ligeriana* (Peyrot, 1938), NHMW 2015/0133/0191, height 2.4 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

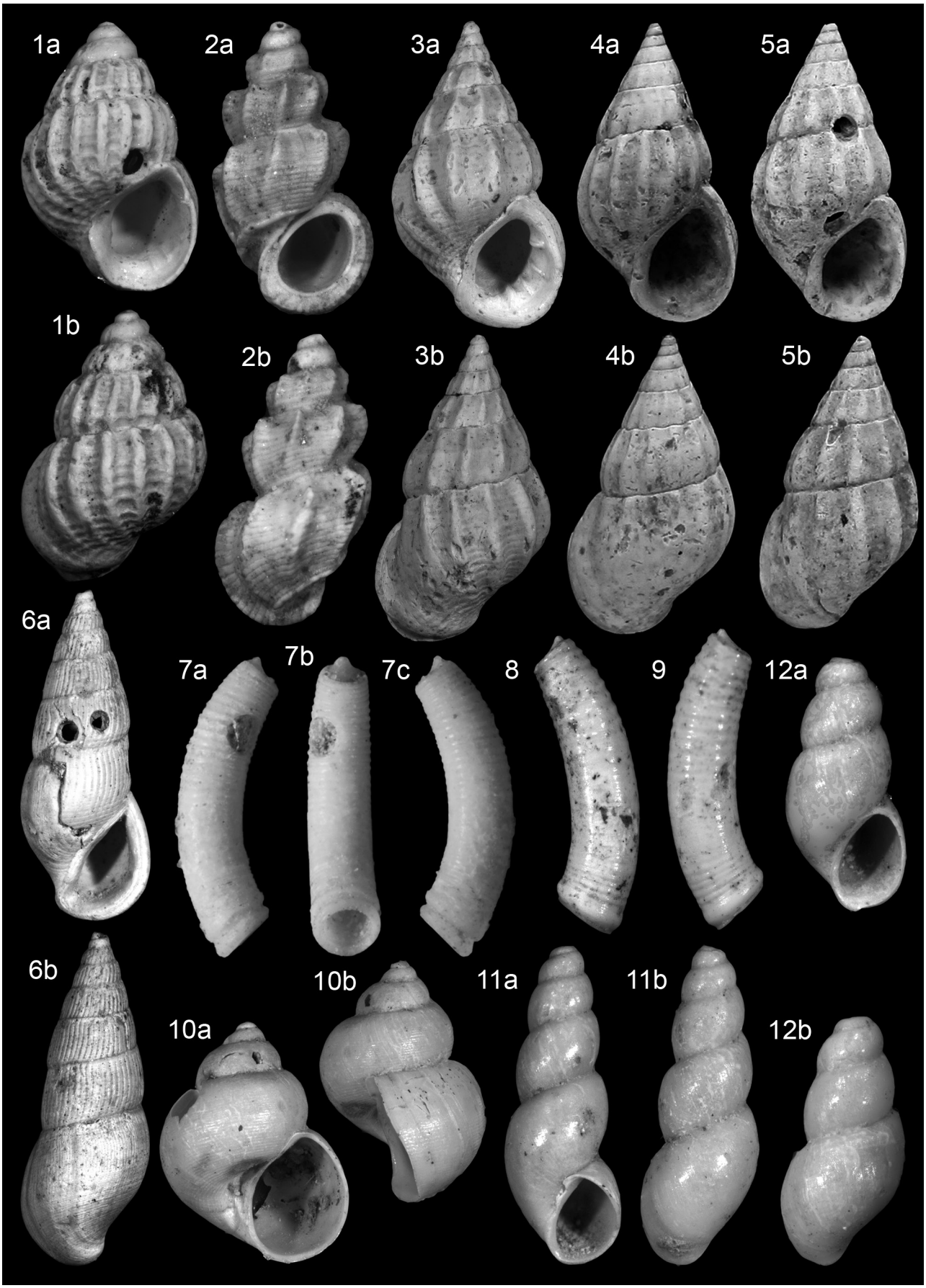
1a
2a
3a
4a
5a
1b
2b
3b
4b
5b
6a
7a
7b
7c
8
9
12a
6b
10b
11a
11b
10a
12b

Plate 10

Plate 11

1. *Crisilla* sp., NHMW 2015/0133/0362, height 2.2 mm.
2. *Rissoa s.l.* sp., NHMW 2015/0133/0194, height 3.6 mm.
3. *Caecum aartseni* nov. sp., paratype 1 NHMW 2015/0133/0197, height 2.5 mm.
4. *Caecum aartseni* nov. sp., paratype 2 NHMW 2015/0133/0198, height 2.7 mm.
5. *Caecum glabrum* (Montagu, 1803), NHMW 2015/0133/0196, height 3.1 mm.
6. *Ceratia falunica* (Glibert, 1949), NHMW 2015/0133/0192, height 2.4 mm.
7. *Pseudonoba* aff. *striata* (Hörnes, 1856), NHMW 2015/0133/0193, height 4.8 mm.
8. *Tornus primitivus* Moroni & Ruggieri, 1985, NHMW2015/0133/0178, maximum diameter 2.3 mm.
9. *Tornus subcarinatus* (Montagu, 1803), NHMW2015/0133/0176, maximum diameter 2.5 mm.
10. *Crisilla ariejansseni* nov. sp. Holotype NHMW 2015/0133/0361, height 2.1 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

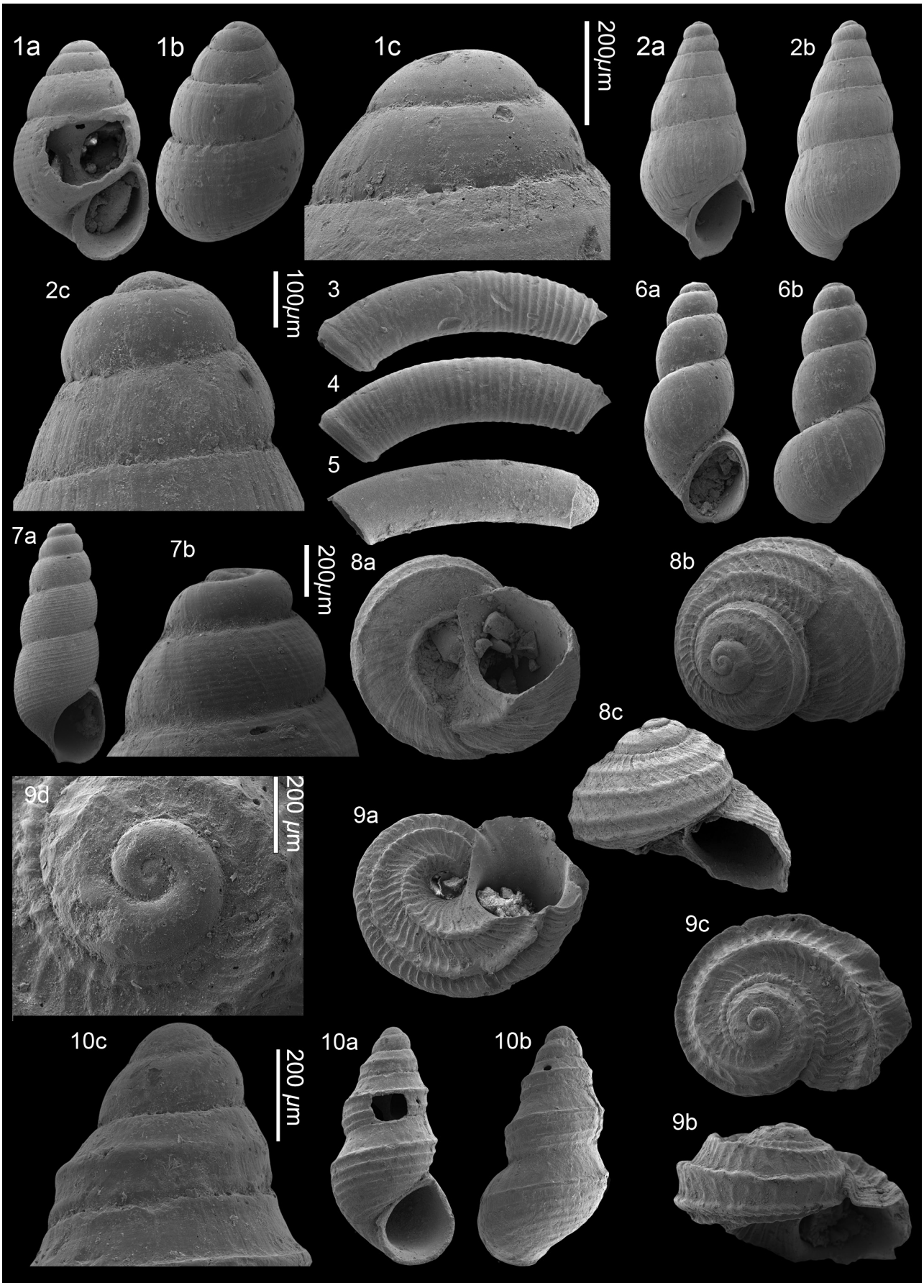
1a
1b
1c
200µm
2a
2b
2c
100µm
3
4
5
6a
6b
7a
7b
200µm
8a
8b
8c
9d
200 µm
9a
9c
10c
200 µm
10a
10b
9b

Plate 11

Plate 12

1. *Nystia guillotini* nov. sp., holotype NHMW 2015/0133/0268, height 3.9 mm.
2. *Bouryia cylindrica* (Cossmann & Peyrot, 1918), NHMW 2015/0133/0187, height 6.0 mm.
3. *Tornus subcarinatus* (Montagu, 1803), NHMW2015/0133/0175, maximum diameter 2.8 mm.
4. *Solariorbis woodi* (Hörnes, 1856), NHMW2015/0133/0172, maximum diameter 3.1 mm.
5. *Solariorbis woodi* (Hörnes, 1856), NHMW2015/0133/0173, maximum diameter 3.9 mm.
6. *Malea orbiculata* (Brocchi, 1814), FVD coll., length 83.7 mm (photo FVD).
7. *Galeodea echinophora* (Linnaeus, 1758), NHMW 2015/0133/0306, height 54.7 mm.
8. *Galeodea echinophora* (Linnaeus, 1758), NHMW 2015/0133/0249, height 46.7 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

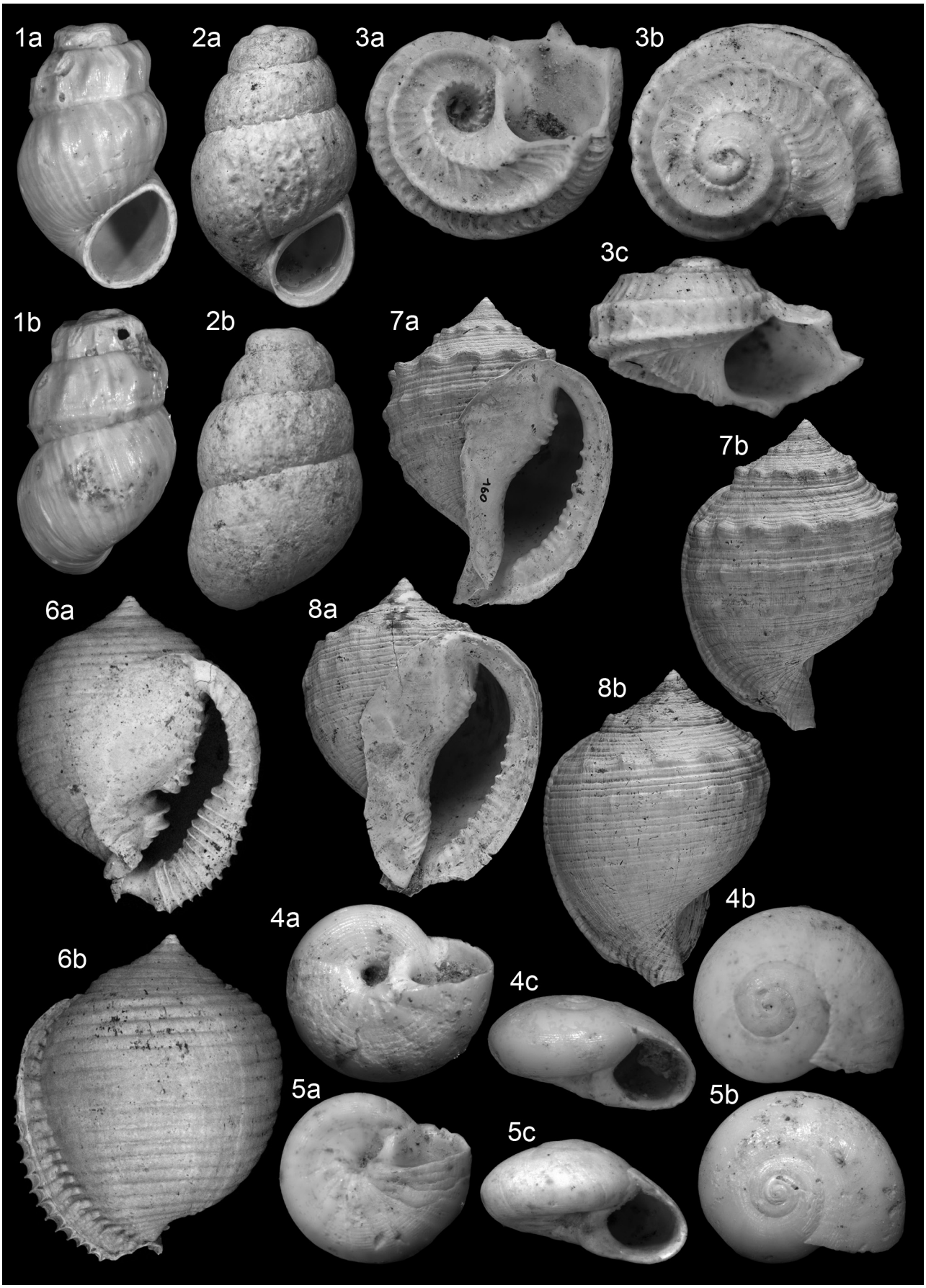

Plate 12

Plate 13

1. *Galeodea echinophora* (Linnaeus, 1758), NHMW 2015/0133/0307, height 53.9 mm.
2. *Semicassis laevigata* (Defrance, 1817), LC coll., height 45.2 mm.
3. *Monoplex corrugatus* (Lamarck, 1816), NHMW 2015/0133/0359, height 20.7 mm.
4. *Monoplex heptagonus* (Brocchi, 1814), LC coll., height 25.9 mm.
5. *Ficus geometra* (Borson, 1825), NHMW 2015/0133/0243, height 56.8 mm.
6. *Ficus geometra* (Borson, 1825), MNHN.F.A53615, height 35.9 mm (photo MNHN).
7. *Petaloconchus intortus* (Lamarck, 1818), NHMW 2015/0133/0275, maximum diameter 6.2 mm.
8. *Thylacodes arenarius* (Linnaeus, 1758), NHMW 2015/0133/0172, maximum diameter 30.4 mm.
9. *Aclis pacaudi* nov. sp., Holotype NHMW 2015/0133/0217, height 2.8 mm.
10. *Eulima* sp., NHMW2015/0133/0252, height 20.4 mm.
11. *Melanella spiridioni* (Dautzenberg & Fischer, 1896), NHMW 2015/0133/0254, height 6.7 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

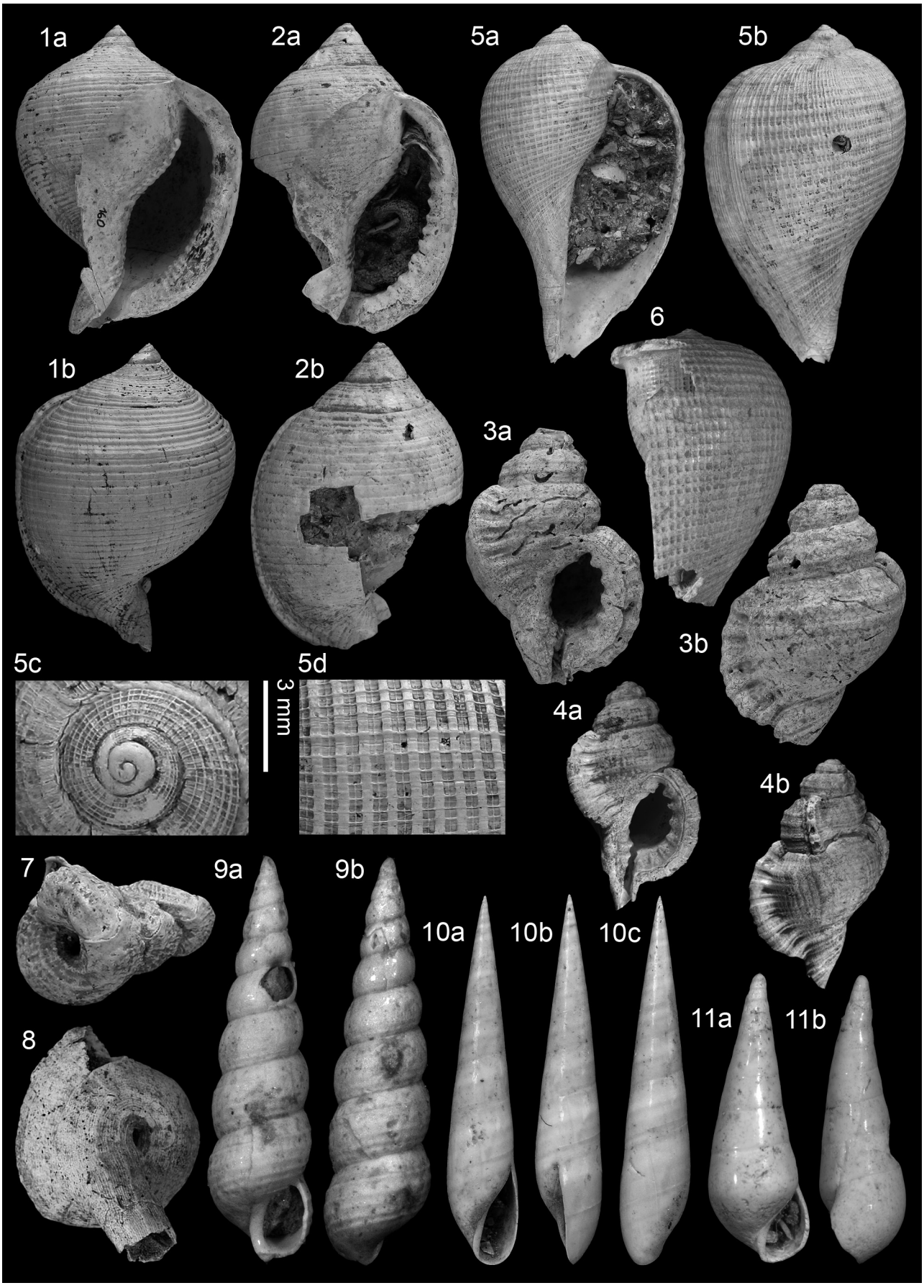

Plate 13

Plate 14

1. *Melanella alba* (Da Costa, 1778), NHMW 2015/0133/0292, height 17.3 mm.
2. *Melanella spiridioni* (Dautzenberg & Fischer, 1896), NHMW 2015/0133/0255, height 7.9 mm.
3. *Niso dollfusi* nov. sp., holotype MNHN.F.A57394, height 13.9 mm.
4. *Niso dollfusi* nov. sp., paratype 1 NHMW 2015/0133/0258, height 7.4 mm.
5. *Macromphalus reticulatus* Wood, 1842, NHMW 2015/0133/0180, height 3.8 mm.
6. *Macromphalina* sp., NHMW 2015/0133/0409, maximum diameter 1.5 mm (incomplete), height 800 μm.
7. *Mashallora* cf. *adversa* (Montagu, 1803), NHMW 2015/0133/0225, height 4.3 mm.
8. *Mashallora* cf. *adversa* (Montagu, 1803), NHMW 2015/0133/0226, height 3.4 mm (SEM).
9. *Obesula* sp., NHMW 2015/0133/0228, height 2.0 mm.
10. *Obesula* sp., NHMW 2015/0133/0229, height 2.0 mm (SEM).
11. *Cerithiopsis* cf. *tubercularis* (Montagu, 1803), NHMW 2015/0133/0221, height 6.7 mm.
12. *Dizoniopsis* cf. *bilineata* (Hörnes, 1848), NHMW 2015/0133/0219, 5.4 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

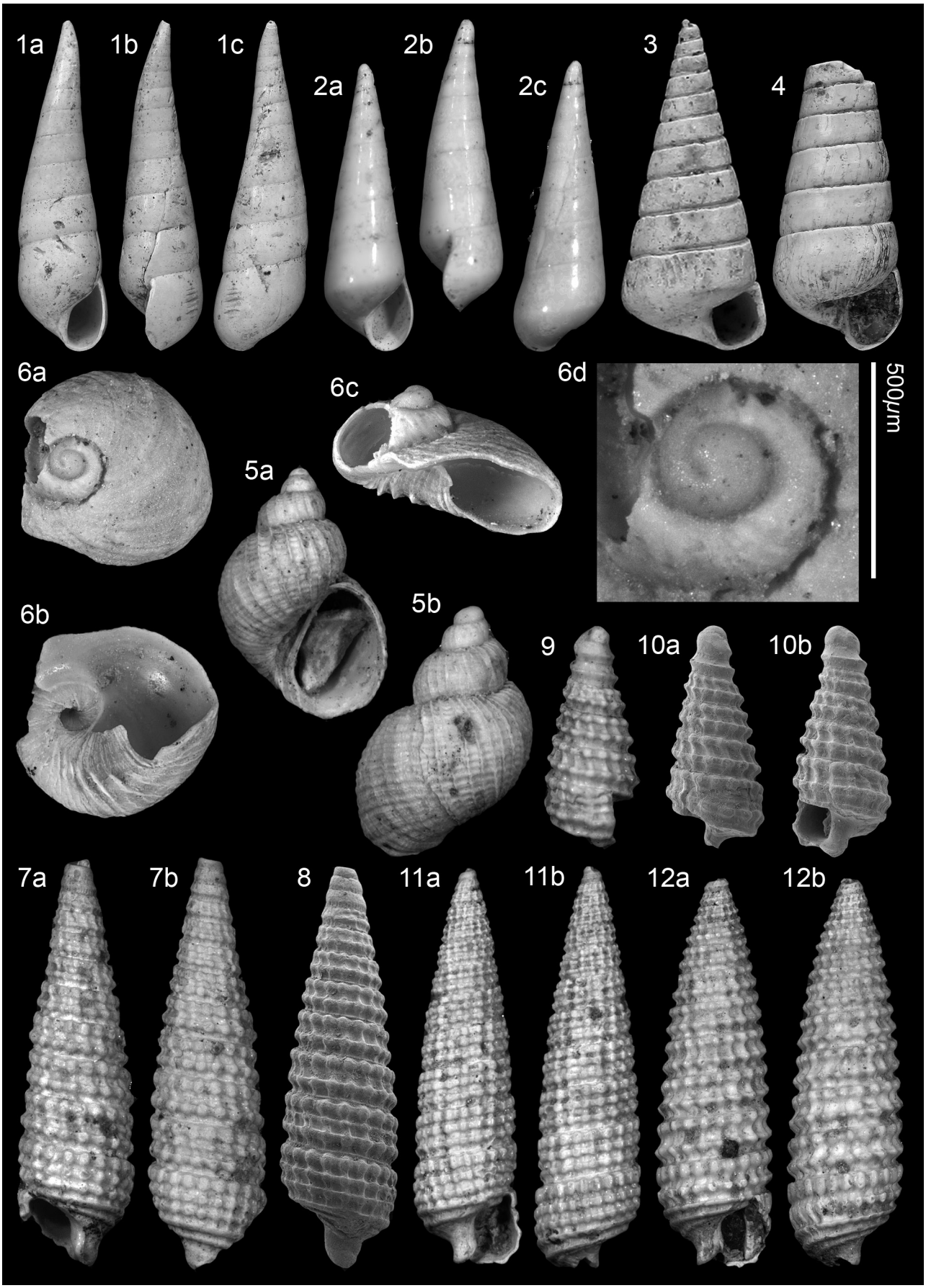
1a
1b
1c
2a
2b
2c
3
4
6a
6c
6d
500μm
5a
6b
5b
9
10a
10b
7a
7b
8
11a
11b
12a
12b

Plate 14

Plate 15

1. *Seila suttonensis* Marquet, 2001, NHMW 2015/0133/0223, height 7.2 mm.
2. *Epitonium* aff. *candidissimum* (Monterosato, 1877), NHMW 2015/0133/0296, height 10.2 mm.
3. *Epitonium frondiculum* (Wood, 1848), NHMW 2015/0133/0293, height 13.7 mm.
4. *Epitonium frondiculum* (Wood, 1848), NHMW 2015/0133/0294, height 14.7 mm.
5. *Epitonium* aff. *subulatum* (J.D.C. Sowerby, 1823), NHMW 2015/0133/0297, height 14.4 mm.
6. *Epitonium* aff. *subulatum* (J.D.C. Sowerby, 1823), NHMW 2015/0133/0298, height 9.5 mm.
7. *Amaea* (*Acrilla*) *stefanii* (de Boury, 1890), NHMW 2015/0133/0260, height 18.3 mm.
8. *Clathroscala bureaui* de Boury in Cossmann, 1912, NHMW 2015/0133/0299, height 29.1 mm.
9. *Clathroscala cancellata* (Brocchi, 1814), NHMW 2015/0133/0301, height 14.8 mm.
10. *Nodiscala scacchii* (Hörnes, 1856), LC coll., height 4.4 mm.
11. *Acirsa semicorrugata* Chirli, 2009, NHMW 2015/0133/0303, height 12.7 mm.
12. *Cirsotrema fimbriosum* (Wood, 1848), NHMW 2015/0133/0264, height 20.6 mm.
13. *Cirsotrema funiculus* (Wood, 1878), NHMW 2015/0133/0266, height 20.9 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France (Zanclean, lower Pliocene).

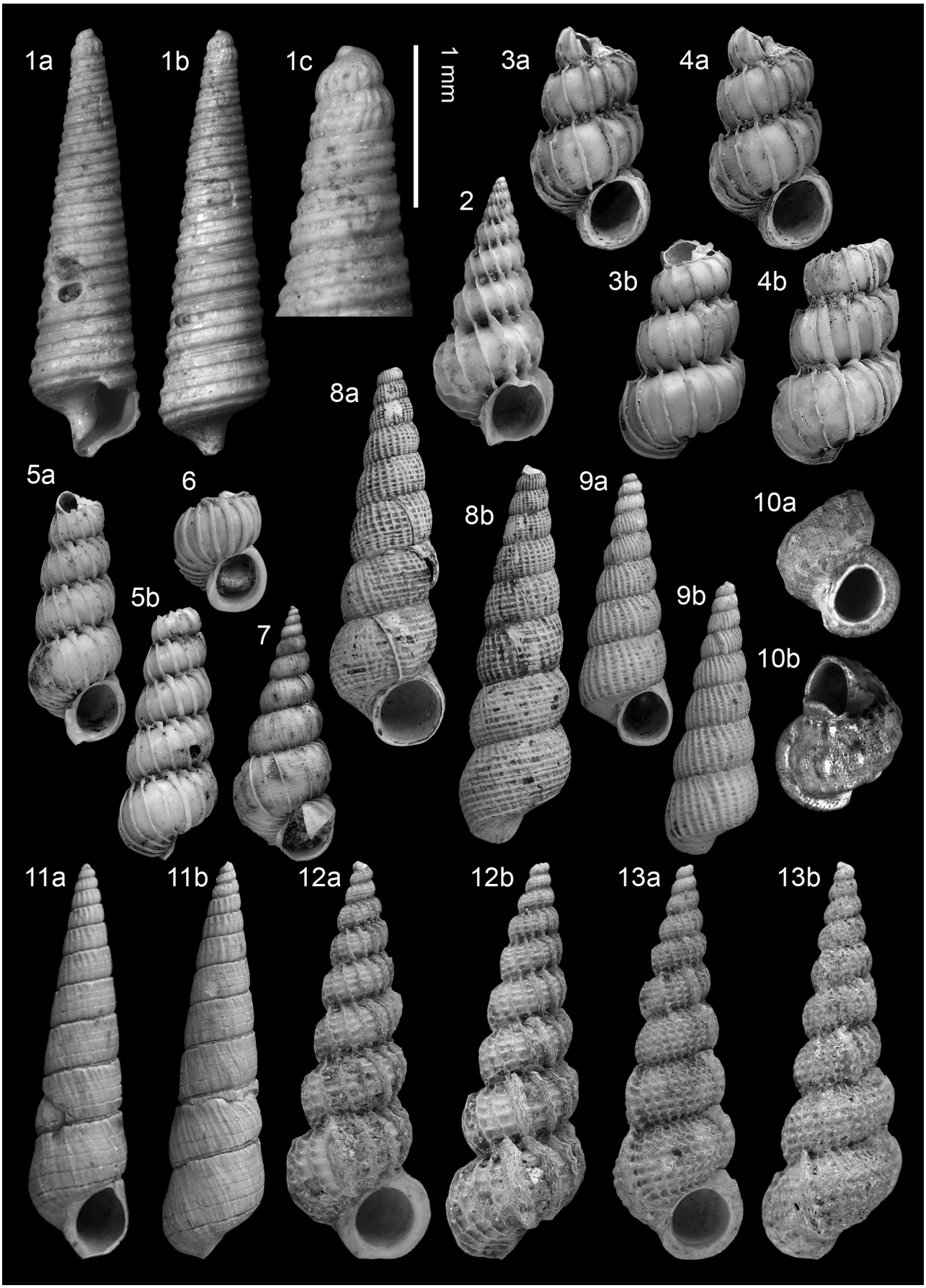
1a
1b
1c
1 mm
3a
4a
2
3b
4b
8a
5a
6
8b
9a
10a
5b
7
9b
10b
11a
11b
12a
12b
13a
13b

Plate 15