The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, Northwest France). Patellogastropoda and Vetigastropoda

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

[1] *Avenue Général Naessens de Loncin 1, B-1330 Rixensart, Belgium; luc.ceulem@skynet.be*
[2] *Cambeenboslaan A 11, B-2960 Brecht, Belgium; fvd@telenet.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; bernielandau@sapo.pt*
[4] *corresponding author*

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In this paper we review the Patellogastropoda and Vetigastropoda of the Zanclean lower Pliocene assemblage of Le Pigeon Blanc, Loire-Atlantique department, France, which we consider the 'type' locality for Assemblage III of Van Dingenen *et al*. (2015). Three patellogastropod and 28 vetigastropod species are recorded, of which eleven are new: *Emarginula brebioni* nov. sp., *Jujubinus armatus* nov. sp., *Jujubinus pigeonblancensis* nov. sp., *Jujubinus condevicnumensis* nov. sp., *Jujubinus ligeriensis* nov. sp., *Gibbula provosti* nov. sp., *Gibbula milleti* nov. sp., *Colliculus neraudeaui* nov. sp., ?*Tectus columbinus* nov. sp., *Calliostoma namnetense* nov sp. and *Microgaza landreauensis* nov. sp. This includes possibly the first European Pliocene record for the genus *Tectus*. *Calliostoma tauromiliare* (Sacco, 1896) is considered a junior synonym of *Calliostoma baccatum* (Millet, 1865).
Based on the data presented here, we suggest that the average Sea Surface Temperatures off the NW French coast in the Zanclean lower 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, Gastropoda, new taxa

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al*., 2014; Van Dingenen *et al*., 2014, 2015). Gastropods of the subclasses Patellogastropoda and Vetigastropoda 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 gastropods (of Van Dingenen *et al*., 2015; see below).
In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded no Patellogastropoda and 15 Vetigastropoda species from Le Pigeon Blanc, many of which were described as new. However, as the thesis was never published, the names do not comply with article 13 of the ICZN code (1999) and must be considered *nomina nuda*.
As discussed in Van Dingenen *et al*. (2015), the revision of these northwestern French assemblages is a huge task, which will take several years. We have started a systematic taxonomic revision of the Zanclean Le Pigeon Blanc assemblage because new material is available. Other northwestern French Tortonian-Gelasian assemblages will be revised in due course.

Geological setting

The Le Pigeon Blanc (Le Landreau) locality (Fig. 1) was included in the 'Redonien' of Brébion (1964) and is one of the localities in the 'Redonien froid' of Lauriat-Rage (1981) in the region of Nantes and Vendée. The numerous problems surrounding the term 'Redonien' were highlighted by Van Dingenen *et al*. (2015), who concluded that it was best to restrict the term to the 'Redonien Stratotypique' of Néraudeau *et al*. (2003). Van Dingenen *et al*. (2015) recognised four major stratigraphic sequences in the post mid-Miocene of northwestern France, characterised by distinct gastropod fossil assemblages designated by them as Assemblages I-IV. Van Dingenen *et al*. (2015, p. 78, fig. 2) correlated these sequences with the upper Miocene to lower Pleistocene formations of Cornwall and East Anglia in England, and Belgium).
We consider Le Pigeon Blanc the 'type' locality for Assem-

blage III. This assemblage includes *Megacardita striatissima* (Cailliaud *in* Mayer, 1868), which was regarded by Lauriat-Rage (1981) and Brault *et al*. (2004) to be a biostratigraphic index species for the lower Pliocene in that region. Other Assemblage III localities are La Dixmérie (Loire-Atlantique), Le Girondor (Vendée) and Palluau (Vendée) (Brébion, 1964, p. 16).

Material and methods

The material described here is part of the Brébion collection, which is housed in the collection de Paléontologie of Muséum national d'Histoire naturelle (Paris), the Muséum d'Histoire naturelle de Nantes, and the Musée de Géologie de l'Université de Rennes, all France. It is the same material used by Brébion in his unpublished thesis (1964). We were unable to locate two of Brébion's 'types' said to be deposited in the Institut Catholique d'Angers (Angers): the 'types' of *Calliostoma caveti nomen nudum* and *Margarites peneui nomen nudum*. In order to understand and adequately characterise the species groups suggested by Brébion, new photographs of Brébion's material were obtained from the respective institutions.
Wherever possible we have used Brébions specimens as holotypes, renaming the species with names quite different from the manuscript names used by Brébion to avoid any confusion.

Type material was deposited in the Muséum national d'Histoire naturelle, Paris (collection de Paléontologie), Muséum d'Histoire naturelle de Nantes and the Naturhistorisches Museum Wien, Vienna, Austria. Further material is present in the personal collections of Luc Ceulemans, Rixensart (Belgium) and Frank Van Dingenen, Brecht (Belgium).
For a discussion on some of the literature relevant to these 'Redonian' assemblages see Landau *et al*. (2016).
We have not included in the synonymy species listed by Bardin (1882, 1883) and Couffon (1907, 1908, 1915), as these are not illustrated and we cannot therefore be certain to which species these authors refer.
Photographs in this work were made by B.M. Landau, unless stated otherwise.

Repository:

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

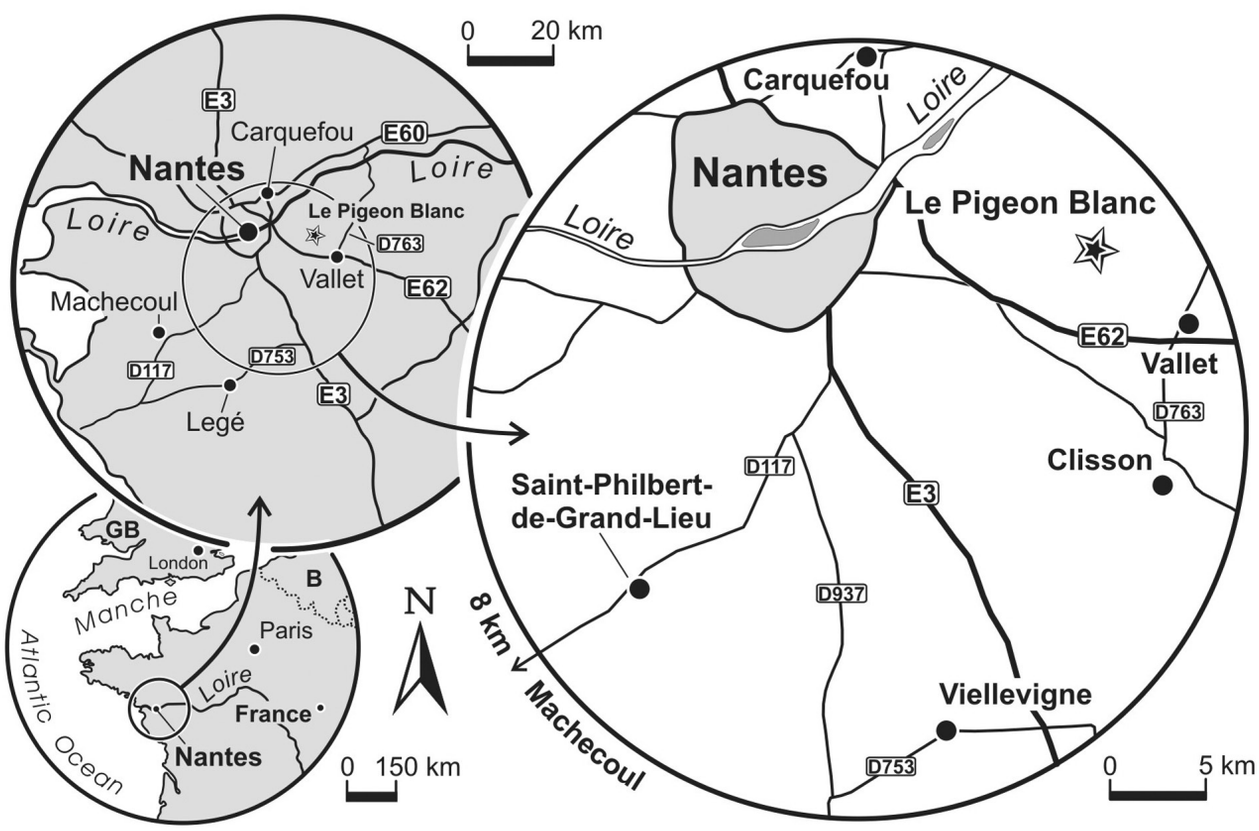

Figure 1. Geographic location of Le Pigeon Blanc.

Systematic palaeontology

Subclass Patellogastropoda Lindberg, 1986
Superfamily Patelloidea Rafinesque, 1815
Family Patellidae Rafinesque, 1815
Genus *Patella* Linnaeus, 1758

Type species (by subsequent designation, Fleming, 1818) – *Patella vulgata* Linnaeus, 1758, present-day, Europe.

1758 *Patella* Linnaeus, p. 780.
1807 *Patelligenus* Renier, pl. 8. Established for the animal occupying the shell of *Patella*. Not available: published in a work placed on the Official Index by Opinion 427 (ICZN, 1956).
1810 *Patellus* de Montfort, p. 66. Invalid: unjustified emendation of *Patella* Linnaeus, 1758.
1839 *Ansates* G.B. Sowerby, II, p. 123. Type species (by monotypy): *Patella pellucida* Linnaeus, 1758, present-day, Europe.
1884 *Patellastra* Monterosato, 1884a, p. 35, 1884b, p. 103. Type species (by monotypy): *Patella lusitanica* Gmelin, 1791 (= *Patella rustica* Linnaeus, 1758), present-day, Europe.
1912 *Costatopatella* Pallary, p. 148, 196. Type species (by original designation): *Patella ferruginea* Gmelin, 1791, present-day, Mediterranean.

Note – Based on molecular data, Koufopanou *et al*. (1999) showed that the typical European *Patella* species formed a monophyletic clade, within which there was little molecular divergence. Moreover, their analysis confirmed that *Ansates pellucidum* (Linnaeus, 1758) belongs in the clade *Patella s.s.*, as suggested by Ridgway *et al.* (1998). Therefore *Ansates* G.B. Sowerby, II, 1839 and *Patellastra* Monterosato, 1884, used in Landau *et al*. (2003), are synonymised with *Patella* Linnaeus, 1758.

Patella* cf. *caerulea Linnaeus, 1758
Plate 1, fig. 1.

cf. *1758 *Patella caerulea* Linnaeus, p. 782.
cf. 2003 *Patella* (*Patella*) *caerulea* Linnaeus, 1758 – Landau *et al*., p. 5, pl. 4, figs 6, 7 (*cum syn*.).
cf. 2004 *Patella caerulea* Linné, 1758 – Chirli, p. 21, pl. 7, figs 12-15.

Material and dimensions – LC (1, Pl. 1, fig. 1), diameter 12.6 x 10.2 mm; height 2.8 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – *Patella caerulea* Linnaeus, 1758 is variable in shape and strength of radial ribbing, but is characterised by having a thin, depressed shell, with six or seven marginal angles and 7-9 prominent radial folds. The single specimen from Le Pigeon Blanc is a juvenile and we cannot be absolutely certain it represents this species, but it corresponds to the morphotype *stellata* Bucquoy, Dautzenberg & Dollfus, 1886.
Patella caerulea was described from the lower and upper Pliocene Mediterranean, Estepona (Landau *et al*., 2003; Chirli, 2004) and it, or a species very similar to it, was recorded from the middle Miocene Langhian of the Loire Basin (Glibert, 1949), which would be the oldest stratigraphic record for the species.
Brébion (1964, pl. 1, figs 13, 14) illustrated a small patellid from Assemblage I localities (Sceaux d'Anjou, St-Michel, Contigné) as *P. protea* Doderlein, 1862, which was originally described from the upper Miocene Tortonian of Italy and said to be common at Montegibbio. Numerous specimens at hand from the Assemblage I locality of St-Clément-de-la-Place resemble tiny specimens of *P. caerulea*, but differ in having an anterior primary rib placed at six o'clock, when the dorsum is viewed on its antero-posterior axis, posterior border placed at the top, whereas in *P. caerulea* the anterior ribs are placed at five o'clock and seven o'clock. They are also considerably smaller: according to Brébion 10-15 mm diameter vs. 20-50 mm diameter for present-day *P. caerula*. The specimens at hand from St-Clément-de-la-Place are even smaller, similar in size to specimens of *P. protea* from the type locality of Montegibbio (3-6.5 mm; Sacco, 1986, p. 23).

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

***Patella pellucida* Linnaeus, 1758**
Plate 1, fig. 2.

*1758 *Patella caerulea* Linnaeus, p. 1260.
2003 *Ansates pellucidum* (Linnaeus, 1758) – Landau *et al*., p. 7, pl. 5, fig. 2 (*cum syn*).
2006 *Patella pellucida* Linnaeus, 1758 – Silva *et al*. p. 227, fig. 3/1-8.

Material and dimensions – NHMW 2015/0133/0403 (1, Pl. 2, fig. 2), maximum diameter 6.0 mm (incomplete). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – *Patella pellucida* Linnaeus, 1758 is represented in the Le Pigeon Blanc assemblage by a single, incomplete specimen. However, this species is so characteristic, with its elongated dome-shaped shell, with the apex placed at, or overhanging the dorsal margin and its colour pattern of dots radiating from the apex, that the specific assignment is certain.
Patella pellucida is a north-western Atlantic shallow water grazing gastropod typically living and feeding on laminarian algae. Today the species is usually considered to be primarily a northern cooler water species, inhabiting the Atlantic coasts of Europe, but rarely found off the Atlantic NW African coast and westernmost Mediterranean. At higher sea surface temperatures laminarian algae become physiologically stressed and are found only where seasonal upwelling of cooler nutrient-rich waters

occurs. Such oceanographic conditions exist today, e.g., off the western coast of Iberia.
To explain its occurrence in the warm, subtropical to tropical, Pliocene Atlantic and Mediterranean Iberian waters, Silva *et al*. (2006) suggested that similar upwelling conditions were already in place in western Iberia and in the Alboran Sea during Pliocene times and that the distribution of *P. pellucida* was dictated by upwelling of nutrient-rich, cooler waters, and high productivity conditions rather than sea surface temperature alone. Thus, the unexpected Pliocene geographic distribution of *P. pellucida* demonstrates that high productivity associated with upwelling may, at least in the Atlanto-Mediterranean area, override the dominant biogeographic pattern resulting from the latitudinal sea surface temperature gradient of water masses. Although this single specimen may have been transported some distance, this record for *P. pellucida* in the subtropical lower Pliocene of NW France suggests that upwelling may have also been present closeby.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Upper Pliocene: Atlantic, Modego Basin, Portugal (Silva, 2001; Silva *et al*., 2006); western Mediterranean, Estepona Basin (Landau *et al*., 2003). Pleistocene: Atlantic, Iceland (Gladenkov *et al*., 1980), British Isles (Harmer, 1921), Morocco (Lecointre, 1952). Present-day: Atlantic, northern Norway to Portugal, Iceland (Poppe & Goto, 1991).

***Patella* sp.**
Plate 1, figs 3, 4.

Material and dimensions – NMHW2015/0133/0164 (1, Pl. 1, fig. 3), NMHW2015/0133/0165 (1, Pl. 1, fig. 4). Maximum diameter of smaller specimen 23.6 mm (larger fragment suggests a maximum diameter of at least 40 mm). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Description – Shell of medium size and thickness, patelliform, oval, depressed, with apex subcentrally, slightly towards posterior margin. Axial sculpture consists of 8-9 sharp, narrow, elevated primary radial ribs, with a secondary rib intercalated in some of the interspaces. Primary ribs extending slightly beyond shell margin, forming a crenulate edge. Shell surface irregular, roughened.

Discussion – Unfortunately, this species is represented in the material available by two fragments, the smaller is half complete and has the apex preserved (NMHW2015 /0133/0164), the larger (NMHW2015/0133/0165) represents a portion of the margin of a larger shell, with stronger sculpture. It is most similar to *Patella ferruginea* Gmelin, 1791, but this species is larger, thicker-shelled and has more numerous and stronger radial ribs that deeply corrugate the shell margin. The apex in *P. ferruginea* is also more centrally placed than it is in the species from NW France (see Giannuzzi-Savelli *et al*., 1994, figs 11-14). The material at hand is insufficient to formally describe this species, which is probably new. Brébion (1964, p. 66) recorded two congeners from the NW French assemblages: *P. protea* Doderlein, 1862 from Assemblage I localities (see above), which differs from *Patella* sp. in being smaller-shelled, the apex is placed further towards the posterior edge and sculpture consists of more numerous primary ribs with numerous secondary cordlets in the interspaces, the primaries not markedly crenulating the edge. A second species, *P. couffoni* Brébion, 1964 (*nomen nudum*), was described based on a single specimen from an Assemblage I locality (St-Michel) and a second specimen from an Assemblage IV locality (St-Jean-la-Poterie). The illustrated material seems to represent a species with even finer radial sculpture.

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

Subclass Vetigastropoda Salvini-Plawen, 1980
Superfamily Fissurelloidea Fleming, 1822
Family Fissurellidae Fleming, 1822
Subfamily Emarginulinae Children, 1834
Tribe Diodorini Odhner, 1932
Genus *Diodora* Gray, 1821

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

1821 *Diodora* Gray, p. 233.
1934 *Austroglyphis* Cotton & Godfrey, p. 52. Type species (by original designation): *Diodora lincolnensis* Cotton, 1930, present-day, southern Australia.
1857 *Capiluna* Gray, p. 166. Type species (by monotypy): *Capiluna cuvieri* Gray, 1857, present-day, *taxon inquirendum*.
1924 *Elegidion* Iredale, p. 182. Type species (by monotypy): *Elegidion audax* Iredale, 1924, present-day, Australia.
1840 *Fissuridea* Swainson, p. 356. Type species (by monotypy): *Fissuridea pileus* Swainson, 1840, present-day, *taxon inquirendum*.
1857 *Glyphis* Carpenter, p. 223. Invalid: junior homonym of *Glyphis* Agassiz, 1843 [Pisces].

***Diodora graeca* (Linnaeus, 1758)**
Plate 1, figs 5, 6

*1758 *Patella graeca* Linnaeus, p. 784.
1854 *Fissurella Labiatoides* Millet, p. 166 (*nomen nudum*).
1864 *Fissurella labiatoides* Millet, p. 680.
1954 *Diodora apertura* Montagu, 1803 – Van Regteren Altena, p. 58, pl. 1, fig. 7.
1964 *Diodora apertura* Montagu, 1803 – Brébion, p. 63, pl. 1, fig. 2.
2003 *Diodora graeca* (Linnaeus, 1758) – Landau *et al*., p. 26, pl. 4, fig. 4 (*cum syn.*).
2004 *Diodora graeca* (Linné, 1758) – Chirli, p. 30, pl.

10, figs 3-6.
2006 *Diodora graeca* (Linnaeus, 1758) – Marquet & Landau, p. 17, fig. 2/3a-b.
2008 *Diodora graeca* (Linné, 1758) – Chirli & Richard, p. 13, pl. 1, fig. 1.
2011 *Diodora graeca* (Linné, 1758) – Wesselingh & Pouwer, p. 139, figs 30, 31.

Material and dimensions –NHMW 2015/0133/050 (1, Pl. 1, fig. 5), NHMW 2015/0133/052 (12); LC (1, Pl. 1, fig. 6; 50+ adults and juveniles); FVD (23 adults and juveniles). Maximum diameter 23.6 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Distinguished from *D. gibberula* (Lamarck, 1822) by its larger size, more central apical hole and more prominent sculpture. Most recent authors do not distinguish this species from *Diodora apertura* (Montagu, 1803). Marquet (1998) synonymised *D. apertura* with *D. graeca* (Linnaeus, 1758), suggesting the former was the form found along the north-eastern Atlantic frontage, whilst *D. graeca* occurred in the Mediterranean. *Diodora graeca* does, however, occur in the North Sea Basin Pliocene, as recorded by Harmer (1923) and by material collected from Doel (Belgium) (Landau *et al*., 2003). Most of Le Pigeon Blanc material is attributed to *D. graeca*, although the sculpture is somewhat weaker than is usual in Mediterranean fossil (Landau *et al*., 2003, pl. 4, fig. 5) and present-day (Giannuzzi-Savelli *et al*., 1994, figs 56-58) populations. However, one large specimen in the LC collection (Pl. 1, fig. 6) has the finer, more regular sculpture illustrated by Fretter & Graham (1976, p. 15, fig. 11) and Marquet (1998, p. 24, fig. 1) for the *D. apertura* form. We provisionally follow Marquet (1998) and consider the Atlantic and Mediterranean specimens to represent a single species, *D. graeca*.
Brébion (1964, p. 65) reported this species (as *D. apertura*) in localities representing Assemblages II-IV.

Distribution – Middle Miocene: Paratethys, Badenian, Poland (Bałuk, 1975); Hungary (Strausz, 1966). Upper Miocene: Atlantic, Messinian, NW France (Brébion, 1964); Tethys, Tortonian: Po valley, Italy (Sacco, 1896). Lower Pliocene: Atlantic, NW France (Brébion, 1964); Coralline Crag, England (Harmer, 1923), Luchtbal Formation, Belgium (Marquet & Landau, 2006); central Mediterranean, Italy (Chirli, 2004). Upper Pliocene: Red Crag, England (Harmer, 1923); western Mediterranean, Estepona, S. Spain (Landau *et al*., 2003); France (Chirli & Richard, 2008); central Mediterranean, Italy (Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992). Pliocene (unspecified): central Mediterranean, Italy (Brambilla & Lualdi, 1988); Atlantic Morocco (Lecointre, 1952). Upper Pliocene-lower Pleistocene: Atlantic, NW France (Brébion, 1964); central Mediterranean, Italy (Cerulli-Irelli, 1916; Malatesta, 1960). Pleistocene (unspecified): western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); Atlantic, Morocco (Lecointre, 1952). Upper Pleistocene: England, Ireland (Harmer, 1923), The Netherlands (Wesselingh & Pouwer, 2011). Present-day: Atlantic British Isles to Canaries, Mediterranean and Black Sea, rocky shores under stones and rocks, especially where a little silt occurs, living near sponges, on which it feeds (Poppe & Goto, 1991).

Tribe Emarginulini Children, 1834
Genus *Emarginula* Lamarck, 1801

Type species (by monotypy) – *Emarginula conica* Lamarck, 1801 [= *Emarginula fissura* (Linnaeus, 1758)], present-day, Europe.

1801 *Emarginula* Lamarck, p. 69.
1867 *Semperia* Crosse, p. 74. Type species (by subsequent designation, Cossmann, 1888): *Semperia paivana* Crosse, 1867, present-day, Madeira.
1924 *Subzeidora* Iredale, p. 182, 217. Type species (by original designation): *Emarginula connectens* Thiele, 1915, present-day, Kermadec Islands.
1945 *Entomella* Cotton, p. 14. Type species (by original designation): *Emarginula candida* A. Adams, 1852, present-day, South Australia. Invalid: junior homonym of *Entomella* Cossmann, 1888.
1957 *Notomella* Cotton, p. 127. Type species (by typification of replaced name): *Emarginula candida* A. Adams, 1852, present-day, South Australia. *Nom. nov. pro Entomella* Cotton, 1945, *non* Cossmann, 1888.

***Emarginula brebioni* nov. sp.**
Plate 1, figs 7, 8

1964 *Emarginula dollfusi* Brébion, p. 59, pl. 1, fig. 9 (*nomen nudum*).

Type material – Holotype MNHN.F. A53407 (Pl. 1, fig. 7), height 3.1 mm, maximum diameter 6.5 mm; paratypes 1-9 MNHN.F.A53408/1-9; paratype 10 NHMW 2015/0133/0054 (Pl.1, fig. 8), height 6.5 mm, maximum diameter 10.1 mm; paratype 11 NHMW 2015/0133/0098, height 4.4 mm, maximum diameter 8.4 mm. Paratypes 10, 11 from Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Other material – NHMW 2015/0133/0099 (11); LC (31). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Etymology – Named after Philippe Brébion of the Museum National d'Histoire Naturelle, Paris, in recognition of his work on the French Redonian assemblages. *Emarginula* gender feminine.

Locus typicus – Le Girondor, Boufféré, Vendée department, NW France.

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Emarginula* species with a tall domed shell, the apex placed midline, close to, but not overhanging, the posterior margin; coarse reticulate sculpture composed of about 25 axial ribs and widely spaced concentric cords, with tubercles developed at the intersections, secondary axial ribs are intercalated towards the periphery, and a narrow, deeply slit selenizone, the lamellae on the selenizone placed lower than the surface sculpture.

Description – Shell small, solid, patelliform, oval, convex, moderately elevated, with a recurved apex placed midline, posteriorly, four-fifths from anterior margin, not overhanging posterior margin. Selenizone narrow, bearing close-set ridges, which run parallel to shell margin, the apex of the ridges placed lower than the surface sculpture; deeply slit at periphery. Dorsum bearing about 25 broad, elevated primary axial ribs, with a single weaker secondary in interspaces developed towards periphery. Axial ribs crossed by relatively widely spaced concentric cords, narrower than the ribs, forming cancellate surface sculpture with small tubercles developed at the intersections.

Discussion – *Emarginula brebioni* nov. sp. is characterised by its coarse reticulate sculpture, with tubercles developed at the sculptural intersections. It has a similar number of axial ribs to *E. reticulata* J. Sowerby, 1813 (about 25). However, *E. brebioni* has a strongly convex dorsum, with the apex placed close to the posterior margin, whereas *E. reticulata* has a conical dorsum with the apex placed closer to the centre. *Emarginula rosea* Bell, 1824 differs in having a much taller conical dorsum. *Emarginula adriatica* Costa, 1829 from the Pliocene to present-day Atlantic and Mediterranean coasts of Europe has the apex placed in a similar position to *E. brebioni*, but is more elongated in shape and has finer sculpture composed of about 40 primary axial ribs. *Emarginula tuberculosa* Libassi, 1859 from the Pliocene of Italy also has relatively coarse sculpture, but differs from *E. brebioni* in having a more strongly recurved apex and secondary axial ribs intercalated in the interspaces from the apex, whereas in *E. brebioni* the secondary rib only appear towards the periphery. The ridges on the selenizone are far coarser and wider apart than those seen in *E. brebioni*. *Emarginula octaviana* Coen, 1939 from the Pliocene to present-day Mediterranean has 30-35 primary axial ribs and also has secondary ribs developed towards the periphery. It differs from *E. brebioni* in having a more depressed shell, the apex placed slightly less posteriorly and in having more numerous concentric lamellae forming more prominent spinose tubercles where they cross the axial ribs. The shell identified as *E. clathrataeformis* Eichwald, 1830 from the Langhian middle Miocene Loire Basin of France by Glibert (1949, pl. 1, fig. 6) is similar in shape and in the position of the apex, but has finer cancellate sculpture than *E. brebioni*. *Emarginula dujardini* Dollfus & Dautzenberg, 1886 also from the Loire Basin middle Miocene has a more depressed shell, the apex is placed further from the posterior margin and its cancellate sculpture is much finer.
Brébion (1964, p. 60) recorded this species from Le Girondor and La Gauvinière. These, together with Le Pigeon Blanc, are all Assemblage III localities.

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

***Emarginula dujardini* Dollfus & Dautzenberg, 1886**
Plate 2, fig. 1

*1886	*Emarginula Dujardini* Dollfus & Dautzenberg, p. 142.
1938	*Emarginula Dujardini* Dollfus & Dautzenberg, mss. – Peyrot, p. 19.
1949	*Emarginula dujardini* Dollfus et Dautzenberg, 1886 – Glibert, p. 20, pl. 1, fig. 7.
1964	*Emarginula dujardini* Dollfus et Dautzenberg, 1886 – Brébion, p. 60, pl. 1, figs 10, 11.

Material and dimensions – NHMW 2015/0133/0166 (1, Pl. 2, fig. 1), diameter 18.3 mm x 12.6 mm, height 6.2 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Despite the original description being short; '*Espèce de grande taille à treillis fin et élevé*' (Dollfus & Dautzenberg, 1886, p. 142), it is unambiguous and valid under Article 12 for names published before 1931 (ICZN 1999). A full description was provided by Peyrot (1938, p. 19) and Glibert (1949, p. 20).
This rather large emarginulid is characterised by its flattened shell, somewhat expanded in the posterior half, its recurved apex placed at about two-thirds distance from the anterior edge, fine radial sculpture composed of ribs of irregularly alternating strength, cut by close-set growth lines, forming a finely reticulated pattern, and rather short anterior slit on the selenizone. There seems to be quite some intraspecific variability. One shell at hand from the Tortonian Assemblage I locality of St-Clément-de-la-Place has a slightly more elevated shell. This variability in shell height in the 'Redonian' specimens was remarked on by Brébion (1964, p. 61). The sculpture in the few Tortonian to Zanclean specimens at hand is strongly squamous, as described by Peyrot (1938), whereas Glibert (1949) referred to pointed tubercles formed at the sculptural intersections. As described by Peyrot (1938), the basal perimeter is flat, or almost so, in the Tortonian to Zanclean specimens, whereas it is markedly concave in the specimen illustrated by Glibert (1949, pl. 1, fig. 7b). The most important difference is the number of primary axial ribs. The Tortonian to Zanclean specimens have 40-44 primary ribs. Glibert (1949) counted 24 primary ribs in his specimens from the Middle Miocene Loire Basin. Peyrot (1938) described the shell as having numerous primary ribs, without being specific. We provisionally consider these all to fit within the range of variability for *E. dujardini*.
Emarginula dujardini is closely similar in shape and sculpture to the chronologically older *E. squammata* Grateloup, 1835 from the Aquitanian and Burdigalian of

the Aquitaine Basin of France, but differs in being larger shelled and having more numerous ribs, producing a finer reticulate surface sculpture. The present-day Mediterranean *E. huzardii* (Payraudeau, 1826) is also similar in shape and sculpture, also with a shallow slit on the selenizone, but is larger-shelled, more dilated posteriorly, with the apex placed more centrally.
Brébion (1964, p. 61) recorded *E. dujardini* in Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, Chalonnes), Assemblage II (Apigné) and Assemblage III (Le Girondor, La Gauvinière); to this last group we add Le Pigeon Blanc.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Dollfus & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1949). Upper Miocene: Atlantic, Tortonian and Messinian, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Emarginula fissura* Linnaeus, 1758**
Plate 2, fig. 2

*1758	*Emarginula fissura*	Linnaeus, p. 784.
1813	*Emarginula reticulata*	J. Sowerby, 1813, p. 74, pl. 33.
1848	*Emarginula fissura*	Linn. v. *vulgaris* Wood, p. 164, pl. 17, fig. 3b (*non* v. *punctura*, pl. 17, fig. 3b = *Emarginula punctura* Wood, 1848).
1854	*Emarginula Rostrata*	Millet, p. 166 (*nomen nudum*).
1865	*Fissurella rostrata*	Millet, p. 599.
1878	*Emarginula fissura*	Lin. – Nyst, pl. 7, fig. 9.
1882	*Emarginula fissura*	Lin. – Nyst, p. 114.
1923	*Emarginula fissura*	Linné – Harmer (*partim*), p. 776, pl. 62, fig. 7.
1923	*Emarginula fissura*	var. *depressa* Harmer, p. 777, pl. 62, fig. 8.
1949	*Emarginula reticulata*	Sowerby, 1813 – Glibert, p. 15, pl. 1, fig. 2.
1954	*Emarginula reticulata*	J. Sowerby, 1813 – Van Regteren Altena, p. 57, pl. 1, fig. 2.
1964	*Emarginula reticulata*	Sowerby, 1813 – Brébion, p. 59, pl. 1, fig. 9.
1995	*Emarginula fissura*	form *reticulata* Sowerby, 1813 – Marquet, p. 62, pl. 1, fig. 3.
1998	*Emarginula fissura reticulata*	Sowerby, 1813 – Marquet, p. 27, fig. 4.
2003	*Emarginula fissura*	(Linnaeus, 1758) – Landau *et al*., p. 20, pl. 3, fig. 4 (*cum syn*.).
2011	*Emarginula fissura*	(Linnaeus, 1758) – Landau *et al*., p. 7, pl. 1, fig. 2.
2011	*Emarginula fissura*	(Linné, 1758) – Wesselingh & Pouwer, p. 135, fig. 12.

Material and dimensions – NHMW 2015/0133/0053 (1, Pl. 2, fig. 2), maximum diameter 8.6 mm, height 5.8 mm; NHMW 2015/0133/0153 (4); LC (18); FVD (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – *Emarginula fissura* (Linnaeus, 1758) is characterised by its solid shell, conical profile and thick apex placed two-thirds distance from the anterior edge to sub-centrally. Marquet (1995, 1998), separated the Pliocene North Sea Basin forms based on them being slightly larger with a greater height/width ratio. However, Wesselingh & Pouwer (2011) drew attention to the considerable variability in shape and size in the fossil specimens from the Dutch coasts and concluded that separation of the fossil forms was not justified. It is difficult to draw too many conclusions based on the Dutch material, which is dredged and therefore its stratigraphic origin is unclear. The Le Pigeon Blanc specimens are small and have an elevated dorsum, similar to those from the North Sea Basin illustrated by Marquet (1995, 1998). The small size of the shells negates one of the two distinguishing characters between the Pliocene and present-day forms suggested by Marquet (1995, 1998). We therefore provisionally follow Wesselingh & Pouwer (2011) in considering them all a single species, although separation of the Pliocene forms as a chronosubspecies may eventually be justified.
Emarginula rosea Bell, 1824 from the Pliocene to present-day eastern Atlantic and Mediterranean has a similar conical elevated dorsum, but has a more pronounced and recurved apex.
Brébion (1964) recorded this species from numerous localities, representing Assemblage I-IV.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene: Tortonian-Messinian, Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964); NSB, Coralline Crag, England (Wood, 1848; Harmer, 1923), Kattendijk Formation, Belgium (Marquet, 1998); western Mediterranean, Guadalquivir Basin, S. Spain (Landau *et al*., 2011); central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: Red Crag, England (Wood, 1848; Harmer, 1923); Oorderen and Kruisschans Sands, Belgium (Marquet, 1998); central-west Portugal (Silva, 1990, 2001); western Mediterranean, Estepona, S. Spain (Landau *et al*., 2003); central Mediterranean (Piani, 1984; Cavallo & Repetto, 1992). Upper Pliocene-lower Pleistocene: NW France (Brébion, 1964). Pleistocene (indeterminate): central Mediterranean, Italy (Sacco, 1896; Cerulli-Irelli, 1916). Present-day: Atlantic coasts of Europe north to Scandinavia and Mediterranean, 0-700 m (Piani, 1984).

***Emarginula octaviana* Coen, 1839**
Plate 2, fig. 3

1829	*Emarginula elongata*,	Costa, p. 10 (*non* Defrance, 1819; *non* G.B. Sowerby I, 1823; *non* Gray, 1825).
*1839	*Emarginula octaviana*	Coen, p. 71.
1854	*Emarginula Ornata*	Millet, p. 166 (*nomen nudum*).
1864	*Emarginula ornata*	Millet, p. 599.
1949	*Emarginula elongata*	Da Costa – Glibert, p. 20, pl. 1, fig. 9.
1964	*Emarginula elongata*	Costa, 1829 – Brébion, p.

58, pl. 1, figs 7, 8.
1982 *Emarginula octaviana* Coen, 1939 – Piani, p. 206, figs 26-36.
1994 *Emarginula octaviana* Coen, 1939 – Giannuzzi-Savelli *et al*., p. 46, fig. 77.

Material and dimensions – NHMW 2015/0133/0167 (1, Pl. 2, fig. 3), diameter 12.0 mm (incomplete) x 8.0 mm, height 4.4 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – The salient characters of this species were described by Glibert (1949, p. 20; as *E. elongata*): the low, elongated shell shape, coarse reticulate sculpture and most importantly the lamellae on the selenizone, which are relatively coarse and raised above the level of the reticulate sculpture. This last character separates *Emarginula octaviana* Coen, 1839 from *E. clathrataeformis* Eichwald, 1830, present in the Middle-Upper Miocene of NW France and *E. subclathrata* d'Orbigny, 1852, from the Lower Miocene Aquitanian and Burdigalian Aquitaine Basin of France, both of which have finer lamellae on the selenizone, the crests of which lie below the height of the dorsal reticulate sculpture. *Emarginula clathrataeformis* also differs in being taller-shelled, in having finer reticulated sculpture, and having a more recurved apex, placed closer to the posterior edge. The only diagnostic character not seen in the fossil specimens from NW France is the series of six minute pits in the sculptural interspaces (see Piani, 1984, fig. 28), but this feature may be eroded, as the preservation is not perfect.
Brébion (1964, p. 59) recorded *E. octaviana* (as *E. elongata*) in Assemblage I localities (Reneauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, Chalonnes) and a single specimen from Assemblage IV (Gourbesville). Here we add Assemblage III with this record from Le Pigeon Blanc.

Distribution – Upper Miocene: Atlantic, Tortonian, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-lower Pleistocene: NW France (Brébion, 1964). Present-day: Atlantic Canaries, Portugal, Morocco and Mediterranean (Poppe & Goto, 1992).

Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Trochinae Rafinesque, 1815
Genus *Clanculus* de Montfort, 1810

Type species (by original designation) – *Trochus pharaonius* Linnaeus, 1758, present-day, Red Sea.

1810 *Clanculus* de Montfort, p. 191.
1826 *Otavia* Risso, p. 132. Type species (by subsequent designation, Gray, 1847): *Trochus corallinus* Gmelin, 1791, present-day, Mediterranean.
1840 *Fragella* Swainson, p. 352. Type species (by subsequent designation, Herrmannsen, 1847): *Trochus pharaonius* Linnaeus, 1758, present-day, Red Sea. Invalid: junior objective synonym of *Clanculus* de Montfort, 1810, with the same type species.
1879 *Belangeria* Fischer, p. 415. Type species (by monotypy): *Trochus scabrosus* Philippi, 1850, present-day, Indo-Pacific.
1934 *Macroclanculus* Cotton & Godfrey, p. 78. Type species (by original designation): *Monodonta undata* Lamarck, 1816, present-day, Australia.

Subgenus *Clanculopsis* Monterosato, 1880

Type species (by subsequent designation, Sacco, 1896, p. 21) – *Trochus cruciatus* Linnaeus, 1758, present-day, Mediterranean.

1880 *Clanculopsis* Monterosato, p. 222.

***Clanculus* (*Clanculopsis*) *baccatus* (Defrance, 1824)**
Plate 2, fig. 4

*1824 *Monodonta baccata* Defrance, 1824, p. 475.
1854 *Monodonta Baccata* Defr. – Millet, p. 157.
1938 *Clanculus* (*Clanculopsis*) *baccatus* Defrance – Peyrot, p. 20.
1949 *Clanculus baccatus* Defrance, 1824 – Glibert, p. 65, pl. 4, fig. 1.
1964 *Clanculus baccatus* (Defrance, 1824) – Brébion, p. 122.

Material and dimensions –NHMW 2015/0133/055 (1, Pl. 2, fig. 4), NHMW 2015/0133/056 (24); LC (50+); FVD (6). Maximum diameter 8.0 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – *Clanculus baccatus* (Defrance, 1824) differs from the Pliocene to present-day *Clanculus corallinus* (Gmelin, 1791) by the presence of a single abapical columellar tooth; in *C. corallinus* the anterior tooth is bifid. This places it in the subgenus *Clanculopsis* (Monterosato, 1880). The French Atlantic Miocene-Pliocene forms differ from the type species of the subgenus *C. cruciatus* (Linnaeus, 1758) in having a much more strongly developed anterior columellar tooth.
How many species occur in the French Atlantic Miocene is controversial. *Clanculus araonis* (de Basterot 1825) was described based on lower Miocene Burdigalian material. According to Cossmann & Peyrot (1917, p. 89) the lower Miocene Aquitanian and Burdigalian French Atlantic specimens differed from those of the middle Miocene of Touraine in that the Touraine shells were '*plus évasée, et que son ombilic est invariablement plus ouvert; si l'on tient compte d'autres differences dans les characters de l'ouverture, on conclut qu'il s'agit d'une mutation bien distincte*'. What these other apertural differences were is not specified in the text. Peyrot (1938, p. 21) stressed the intraspecific variability seen in the shape

and sculpture within the specimens from Touraine. He commented that most of the Touraine shells had three primary beaded cords with three weaker cords in the interspaces. However, there were some specimens in which all six cords were of sub-equal strength. He went on to point out that in the lower Miocene forms specimens with six sub-equal cords predominated, but there was overlap between the populations and that they were probably the same species, giving seniority to Defrance (1924) over de Basterot (1825). Glibert (1949, p. 66) agreed with Peyrot (1938): '*Les charactères qui différencient* C. araonis *de* C. baccatus *sont faibles et si inconstants, qu'il serait excessif de leur accorder une valeur spécifique*'. However, he did not include references to *C. araonis* in his synonymy, and in Glibert (1962, p. 60) he separated the Aquitanian and Burdigalian specimens as *C.* (*C.*) *araonis* from those of Touraine as *C.* (*C.*) *baccatus*. Brébion (1964, p. 122) did not include the lower Miocene forms in his synonymy of *C. baccatus* either. Lozouet *et al*. (2001) recorded the lower Miocene Aquitanian specimens from Lariey as *C.* (*C.*) *araonis*, without offering any discussion.
The specimens from Le Pigeon Blanc have beaded cords of strongly alternating strength and are therefore typical *C.* (*C.*) *baccatus*. The difference in umbilical width described by Cossmann & Peyrot (1917) is not convincing. We provisionally follow Lozouet *et al*. (2001) in considering the two forms distinct based on sculpture, although they undoubtedly form part of an evolutionary lineage with some overlap in sculpture between populations.
Brébion (1964) recorded this species from numerous localities, representing Assemblage I, III and IV.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic, Tortonian, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-lower Pleistocene: Atlantic, NW France (Brébion, 1964).

Subfamily Cantharidinae Gray, 1857
Genus *Jujubinus* Monterosato, 1884

Type species (by subsequent designation, Crosse, 1885, p. 140) – *Trochus matonii* Payraudeau, 1826 [= *Jujubinus exasperatus* (Pennant, 1777), present-day, Mediterranean.

1884a *Jujubinus* Monterosato, p. 109
1917 *Mirulinus* Monterosato, p. 10. Type species (original designation): *Trochus striatus* Linnaeus, 1758, present-day, Europe.

***Jujubinus armatus* nov. sp.**
Plate 2, figs 5-7; Plate 3, fig. 1

1964 *Jujubinus termieri* Brébion, p. 117, pl. 3, figs 9, 10 (*nomen nudum*).

Type material – Holotype MNHN.F.A53413 (Pl. 2, fig. 5), maximum diameter 7.5 mm, height 10.3 mm; paratype 1 MNHN.F.A53414/1 (Pl. 2, fig. 6), maximum diameter 7.7 mm, height 10.4 mm; paratype 2 MNHN.F.A53414/2 (Pl. 2, fig. 7), maximum diameter 6.0 mm, height 7.2 mm; paratypes 3-5 MNHN.F.A53414/3-5; paratype 6 NHMW 2015/0133/0057 (Pl. 3, fig. 1), maximum diameter 7.0 mm, height 9.7 mm; paratype 7 NHMW 2015/0133/0058, maximum diameter 7.5 mm, height 9.6 mm; paratype 8 NHMW 2015/0133/0059, maximum diameter 7.6 mm, height 9.9 mm.

Other material –NHMW 2015/0133/0060 (30); LC (50+); FVD (6). Maximum height 16.0 mm. Type locality.

Etymology – Latin '*armatus*', adjective meaning armed. Name reflecting the unusually strongly-developed apertural armature seen in this species. *Jujubinus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Jujubinus* species with a solid shell, whorls with a broad, strongly concave infrasutural ramp delimited by a narrow, prominent suprasutural collar, weak, smooth or indistinctly-beaded spiral sculpture, a flattened, imperforate base and strong apertural armature, consisting of ridges and tubercles on both labial and columellar sides of aperture.

Description – Shell small, solid, conical, with elevated spire, flattened base. Protoconch consisting of 1.5 smooth convex whorls, with medium-sized nucleus. Teleoconch consisting of about six whorls, with periphery at abapical suture. First two whorls weakly convex. Abapically whorls strongly concave above rounded shoulder, which is placed low, just above suture. The result is a broad, concave subsutural ramp delimited by a narrow, rounded, elevated suprasutural collar. Suture linear, impressed. Sculpture consisting of about eight narrow, weakly developed, smooth or indistinctly-beaded spiral cords, narrower than their interspaces. Last whorl strongly, but roundly angled at peripheral carina. Base imperforate, flattened, bearing eight non-beaded concentric ribs, separated by wide interspaces. Aperture tangential; peristome discontinuous, outer lip not thickened, angled at periphery, bearing an internal ridge bordering the broad, shallow, rounded anal canal and two tubercles abapically, all placed a short distance within aperture. Columella deeply excavated in mid-portion, bearing single, prominent, basal columellar tooth and moderately developed parietal tubercle. A colour pattern consisting of narrow, comma-shaped flammules is preserved in some specimens (Pl. 2, fig. 6b).

Discussion – As the name would suggest, the most remarkable shell character in this new species is the complex apertural dentition developed within the aperture. In

shell shape it is most similar to the Pliocene to present-day Mediterranean *Jujubinus exasperatus* (Pennant, 1777), which also has an elevated suprasutural collar with the whorl profile above concave, but in this species the spiral sculpture is more strongly developed and it lacks the complex apertural dentition. Another present-day Mediterranean species, *J. unidentatus* (Philippi, 1844) also has a similar shell shape, and has a sharp basal columellar tooth developed, but lacks the labial and parietal denticles. Brébion (1964) compared this species with *Jujubinus matonii* (Payaudeau, 1826) and *J. striatus* var. *monterosatoi* Bucquoy, Dautzenberg & Dollfus, 1884, both of which are now considered a synonym of *J. exasperatus*. Apart from Le Pigeon Blanc, Brébion (1964, p. 118) reported this species from La Gauvinière.

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

***Jujubinus pigeonblancensis* nov. sp.**
Plate 3, figs 2-4

1964 *Calliostoma bureaui* Dollfus mss. – Brébion, p. 88, pl. 2, figs 8, 9 (*nomen nudum*).

Type material – Holotype MNHN.F.A53409 (Pl. 3, i. 2), height 7.1 mm, maximum width 6.4 mm; paratype 1 MNHN.F.A53410 (Pl. 3, fi. 3), height 7.2 mm, maximum width 6.6 mm; paratype 2 NHMW 2015/0133/0080 (Pl. 3, fig 4), height 7.1 mm, maximum width 7.4 mm; paratype 3 NHMW 2015/0133/0081, height 8.5 mm, maximum width 7.6 mm; paratype 4 NHMW 2015/0133/0082, height 7.0 mm, maximum width 6.5 mm.

Other material – NHMW 2015/0133/0083 (50+); LC (50+); FVD (4). Type locality.

Etymology – Named after type locality of Le Pigeon Blanc. *Jujubinus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Jujubinus* species with a moderately low spire of cyrtoconoid profile, last two teleoconch whorls with a prominent suprasutural cord making the whorl profile above concave, fine, weakly beaded spiral sculpture and a strongly carinate last whorl, sharply angling the outer lip.

Description – Shell small, of medium thickness, conical, with moderately low cyrtoconoid spire, flattened base. Protoconch eroded in all specimens. Teleoconch consisting of about 4-5 whorls, with periphery at abapical suture. First two whorls weakly convex to flat-sided. Prominent suprasutural cord develops on penultimate whorl, forming periphery on last whorl. Surface covered in fine, irregular, close-set spiral cords and threads, weakly and irregularly beaded by prosocline growth lines. Suture linear, impressed. Last whorl strongly, but roundly angled at peripheral carina, whorl profile concave above peripheral cord. Base imperforate, flattened, bearing numerous concentric cords and threads, strengthening towards the centre. Aperture strongly tangential; peristome discontinuous, outer lip not thickened, strongly angled at periphery, smooth within. Columella straight, bearing a small denticle mid-columella.

Discussion – Brébion (1964, p. 88) placed this species in the family Calliostomatidae, however, there is a small but distinct denticle on the columella, placing it in the subfamily Cantharidinae, moreover, the interior of the aperture is not nacreous. *Jujubinus pigeonblancensis* nov. sp., with its low, cyrtoconoid spire and strongly carinate later adult whorls is a very distinctive species. Other congeners such as *J. exasperatus* (Pennant, 1777), *J. unidentatus* (Philippi, 1844) and the coeval *J. armatus* nov. sp. also have a prominent suprasutural cord, but all of these are much higher-spired.
Brébion (1964, p. 88) recorded this species from Le Girondor and La Gauvinière. These, together with Le Pigeon Blanc, are all Assemblage III localities.

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

***Jujubinus condevicnumensis* nov. sp.**
Plate 3, figs 5, 6

1964 *Calliostoma caveti* nov. sp. Brébion, p. 87, pl. 2, figs 6, 7 (*nomen nudum*).

Type material – Holotype MNHN.F.A57386, maximum diameter 5.8 mm, height 6.3 mm; paratype 1 NHMW 2015/0133/0085 (Pl. 3, fig. 5), maximum diameter 6.6 mm, height 6.8 mm; paratype 2 NHMW 2015/0133/0086 (Pl. 3, fig. 6), maximum diameter 5.5 mm, height 5.5 mm; paratype 3 NHMW 2015/0133/0084 maximum diameter 5.4 mm, height 5.5 mm.

Other material – NHMW 2015/0133/0087 (14); LC (50+); FVD (1). Type locality.

Etymology – Latinisation of the Gallic name of the Namnete capital city '*Condevicnum*' (= Nantes) during Roman domination, before the 3rd century when it was known as '*Portus Namnetum*'. *Jujubinus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Jujubinus* species with a canaliculated suture, resulting in a weakly scalate spire, spiral sculpture composed of seven narrow, elevated, strongly

but finely beaded cords, a convex base with ten concentric, beaded cords, a narrow, shallow umbilicus, and an aperture with a ridge internally, parallel to the lip edge.

Description – Shell small, relatively solid, turbinate, with weakly scalate spire, base weakly convex, perforate. Protoconch not preserved. Teleoconch consisting of 4-5 straight-sided whorls. Suture linear, canaliculated. Spire whorls bearing seven elevated, narrow cords, finely beaded by crowded, prosocline growth lines, adapical cord bordering canaliculated suture most strongly developed. Last whorl strongly angled at basal carina, whorl profile above concave, sculptured by seven finely beaded cords above carina; basal carina composed of three close-set cords. Base weakly convex, bearing ten narrow, elevated, concentric cords. Umbilicus narrow, shallow, smooth within. Aperture tangential; peristome continuous, outer lip not thickened, smooth edged, angled at periphery, bearing an internal ridge running parallel to the lip edge, in some specimens a second ridge extends inwards from lip angulation. Columella straight, leaning abaxially, bearing single columellar tooth mid-columella. Columellar callus somewhat thickened, appressed, forming medial border of umbilicus.

Discussion – We were unable to locate Brébion's 'type' for *Calliostoma caveti nomen nudum*, said to be deposited in the Institut Catholique d'Angers (Angers) and have therefore chosen a 'new holotype'. *Jujubinus condevicnumensis* nov. sp. is quite a distinctive little species due to its canaliculated suture resulting in a scalate spire and elevated, narrow spiral cords that are finely, but sharply beaded. The ridge running a short distance within the aperture along the entire outer lip edge is also a distinctive feature in this species. In some specimens the ridge is interrupted within the outer lip angulation, whereas in others it is continuous and in some specimens a second ridge extends inwards from the lip angulation. This same apertural armature is also seen in other French Atlantic *Jujubinus* species, such as *J. subturgidulus* (d'Orbigny, 1852) from the Atlantic Aquitanian of France (Lozouet *et al*., 2001, pl. 4, fig. 5) and the present-day *J. exasperatus* (Pennant, 1777). Otherwise *J. condevicnumensis* is remarkably constant in size and sculpture. As with several other NW French trochids, Brébion (1964) included this species in the genus *Calliostoma* Swainson, 1840, however, the presence of a columellar denticle places it in the subfamily Cantharidinae.
Brébion (1964, p. 87) recorded this species from several other Assemblage III localities (Le Girondor, La Gauvinière and Palluau).

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

***Jujubinus ligeriensis* nov. sp.**
Plate 4, figs 2-4

1964 *Jujubinus* (*Strigosella*) *quadristriatus* Dubois de Montpereux, 1831 – Brébion (*partim*), p. 119, pl. 3, fig. 11 (not fig. 12) (*non Trochus quadristriatus* Dubois de Montpereux, 1831).

Type material – Holotype MNHN.F.A57387 (Pl. 4, fig. 2), maximum diameter 5.6 mm, height 6.0 mm; paratype 1 NHMW 2015/0133/0062 (Pl. 4, fig. 3), maximum diameter 6.2 mm, height 7.1 mm; paratype 2 NHMW 2015/0133/0064 (Pl. 4, fig. 4), maximum diameter 6.4 mm, height 7.4 mm; paratype 3 NHMW 2015/0133/0061, maximum diameter 6.2 mm, height 7.1 mm.

Other material – NHMW 2015/0133/0063 (15); LC (50+); FVD (4). Type locality.

Etymology – Named after the Latin name for the Loire River, '*Liger*'. *Jujubinus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Jujubinus* species with a conical spire, spiral sculpture composed of 5-6 narrow, elevated, strongly but finely beaded cords, a convex base with ten concentric, beaded cords, a narrow, shallow umbilicus, and an aperture with a ridge internally, parallel to the lip edge.

Description – Shell small, solid, turbinate, with conical spire, base convex, perforate. Protoconch not preserved. Teleoconch consisting of five weakly convex to straight-sided whorls. Suture linear, impressed. Spire whorls bearing 5-6 elevated, narrow, irregular cords, finely beaded by crowded, prosocline growth lines, adapical two cords closer-set. Last whorl weakly angled at periphery, whorl profile above convex, sculptured by five finely beaded cords above carina; basal carina composed of two narrower, close-set cords. Base convex, bearing ten narrow, elevated, concentric cords. Umbilicus narrow, shallow, smooth within. Aperture tangential; peristome continuous, outer lip not thickened, smooth edged, rounded at periphery, bearing an internal ridge running parallel to the lip edge, in some specimens a second ridge extends inwards from lip angulation. Columella straight, leaning abaxially, bearing single columellar tooth mid-columella. Columellar callus somewhat thickened, appressed, forming medial border of umbilicus.

Discussion – *Jujubinus ligeriensis* nov. sp. is closely similar to *Jujubinus condevicnumensis* nov. sp. (see above) in size and sculpture, but differs in 1) not having a canaliculated suture; in some specimens there is a narrow subsutural ramp, but the suture is never canaliculated, 2) having a conical rather than scalate spire, 3) having fewer spiral cords (5-6 vs. 7), 4) having the last whorl above the basal carina convex rather than concave, 5) in having a less prominent basal carina composed of two spiral cords as opposed to three in *J. condevicnumensis*, and 6)

having a more convex base. The apertural and umbilical characters are similar in both species.
The shell illustrated by Brébion (1964, pl. 3, fig. 11) from Le Pigeon Blanc as *Jujubinus* (*Strigosella*) *quadristriatus* Dubois de Montpereux, 1831 is this species, whereas the specimen from Manoir St-Jacques is not, therefore we have not included the other localities given by Brébion in the distribution. The shells illustrated by Glibert (1949, pl. 3, fig. 3) as *Callisotoma quadristriatum* (Dub.) from the middle Miocene Loire Basin have fewer spiral cords, a sharper basal angulation, a flatter base and a deeper umbilicus. Another species illustrated by Glibert (1949, pl. 3, fig 2) as *Callisotoma* cf. *turgidulum* (Brocc.), also from the Loire Basin middle Miocene has a similar number of beaded cords, but differs in being higher spired, having a sharper basal angulation, flatter base and deeper umbilicus. *Colliculus beetsi* (van Regteren Altena, 1954) from the Pliocene North Sea Basin Belgian and Dutch deposits is superficially similar to *J. ligeriensis*, with a similar number of finely beaded cords, but is lower spired, is imperforate, or almost so, and does not have denticulation within the aperture. Pouwer (2014) illustrated the holotype of *C. beetsi* with a somewhat scalate spire, resembling *J. condevicnumensis*, but it differs from this species in having fewer spiral cords, and in the same umbilical and apertural characters which distinguish it from *J. ligeriensis*.

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

***Jujubinus striatus* (Linnaeus, 1758)**
Plate 4, fig. 5

*1758	*Trochus striatus* Linnaeus, p. 759.
1923	*Trochus (Calliostoma) striatus* (Linné) – Harmer, p. 725, pl. 59, figs 4, 5.
2003	*Jujubinus striatus striatus* (Linnaeus, 1767 [*sic*]) – Landau *et al*., p. 44, pl. 10, fig. 2 (*cum syn*.).
2004	*Jujubinus striatus* (Linné, 1758) – Chirli, p. 82, pl.34, figs 1-12.
2011	*Jujubinus striatus striatus* (Linnaeus, 1767 [*sic*]) – Landau *et al*., p. 8, pl. 1, fig. 5.
2012	*Jujubinus striatus* (Linné, 1758) – Pouwer & Wesselingh, p. 159, fig. 26.

Material and dimensions – NHMW 2015/0133/0156 (1, Pl. 4, fig. 5), maximum diameter 6.7 mm, height 5.9 mm, NHMW 2015/0133/0246 (5); LC (6); FVD (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – These small shells from Le Pigeon Blanc probably fit within the enormous variation seen in *Jujubinus striatus* (Linnaeus, 1758). Cretella (1993, p. 41) reported a clinal variation in the species morphology, western forms being sqatter, with a flatter base, stronger axial growth lamellae and fewer spiral cords (western 6-9 *v.s.* eastern 10-12). This would be true of the Le Pigeon Blanc specimens, which are rather squat, with about eight spiral cords per whorl.

Distribution – Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, S. Spain (Landau *et al*., 2011); western Mediterranean, NE Spain (Martinell, 1978); central Mediterranean, Italy (Chirli, 2004). Upper Pliocene: Atlantic, Red Crag, England (Harmer, 1923); western Mediterranean, Estepona, S. Spain (Landau *et al*., 2003); central Mediterranean, Italy (Spadini, 1986; Cavallo & Repetto, 1992). Pleistocene: Atlantic, Britain (Harmer, 1923); The Netherlands (Pouwer & Wesselingh, 2012); western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Italy (Malatesta, 1960; Taviani *et al*., 1998). Present-day: Atlantic, Isle of Man to Canaries, Madeira, Azores and Mediterranean, from the extreme low tide to 200m deep on seaweeds and small stones (Poppe & Goto, 1991).

Genus *Gibbula* Risso, 1826

Type species (by subsequent designation, Herrmannsen, 1847, p. 473) – *Trochus magus* Linnaeus, 1758, present-day, Mediterranean.

1826	*Gibbula* Risso, p. 134.

***Gibbula provosti* nov. sp.**
Plate 4, fig. 6; Plate 5, fig. 1

1964	*Gibbula (Colliculus) varia* Linné, 1766 [*sic*] var. *termieri* nov. sp. Dollfus mss., (emend) – Brébion, p. 109, pl. 3, fig. 3 (*nomen nudum*).

Type material – Holotype MNHN.F.A53415 (Pl. 4, fig. 6), maximum diameter 8.7 mm, height 6.8 mm; paratype 1 NHMW 2015/0133/0068 (Pl. 5, fig. 1), maximum diameter 9.5 mm, height 8.7 mm; paratype 2 NHMW 2015/0133/0069, maximum diameter 9.5 mm, height 8.0 mm; paratype 3 NHMW 2015/0133/0070, maximum diameter 7.3 mm, height 6.8 mm.

Other material – NHMW 2015/0133/0071 (32); LC (50+); FVD (9). Type locality.

Etymology – Named in honour of the family Provost, owners of the land at Le Pigeon Blanc, without whose support this work would not have been possible. *Gibbula* gender feminine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Gibbula* species with a strongly depressed spire, surface covered by finely-beaded, narrow spiral cords, a strongly oblique columella bearing a relatively well-developed tooth, a base bearing prominent

cords and growth lines, and a narrow smooth umbilicus.

Description – Shell small, solid, trochiform, with strongly depressed, conical spire. Protoconch eroded. Teleoconch consisting of four weakly convex whorls, with periphery at abapical suture. Suture linear, impressed. Spiral sculpture consisting of numerous, close-set, narrow, irregular cords, 13 on penultimate whorl, finely beaded by crowded, strongly prosocline growth lines. Last whorl depressed, roundly angled at periphery. Base not clearly delimited, weakly convex, perforate, bearing 12-15 narrow concentric cords, slightly wider-spaced towards centre, and prominent axial growth lines. Aperture subquadrangular, peristome complete, outer lip not thickened, strongly tangential. Columella straight, leaning strongly abaxially, bearing single columellar tooth abapically. Columellar callus thickened, forming medial border of umbilicus. Umbilicus narrow, with a rounded edge, smooth within.

Discussion – We agree with Brébion (1964, p. 109) in separating these shells from *Gibbula varia* (Linnaeus, 1758) from the Pliocene to present-day Mediterranean. The French fossil shells differ from this species in 1) being smaller in size, 2) having a more depressed shell, especially the last whorl, 3) having finely beaded spiral cords, 4) having more prominent sculpture on the base, 5) having a more oblique columella, 6) having a more strongly developed columellar tooth, and 7) having a narrower umbilicus. Even in specimens with an unusually wide umbilicus, such as the shell illustrated by Brébion (1964, pl. 3, fig. 3), it is still narrower than in *G. varia*.
A similar species was figured by Brébion (1964, pl. 3, figs 1, 2) under the name *G. varia* var. *monodontoides* (Millet, 1854) (*nomen nudum*; made available Millet, 1865) from localities in Assemblages I and II. This species has a less depressed shell than *Gibbula provosti* nov. sp., similar to *G. varia*, but was said to differ in the complete absence, or almost so, of the umbilicus, which is covered by a columellar callus. Unfortunately, no basal view was offered by Brébion and this species will be revised in a subsequent paper.
Brébion (1964, p. 110) also recorded *G. provosti* from Le Girondor.

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

***Gibbula milleti* nov. sp.**
Plate 5, figs 2, 3

Type material – Holotype MNHN.F.A57388 (Pl. 5, fig. 2), maximum diameter 6.8 mm, height 5.5 mm; paratype 1 NHMW 2015/0133/0158, maximum diameter 6.4 mm, height 4.5 mm; paratype 2 NHMW 2015/0133/0159, maximum diameter 5.8 mm, height 4.5 mm; paratype 3 NHMW 2015/0133/0171 (Pl. 5, fig. 3), maximum diameter 6.8 mm, height 5.0 mm; paratype 4 NHMW 2015/0133/0247, maximum diameter 7.3 mm, height 7.4 mm; paratype 5 NHMW 2015/0133/0157, maximum diameter 7.2 mm, height 7.0 mm.

Other material – Known only from type series.

Etymology – Named after Pierre-Aimé Millet de la Turtaudière (1783-1873), French naturalist and Secrétaire Général de la Société d'Agriculture d'Angers, in recognition of his early works on the palaeontology of Maine-et-Loire. *Gibbula* gender feminine

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Gibbula* species with a strongly depressed to somewhat elevated spire, sculpture on spire whorls consisting of five cords, a depressed last whorl with a swollen peripheral carina, the carina and base covered in finer cords, and an imperforate, or almost so, flattened base.

Description – Shell small, solid, trochiform, with strongly depressed to somewhat elevated conical spire. Protoconch eroded. Teleoconch consisting of 3.5 whorls, with periphery at abapical suture. Whorl profile of first two whorls weakly convex. Suture linear, impressed. Spiral sculpture consisting of five non-beaded cords. Last whorl depressed, with swollen peripheral carina, whorl profile above weakly concave, bearing five cords above periphery; swollen peripheral carina and base covered in finer cords. Base not sharply delimited, flattened, imperforate or with very small umbilical dimple, bearing 13-14 irregular, narrow, concentric cords, slightly wider-spaced towards centre. Aperture subquadrangular, peristome complete, outer lip not thickened, strongly tangential. Columella straight, leaning strongly abaxially, bearing single columellar tooth abapically. Columellar callus thickened, closing umbilicus.

Discussion – *Gibbula milleti* nov. sp. is the smallest *Gibbula* in the Le Pigeon Blanc assemblage and can be separated from its congeners by its base, which is imperforate or in some specimens with a very small umbilical dimple. Most specimens are strongly depressed, although one specimen (paratype 4) has a somewhat elevated spire. Other low-spired species such as the Pliocene to present-day European *G. umbilicaris* (Linnaeus, 1758) and the fossil *G. solarium* (Nyst, 1836) from the North Sea Basin Pliocene are markedly umbilicate. Harmer (1923, pl. 59, fig. 7) figured a shell from Gelasian Pleistocene of St. Erth, *Trochus multistriata* Wood, *in* Kendall & Bell, 1886 with a very similar lentiform shape and imperforate base, but differing in having very delicate fine spiral sculpture and a convex rather than concave profile to the last whorl. Harmer ascribed this shell in the genus *Calliostoma* Swainson, 1840. Based on its shape and the presence of a small columellar tooth placement in *Gibbula* is more likely, however, we have not seen this species.

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

***Gibbula magus* (Linnaeus, 1758)**
Plate 5, fig. 4, 5

*1758	*Trochus magus* Linnaeus, p. 757.
1964	*Gibbula magus* Linné, 1766 [*sic*] – Brébion, p. 103, pl. 2, fig. 31.
2003	*Gibbula* (*Gibbula*) *magus* (Linnaeus, 1758) – Landau *et al*., p. 46, pl. 10, fig. 4 (*cum syn*.).
2004	*Gibbula* (*Gibbula*) *magus* (Linné, 1758) – Chirli, p. 58, pl. 20, figs 11, 12, pl. 21, figs 1-3.
2010	*Gibbula magus* (Linnaeus, 1758) – Sosso & Dell' Angelo, p. 19, p. 30 fig. third row right.
2011	*Gibbula* (*Gibbula*) *magus* (Linnaeus, 1758) – Landau *et al*., p. 8, pl. 1, fig. 6.
2012	*Gibbula magus* (Linné, 1758) – Pouwer & Wesselingh, p. 153, fig. 7.

Material and dimensions – NHMW 2015/0133/0065 (1, Pl. 5, fig. 4)), height 15.5 mm; width 15.3 mm; NHMW 2015/0133/0066 (1), height 15.4 mm; width 16.1 mm; NHMW 2015/0133/0154 (1, Pl. 5, fig. 5), height 12.2 mm; width 14.7 mm (incomplete); LC (36 incomplete and juveniles); FVD (8). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Two closely similar species occur in the European Neogene. *Gibbula sagus* (Defrance, 1828) from the middle Miocene of the Loire Basin and upper Miocene Tortonian Assemblage I localities of NW France and the Pliocene to present-day *G. magus* (Linnaeus, 1758) until now known in the Pliocene only from the Mediterranean and adjacent Atlantic (Landau *et al*., 2003, 2011), although it has been reported from the Eemian Pleistocene of the North Sea Basin (Pouwer & Wesselingh, 2012). *Gibbula magus* is somewhat more depressed, with a more angular last whorl and a flatter base. The concentric ridges are not as prominent as in the Miocene species, in which the sculpture on the base consists of elevated cords rather than ridges (see Glibert, 1949).
The specimens from Le Pigeon Blanc are highly variable, as seen in the illustrated series. We point out that almost all of the material available is not fully adult or incomplete, but most specimens do not have the folds on the subsutural ramp, although they are present in one specimen (Pl. 5, fig. 5). The character of the base, however, is typical of *M. magus*. Therefore is seems that at some time between the end of the middle Miocene and the beginning of the Pliocene *G. sagus* was replaced along the north-eastern Atlantic frontage by *G. magus*. Brébion (1964, p. 104) reported *G. magus* from Assemblage I localities (Renauleau and Thorigné), so this replacement may have been at the beginning of the Tortonian, but these records need to be confirmed. Either way, this record of *G. magus* in the NW French Zanclean is the chronostratigraphically earliest record for the species outside the Mediterranean.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964), Guadalquivir Basin, S. Spain (Landau *et al*., 2011); western Mediterranean, Morocco (Lecointre, 1952); central Mediterranean, Italy (Chirli, 2004; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona, S. Spain (Landau *et al*., 2003), central Mediterranean, Italy (Sacco, 1896, Malatesta, 1974; Caprotti, 1976; Spadini, 1986; Anfossi *et al*., 1982; Cavallo & Repetto, 1992). Pleistocene: western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1916; Malatesta, 1960; Glibert, 1962; Taviani *et al*., 1998). Upper Pleistocene: Atlantic, British Isles (Harmer, 1923; Glibert, 1962), The Netherlands (Pouwer & Wesselingh, 2012). Present-day: Mediterranean and Atlantic northwards to the Shetland Isles, exceptionally intertidal in the Atlantic, but elsewhere infralittoral, where it prefers muddy bottoms, down to 70 m depth in the Atlantic, probably deeper in the Mediterranean (Poppe & Goto, 1991).

***Gibbula carinifera* (Wood, 1848)**
Plate 5, figs 6, 7

1842	*Trochus cariniferus* Wood, p. 532 (*nomen nudum*).
*1848	*Trochus cariniferus* Wood, p. 132, pl. 14, fig. 6.
1923	*Trochus* (*Gibbula*) *cariniferus* (S.V. Wood) – Harmer, p. 738, pl. 59, fig. 18.
?2012	*Gibbula* spec. 2 – Pouwer & Wesselingh, p. 157, fig. 21.

Material and dimensions – NHMW 2015/0133/0067 (1, Pl. 5, fig. 6), maximum diameter 6.0 mm, height 5.7 mm; NHMW 2015/0133/0404 (1, Pl. 5, fig. 7), maximum diameter 9.4 mm, height 10.2 mm; NHMW 2015/0133/0155 (3), maximum diameter 9.4 mm, height 10.2 mm; LC (7 juveniles and fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Revised description – Shell small, turbinate, base flattened, perforate. Protoconch not preserved. Teleoconch consisting of four angular whorls. First whorl bearing three narrow, strongly elevated spiral cords. On second whorl adapical cord, placed on subsutural ramp, weakens; second cord forming shoulder. On penultimate whorl a third primary cord develops above suture. Last whorl bearing three raised cords, the lowest cord forming the periphery. Suture linear, superficial. Base sharply angled, flattened, bearing five narrow, concentric cords; umbilicus relatively narrow, deep, sharp-edged, smooth within. Whole whorl surface and cords covered in strongly prosocline, elevated lamellae, giving surface a somewhat scabrous appearance. Aperture tangential; peristome continuous, outer lip not thickened, angled at periphery, edge coarsely crenulated by ends of primary cords. Columella straight, erect, forming medial border of umbilicus, bearing broad, indistinct thickening mid-columella. Parietal callus not developed.

Discussion – We consider these shells to be conspecific

with that illustrated by Harmer (1923, pl. 59, fig. 18) as *Trochus* (*Gibbula*) *cariniferus* (S.V. Wood). This is an extremely distinctive species. The three strong spiral keels on the spire whorls, axial lamellae giving the surface a scabrous appearance and flat base immediately separate it from all other *Gibbula* species. One of the shells illustrated (Pl. 5, fig. 6) is not fully grown, but is chosen for its perfectly preserved sculpture. Fragments in the LC collection suggest a fully adult size at least four times the size of the holotype. The Le Pigeon Blanc specimens have a more flattened base than the shell from Little Oakley, Red Crag illustrated by Harmer, but with the small amount of material available we consider this to be intraspecific variability. Pouwer & Wesselingh (2012, fig. 21) illustrated a small fossil shell from De Kaloot, The Netherlands, considered to be Pliocene, as *Gibbula* spec. 2. It is extremely similar to the smaller juvenile shell here illustrated (Pl. 5, fig. 6), but again has a less flattened base. We provisionally include it in the synonymy, with some reservation.
We can find few other *Gibbula* species with strongly elevated spiral cords with which to compare this new species; *G. saeniensis* Chirli & Micali, 2002 from the lower Pliocene of Italy also has elevated cords, but these are more numerous.

Distribution – Lower Pliocene: Atlantic, NW France (this paper), Coralline Crag, England (Wood, 1842, 1848; Harmer, 1923). Upper Pliocene: Atlantic, Red Crag, England (Harmer, 1923). Pliocene (indeterminate): ?The Netherlands (Pouwer & Wesselingh, 2012).

Genus *Colliculus* Monterosato, 1888

Type species (by subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1898, p. 773) – *Trochus adansonii* Payraudeau, 1826, present-day, Mediterranean.

1888 *Colliculus* Monterosato, p. 171.
1888 *Glomulus* Monterosato, p. 172. Type species (subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1898, p. 773): *Trochus turbinoides* Deshayes, 1835, present-day, Mediterranean. *Colliculus* given precedence over *Glomulus*, by First Reviser's choice by Cossmann, 1918.

Note – Lozouet *et al*. (2001, p. 18) gave full genus rank to *Colliculus* Monterosato, 1888, whereas the taxon is synonymised (Bouchet & Gofas, WoRMS 2015) with *Gibbula* Risso, 1826. In our opinion it is unlikely that all the species included in the genus *Gibbula* by WoRMS are monophyletic. Barco *et al*. (2013) found that at least *Gibbula (s.l.) adansoni* and *G. (s.l.) adriatica* (Philippi, 1844), both placed in *Colliculus*, formed a monophyletic group. Cossmann (1918, p. 233) highlighted the differences between *Colliculus* and *Gibbula*; *Colliculus* has a narrow umbilicus with a non-callused edge, the aperture is at 45º, and the columellar edge is relatively straight with a swelling, but not a well-developed tooth. The species included below within this genus are similar to *Colliculus aquitanicus* (Cossmann & Peyrot, 1917) from the Atlantic lower Miocene Aquitaine Basin of France (see Lozouet *et al*., 2001, pl. 3, figs 5, 6).

***Colliculus neraudeaui* nov.sp.**
Plate 6, fig. 1

Type material – Holotype NHMW 2015/0133/0168 (Pl. 6, fig. 1), maximum diameter 10.2 mm, height 7.2 mm.

Other material – LC (2 fragments). Type locality.

Etymology – Named after Didier Néraudeau of the Université de Rennes 1 (UMR 6118 Géosciences) in recognition of his help and advice concerning the stratigraphy of NW France. *Colliculus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A small *Colliculus* species with a depressed spire, sculpture on spire whorls consisting of a strong adapical cord delimiting a horizontal, concave subsutural platform, an even stronger peripheral carina delimiting the base, with one weaker cord between, base weakly convex, with mid-width, deep umbilicus.

Description – Shell small, solid, trochiform, with depressed, low, scalate spire. Protoconch eroded. Teleoconch consisting of three whorls, with angular profile, periphery at abapical suture. Spire whorls with horizontal, concave subsutural platform, delimited by strongly developed, raised adapical spiral cord; whorl profile below concave to an even more strongly developed, raised abapical cord, placed immediately above suture; suggestion of beading on abapical cord; a single weaker primary cord runs mid-whorl. Suture linear, superficial. Last whorl depressed, sharply biangular, adapical cord forming a stout peripheral keel delimiting base; secondary spiral threads appear in interspace between mid-cord and adapical cord on last half whorl. Base weakly convex, bearing four cords, perforate; umbilicus moderately wide, round-edged, very deep, bearing close-set spiral grooves within. Aperture subquadrangular, outer lip not thickened, strongly angled at adapical and abapical cords. Columella incomplete.

Discussion – *Colliculus neraudeaui* nov.sp. is represented by a single, somewhat worn specimen, but its outline and sculpture are so peculiar that it warrants description. It seems to form part of a group of NW French Miocene *Colliculus* species with strongly developed spiral cords delimiting the subsutural platform and base, giving the last whorl a biangular profile. We include in this group *C. aquitanicus* (Cossmann & Peyrot, 1917) from the Aquitanian lower Miocene of the Aquitaine Basin, which dif-

fers in having a less depressed shell, with less angular whorls, especially the adapical angulation is weaker; the cords at the angulations less strongly developed, with the secondary spiral sculpture more prominent, only slightly weaker than the primary cords, covering the entire whorl surface. *Colliculus glyphidospira* (Cossmann & Peyrot, 1917) from Aquitanian lower Miocene of the Aquitaine Basin has very strongly developed adapical and abapical primary spiral cords, like *C. neraudeaui*, but differs from it in being higher-spired, the spire conical, lacking the horizontal subsutural platform seen in the new species. *Colliculus sosensis* (Cossmann & Peyrot, 1917), widespread in the NW French Assemblage I localities, is the most similar, but differs from *C. neraudeaui* in being smaller-shelled, in having two primary spiral cords between the stronger adapical and abapical cords, in having numerous finer cords on the base and a narrower, shallower umbilicus. In *C. sosensis* the spiral sculpture is finely beaded by close-set growth lines, absent in the new species. Finally, *C. biangulata* (Eichwald, 1830), which is widespread in the Middle and Upper Miocene NW French assemblages, and is most like *C. aquitanicus*, but lower-spired and more strongly biangular than the Aquitanian species, has narrower and more numerous spiral cords between the angulations.

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

Genus *Paroxystele* Schultz, 1969

Type species (by original designation) – *Trochus patulus* Brocchi, 1814, Neogene, Italy.

1969 *Paroxystele* Schultz, p 217.

***Paroxystele turoniensis* (Glibert, 1949)**
Plate 6, fig. 2

*1949 *Monodonta (Oxystele) amedei turoniensis* Glibert, p. 63, pl. 3, fig. 10.

Material and dimensions – NHMW 2015/0133/0169 (1, Pl. 6, fig. 2)), height 18.1 mm, width 27.0 mm; NHMW 2015/0133/0072 (1), height 21.2 mm, width 25.2 mm (incomplete); FVD (1 adult height 25.2 mm, width 31.6 mm + 2 juveniles). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – As discussed by Landau *et al*. (2013, p. 29), Most Miocene *Paroxystele* species differ from those in the Pliocene in having a completely closed umbilicus and only few Miocene species have subsutural folds, which are usually present in the Plio-Pleistocene *Paroxystele patulum* (Brocchi, 1814). It is therefore noteworthy that in the lower Pliocene assemblage of Le Pigeon Blanc the middle Miocene Loire Basin species *Paroxystele turoniensis* (Glibert, 1949) survived into the Pliocene, rather than being replaced by the Plio-Pleistocene *P. patulum*, which was widely distributed in the Mediterranean since at least the lower upper Pliocene. *Paroxystele turoniensis* is a relatively low-spired species, in which the base is subcarinate, and the whorls are ornamented by seven or eight spiral cords, without secondary sculpture, subsutural folds are absent, and the umbilical callus is broad and closely adherent, filling the umbilicus. The stratigraphically older Aquitanian and Burdigalian Atlantic species *P. burdigalensis* (Cossmann & Peyrot, 1917) differs in being lower spired and having secondary spiral sculpture between the primary spiral cords. *Paroxystele orientale* (Cossmann & Peyrot, 1917) from the middle Miocene eastern Mediterranean and Paratethys differs in having more numerous spiral cords, the base is more rounded and the umbilical callus is narrower, not completely filling the umbilicus.

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

Superfamily Turbinoidea Rafinesque, 1815
Family Turbinidae Rafinesque, 1815
Genus *Bolma* Risso, 1826

Type species (by monotypy) – *Turbo rugosus* Linné, 1767, present-day, Mediterranean.

1767 *Bolma* Risso, 1826, p. 117.

Note – We have not repeated here the list of generic synonyms given by Beu & Ponder (1979), as we do not believe the genus, as envisaged by these authors, to be monophyletic. This is supported by the molecular phylogenetic studies presented by Williams & Ozawa (2006). Landau *et al*. (2003) argued that *Ormastralium* Sacco, 1896 species should be considered a separate subgenus, elevated to genus by Landau *et al*. (2013).

***Bolma rugosa* (Linné, 1767)**
Plate 6, fig. 3

*1767 *Turbo rugosus* Linné, p. 1234.
2003 *Bolma (Bolma) rugosa* (Linnaeus, 1767) – Landau *et al*., p. 32, pl. 7, fig. 4 (*cum syn*.).
2004 *Bolma rugosa* (Linné, 1767) – Chirli, p. 40, pl. 13, figs. 1-9.
2008 *Bolma rugosa* (Linné, 1758 [*sic*]) – Chirli & Richard, p. 14, pl. 1, fig. 3.
2010 *Bolma rugosa* (Linnaeus, 1758 [*sic*]) – Sosso & Dell'Angelo, p. 19, p. 30 fig. bottom right.
2011 *Bolma rugosa* (Linnaeus, 1767) – Landau *et al*., p. 9, pl. 1, figs 11, 12 (*cum syn*.).
2013 *Bolma rugosa* (Linné, 1767) – Landau *et al*., p. 30, fig. 15, figs 3-7.

Material and dimensions – NHMW 2015/0133/0170 (1,

Pl. 6, fig. 3), height 44.6 mm, maximum width 55.6 mm; NHMW 2015/0133/0073 (1), height 35.1 mm, maximum width 42.5 mm; NHMW 2015/0133/0074 (3 juveniles); LC (4 incomplete and juveniles); FVD (4 incomplete and juveniles). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Landau *et al*. (2013, p. 30) discussed the differences between the Miocene species *Bolma meynardi* (Michelotti, 1847) and the Pliocene to present-day species *B. rugosa* (Linné, 1767). In *B. meynardi* the basal callus is significantly larger than in present day *B. rugosa* shells, with Pliocene specimens of *B. rugosa* somewhere in between. The spire is squatter in *B. meynardi* than in present day *B. rugosa* shells, with Pliocene *B. rugosa* having both high and low spires. Dorsal rugae are absent, or weak in present-day *B. rugosa* and are strongly developed in most Miocene and Pliocene forms. Landau *et al*. (2013) considered the most constant distinguishing character the position of the suture on the second half of the last whorl. In *B. meynardi* the suture, when viewed aperturally, is placed between the base and mid-whorl height, whereas in *B. rugosa* the suture is at or below the base. Pliocene and present-day forms of *B. rugosa*, although somewhat different, cannot be separated consistently. The illustrated shell from Le Pigeon Blanc has the suture on the second half of the last whorl positioned at the base and a relatively small basal callus, features consistent with *B. rugosa*. Brébion (1964) reported *Bolma trochleata* (Millet, 1854) (invalid; junior homonym of *T. trochleatus* Münster, 1841), from the Redonian of northwestern France, and recorded it in outcrops representing Assemblages I-IV. The specimens from Le Pigeon Blanc are *B. rugosa*. Those from Assemblage I localities are almost entirely represented by juveniles. We will review this species in the corresponding revision.
This occurrence of *B. rugosa* in the lower Pliocene of northwestern France is the most northerly limit of the species in the fossil record and represents a range expansion compared to that of the species today, which is not found in the Atlantic north of Portugal.

Distribution – Lower Pliocene: Atlantic, Guadalquivir basin, Spain (Landau *et al*., 2011); western Mediterranean, Estepona, S Spain (Landau *et al*., 2003), Empordà, NE Spain (Martinell, 1978), NW. France (this paper); central Mediterranean, Tunisia (Fekih, 1975), Italy (Malatesta, 1974; Anfossi *et al*., 1982; Chirli, 2004; Sosso & Dell'Angelo, 2010). Upper Pliocene: Atlantic, Portugal (Silva, 1990, 2001), Morocco (Lecointre, 1952); western Mediterranean, France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1896; Glibert, 1962; Caprotti, 1976; Cavallo & Repetto, 1992). Pleistocene: Atlantic, Morocco (Lecointre, 1952); Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Sicily (Glibert, 1962), Italy (Cerulli-Irelli, 1916; Malatesta, 1960; Glibert, 1962), Tunisia (Glibert, 1962); western Mediterranean, France (Glibert, 1962). Present-day: Atlantic, Portugal to Madeira, Azores, Canaries and Mediterranean, rock bottoms between 8-50m (Poppe & Goto, 1991).

Family Tegulidae Kuroda, Habe & Oyama, 1971
Genus *Tectus* de Montfort, 1810

Type species (by original designation) – *Tectus pagodalis* Montfort, 1810 [= *Tectus mauritianus* (Gmelin, 1791)], present day, East Africa.

1810 *Tectus* de Montfort, p. 186.
1817 *Pyramis* Schumacher, p. 70, 232. Type species (by monotypy): *Pyramis viridis* Schumacher, 1817 [= *Tectus pyramis* Born, 1778)], present-day, Indian Ocean. Invalid: junior homonym of *Pyramis* Röding, 1798.
1840 *Pyramidea* Swainson, 1840, p. 295. Type species (by subsequent designation, Herrmannsen, 1848): *Trochus obeliscus* Gmelin, 1791 [= *Tectus pyramis* Born, 1778)], present-day, Indian Ocean.

?*Tectus columbinus* nov. sp.
Plate 7, figs 1-5

1964 *Calliostoma quadricingulatum* Brébion, p. 94, pl. 2, fig. 16 (*nomen nudum*).

Material and dimensions – Holotype MHNN.P.020684 (Pl. 7, fig. 4), height 7.9 mm, width 8.2 mm; paratype 1 NHMW 2015/0133/0088 (Pl. 7. Fig. 1), height 25.5 mm (incomplete), width 23.4 mm; paratype 2 NHMW 2015 /0133/0089 (Pl. 7, fig. 2), height 29.0 mm (incomplete), width 24.8 mm; paratype 3 NHMW 2015/0133/0160, height 16.2 mm, width 12.7 mm (juvenile).

Other material – NHMW 2015/0133/0161 (3 fragments and juveniles); LC (14 fragments and juveniles); FVD (2 adults, one of which illustrated Pl. 7, fig. 5). Type locality.

Etymology – Latin '*columbinus, a, um*', adjective, of pigeons; a reference to the type locality of Le Pigeon Blanc (the white pigeon). *Tectus* gender masculine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Tectus* species with a regularly conical shell, straight sided whorls, sculpture composed of four strongly beaded spiral cords, and a flattened base bearing concentric cords.

Description – Shell large, solid, with regularly conical spire. Protoconch eroded. Teleoconch consisting of up to eight straight-sided whorls. Suture linear, impressed. Sculpture on first teleoconch whorl consisting of three coarsely beaded cords. A fourth beaded cord appears above suture on second teleoconch whorl. Abapically all whorls sculptured by four strongly beaded regular cords, with a single spiral thread intercalated in some of the interspaces. Last whorl straight-sided, sharply rounded at

periphery. Base flattened, bearing ten subequal concentric cords. Aperture tangential, sub-quadrangular; outer lip bevelled, with a small tubercle delimiting the lateral border of the short siphonal spout. Columella leaning strongly abaxially, with a single fold abapically delimiting the border of an extremely short, everted, spout-like siphonal canal. Columella callus thickened and somewhat expanded closing umbilicus.

Discussion – Brébion (1964, p. 94) described this species under the name *Calliostoma quadricingulatum nomen nudum*, but examination of the shell characters shows it not to be a calliostomid, but a trochid. The shell is far more solid than usual for *Calliostoma* species and most importantly there is a short spout-like siphonal canal delimited on the medial side by a twisted columellar fold and on the medial side by a small tubercle on the outer lip. We consider this shell to be a tegulid and provisionally place it in the genus *Tectus* de Montfort, 1810. In his review of this paper, Pierre Lozouet pointed out that in *Tectus* species the columellar fold is more strongly developed and continues on earlier whorls and can be seen even in broken shells. In the Le Pigeon Blanc specimens this seems to be less evident, although a slight columellar swelling can be seen in one of the broken shells illustrated (Plate 7, fig. 4a). It is possible that the apertural characters of this new species are convergent and it belongs within another trochid genus. However, the tall conical shape, very solid shell and large size make it unlikely to belong within other Pliocene trochid genera such as *Clanculus*, *Jujubinus*, *Gibbula* or *Paroxystele*. In view of the above, we feel that at present placement in the genus *Tectus* is most appropriate.
Today this genus is Indo-Pacific, but there are a few records of species in the European Tertiary. Of these European species, the sculpture in *Tectus columbinus* nov. sp. is most like that of the Bartonian upper Eocene French species *Tectus monilifer* (Lamarck, 1804), which has the same conical shape and four beaded cords, however, in the Eocene species the lower two cords are slightly elevated on a weak suprasutural collar and the base is flatter with a less strongly developed siphonal canal. The Aquitanian and Burdigalian lower Miocene species *T. rugosus* (Grateloup, 1832) from the Aquitaine Basin of France and *T. vertex* (Michelotti, 1847) from the Po Basin of Italy are both immediately separated by their rugose rather than granulate sculpture. Cossmann & Peyrot (1917) described a second species from lower Burdigalian of the Aquitaine Basin of France [St-Paul-lès-Dax (Cabanes) and Saucats (La Casagne)]: *Trochus* (*Tectus*) *elegantulus*, based on four incomplete or juvenile shells (height 7.0 mm, width, 6 mm). This species is similar in shape and sculpture to ?*T. columbinus*, but the holotype of *T. elegantulus* differs in having five beaded cords on the spire whorls, of which the cords bordering the suture are more strongly developed, whereas ?*T. columbinus* has only four equally developed cords, and having a base with a smooth area peripherally delimited by a strong cord and weaker cords medially to the imperforate centre, whereas in ?*T. columbinus* the entire base is covered in subequal beaded cords. Cossmann & Peyrot (1917, p. 84, footnote 1) noted that the plesiotype from St-Paul-lès-Dax (Cabanes) (not illustrated) had only three cords on the first teleoconch whorl and four on subsequent whorls, like ?*T. columbinus*. Whether this intraspecific variability is correct for *T. elegantulus* we cannot ascertain with the small amount of material described, but all our specimens of ?*T. columbinus* have only four primary spiral cords. It is very unlikely that ?*T. columbinus* is conspecific with the shell from Dax, as the assemblages have no species in common.
The presence of the genus *Tectus* in the Le Pigeon Blanc assemblage is quite unexpected. If this generic attribution is correct, this is the first European Pliocene record, leaving a stratigraphic gap between the Burdigalian lower Miocene and the Zanclean lower Pliocene. It is also unexpected as *Tectus* is a thermophilic genus, found today in warm waters. The Le Pigeon Blanc assemblage has few thermophilic elements (see Van Dingenen *et al*., 2015), although more may be found as the study of the assemblage progresses.
Brébion (1964, p. 95) recorded this species from Le Girondor and La Dixmérie. These, together with Le Pigeon Blanc, are all Assemblage III localities.

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

Family Calliostomatidae Thiele, 1924
Subfamily Calliostomatinae Thiele, 1924
Genus *Calliostoma* Swainson, 1840

Type species (by subsequent designation, Herrmannsen, 1846) – *Trochus conulus* Linnaeus, 1758, present-day, Europe.

1840 *Calliostoma* Swainson, p. 218, 351.
1841 *Conulus* Nardo, p. 244. Type species (by tautonymy): *Trochus conulus* Linnaeus, 1758, present-day, Europe. Invalid: junior homonym of *Conulus* Leske, 1778 [Echinodermata].
1842 *Ziziphinus* Gray, p. 44, 57, 89. Type species (by subsequent designation, Rehder, 1937): *Trochus canaliculatus* (Lightfoot, 1786), present-day, eastern Pacific. *Zizyphinus* is an incorrect subsequent spelling.
1889 *Jacinthinus* Monterosato, p. 79. Type species (by subsequent designation, Pilsbry, 1890): *Trochus conulus* Linnaeus, 1758, present-day, Europe.
1890 *Ampullotrochus* Monterosato, p. 145. Type species (by subsequent designation, Crosse, 1891): *Trochus granulatus* Born, 1778, present-day, Europe.

***Calliostoma multigranum* (Wood, 1848)**
Plate 6, figs 4, 5

*1848 *Trochus multigranus* Wood, p. 127, pl. 13, fig. 3.

1878 *Trochus millegranus* Phil. – Nyst, pl. 6, fig. 3 [*non* Philippi, 1836 = *Clelandella miliaris* (Brocchi, 1814)].
1882 *Trochus multigranus* S. Wood – Nyst, p. 105.
1923 *Trochus* (*Calliostoma*) *multigranus* (S.V. Wood) – Harmer, p. 720, pl. 58, figs 12, 13.
?1923 *Trochus* (*Calliostoma*) *incertus* Harmer, p. 726, pl. 59, fig. 6.
1954 *Calliostoma multigranus* [*sic*] (Wood) – van Regteren Altena *et al*., p. 59, pl. 2, fig. 15.
1957 *Calliostoma* (*Ampullotrochus*) *multigranus* [*sic*] (Wood) – Glibert, p. 15, pl. 1, fig. 9.
1964 *Calliostoma* (*Ampullotrochus*) *multigranum* S.V. Wood, 1848 [*sic*] – Brébion, p. 100, pl. 2, figs 27, 28.
2012 *Calliostoma multigranus* [*sic*] (Wood) – Pouwer & Wesselingh, p. 163, figs 41, 42.

Material and dimensions – Maximum height 19.4 mm (incomplete), width 17.5 mm. NHMW 2015/0133/0078 (1), NHMW 2015/0133/0093 (Pl. 6, fig. 4)-0094 (Pl. 6, fig. 5). (2), NHMW 2015/0133/0079 (5); LC (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – All authors dealing with the North Sea Basin assemblages describe this species as being exceedingly rare (Harmer, 1923; Glibert, 1957; Pouwer & Wesselingh, 2012). There is quite some variation in the shells illustrated under this name; some being more elevated with a rounded base (*i.e*. Harmer, 1923, pl. 58, figs 12, 13), whilst others have a conical shell with a wider apical angle and slightly flattened base (Pouwer & Wesselingh, 2012, figs 41, 42). The strength of the beading is also variable in the figured shells. The Le Pigeon Blanc assemblage is the first to produce a relatively large number of these shells, and we can confirm that these forms intergrade as illustrated. Moreover, the adult shells reach a much greater size than any previously recorded. In the large specimens from Le Pigeon Blanc a suprasutural collar develops on the later adult whorls, not present on the early teleoconch whorls (Pl. 6, fig. 4). As all the North Sea Basin specimens illustrated to date are small, this character had not been observed. This important variability in shell shape in *Calliostoma multigranum* (Wood, 1848) approximates some of the specimens with a wider apical angle and a flatter base to *C. baccatum* (Millet, 1865), also present in the Le Pigeon Blanc assemblage, but this species has finer spiral cords, of which the infrasutural cord is more strongly developed, the beading, when present, is finer and the base is flatter with finer cords that are not beaded (see below).
Brébion (1964) noted that he had examined a specimen from the Gelasian Pleistocene of St Erth which had the same sculpture and differed only in having non-beaded cords on the base. In our material there are also some specimens in which the basal cords are not beaded, and it is likely that this species is a synonym. However, as pointed out by Brébion it is represented by a single incomplete specimen.
Brébion (1964, p. 101) recorded this species from Le Girondor and Palluau, together with Le Pigeon Blanc all Assemblage III localities, and doubtfully from Assemblage II localities of Apigné and Carcé.

Distribution – ?Upper Miocene: Messinian, Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964), Coralline Crag, England (Wood, 1848; Harmer, 1923). Upper Pliocene: Atlantic, Red Crag, England (Harmer, 1923). Pliocene (indeterminate): Belgium (Nyst, 1878, 1882; Glibert, 1959), ?The Netherlands (van Regteren Altena *et al*., 1954; Pouwer & Wesselingh, 2012). ? Lower Pleistocene: St Erth, England (Harmer, 1923).

***Calliostoma namnetense* nov sp.**
Plate 8, figs 1-5

1964 *Calliostoma dollfusi* nov. sp. Brébion, p. 85, pl. 2, fig. 4 (*nomen nudum*).
1964 *Calliostoma tenuicingulatum* nov. sp. Brébion, p. 86, pl. 2, fig. 5 (*nomen nudum*).

Type material – Holotype MNHN.F.A53411 (Pl.8, fig. 1), height 18.9 mm, maximum width 16.8 mm; paratypes 1-4 MNHN.F.A53412/1-4 (one of these Pl. 8, fig. 2); paratype 5 NHMW 2015/0133/0075 (Pl. 8, fig. 3), height 19.1 mm, maximum width 16.7 mm; paratype 6 NHMW 2015/0133/0076, height 12.9 mm (incomplete), maximum width 12.8 mm; paratype 7 NHMW 2015/0133/0090 (Pl. 8, fig. 4), height 11.4 mm, maximum width 11.0 mm; paratype 8 NHMW 2015/0133/0091 (Pl. 8. Fig. 5), height 10.7 mm, maximum width 10.7 mm.

Other material – Maximum height 27.0 mm (incomplete), with 24.1 mm. NHMW 2015/0133/0077 (6 incomplete); LC (21); FVD (50+ adults, juveniles and fragments). Type locality.

Etymology – Named after the Roman name for Nantes in the 3rd century, '*Portus Namnetum*'. *Calliostoma* gender neuter.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A medium-sized *Callisotoma* species with strongly beaded spiral cords on early teleoconch whorls, beading weakening abapically, a broad, elevated suprasutural collar bearing three cords on later teleoconch whorls and a flattened base bearing concentric cords.

Description – Shell of medium size and thickness, with regularly conical spire. Protoconch eroded. Teleoconch consisting of seven whorls. Early whorls straight-sided, later whorls developing broad, elevated suprasutural collar. Suture linear, impressed. Sculpture on first teleo-

conch whorl consisting of five coarsely beaded cords. Abapically, the two lower cords, placed above the suture, strengthen and become elevated on a rounded suprasutural collar, further widened by the appearance of a third cord above the suture. Beading weakens abapically. Last whorl angled at broad, raised peripheral carina composed of three cords, whorl profile concave above. Angulation sharp in juvenile specimens, more rounded in adults. Base flattened, imperforate, bearing about 14 concentric cords. Aperture tangential, sub-quadrangular; outer lip sharp. Columella weakly concave. Columellar callus thickened and somewhat expanded, closing umbilicus.

Discussion – *Calliostoma namnetense* nov. sp. is characterised by its sculpture consisting of five or six spiral cords, coarsely beaded on early teleoconch whorls and the prominent suprasutural collar present on the later teleoconch whorls on which run three of the spiral cords. Brébion (1964) described two similar *Calliostoma* species from the Le Pigeon Blanc locality: *C. dollfusi* (*nomen nudum*) and *C. tenuicingulatum* (*nomen nudum*). The author commented that *C. tenuicingulatum* differed in being smaller shelled, with finer, more strongly beaded spiral cords and in having a sharper peripheral carina. In our opinion, his *C. tenuicingulatum* represents subadult specimens of his *C. dollfusi*, here named *C. namnetense*. In the material at hand both forms are represented and intermediate sized shells are impossible to ascribe to one or other form. Moreover, the sculpture of the early teleoconch whorls is identical.
Some of the more elevated forms of *Calliostoma simile* (J. Sowerby, 1818) from the North Sea Basin Pliocene of Britain, Belgium and The Netherlands, such as the one illustrated by Marquet (1998, p. 35, bottom fig. A, B) are somewhat similar in shape, but differ in having a wider apical angle, more numerous axial ribs that are more finely beaded and lacking the suprasutural collar. *Calliostoma subexcavatum* (Wood, 1848) from the British Red Crag, which Glibert (1957) considered a synonym of *C. simile* and Marquet (1998) a distinct species, differs from *C. namnetense* in the same characters as *C. simile*. It differs from *C. simile* in having a smaller apical angle, similar to *C. namnetense*, and having more strongly beaded cords.
Other species bearing a suprasutural swelling are the present-day Mediterranean *C. laugieri* (Payraudeau, 1826), which is immediately separated by its smooth spiral cords, the present-day Mediterranean *C. gubbiolii* Nofroni, 1984, which has an undulating basal profile. *Callisotoma xavieri* (Dollfus, Cotter & Gomes, 1903) from the middle and upper Miocene Atlantic coasts of France southwards to Portugal differs in having the whorl profile swollen above and below the suture as opposed to just above it, as in *C. namnetense,* and in having finer cords on which the beading disappears earlier.
Brébion (1964, p. 85) also reported this species (under the name *C. dollfusi*) from Le Girondor.

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

***Calliostoma baccatum* (Millet, 1865)**
Plate 9, figs 1, 2

1854	*Trochus Baccatus* Millet, p. 157 (*nomen nudum*).
1865	*Trochus baccatus* Millet, p. 582.
*1896	*Ampullotrochus subexcavatus?* var. *tauromiliaris* Sacco, p. 43, pl. 4, fig. 39.
1949	*Calliostoma tauromiliare* Sacco, 1896 – Glibert, p. 33, pl. 3, fig. 8.
1964	*Calliostoma tauromiliare* Sacco, 1896 – Brébion, p. 75.
non 1985	*Calliostoma (Ampullotrochus) tauromiliare* (Sacco, 1896) – González Delgado, p. 60, pl. 1, figs. 13-14.
non 2003	*Calliostoma (Calliostoma) tauromiliare* (Sacco, 1896) – Landau *et al*., p. 57, pl. 15, figs 1, 2.
2015	*Calliostoma tauromiliare* (Sacco, 1896) – Harzhauser & Landau, p. 88, pl. 1, figs 10-12.

Material and dimensions – Maximum height 14.7 mm (incomplete), height 14.4 mm. NHMW 2015/0133/0161 (1, Pl. 9, fig. 1)), NHMW 2015/0133/0162 (2, one of which Pl. 9, fig. 2), NHMW 2015/0133/0097 (3 fragments); LC (30 fragments and juveniles); FVD (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – We provisionally follow Harzhauser & Landau (2015) in considering the French middle Miocene shells from the Loire Basin illustrated by Glibert (pl. 3, fig. 8) conspecific with *Calliostoma tauromiliare* (Sacco, 1896), described from the lower Miocene of Italy, although we have not seen the Italian material. This would mean that this species was widespread in the Miocene Paratethys, Proto-Mediterranean and Atlantic, where it survived into the lower Pliocene. The upper Pliocene shells from Estepona, Spain, described by Landau *et al*. (2003) as *C. tauromiliare* are not this species and differ in having fewer spiral cords on the whorls and on the base, separated by wider interspaces and do not have two prominent cords at the periphery.
Brébion (1964, p. 75) noted that *C. tauromiliare* had been named *Trochus baccatus* by Millet, but must have considered both Millet 1854 an 1866 (which is a reprint of part of Millet, 1865) *nomina nuda*, as he did not give it priority over Sacco's much later name of 1896. However, Millet (1865, p. 582) gave a valid description of this species. It would have been beneficial to retain Sacco's (1896) name *Calliostoma tauromiliare*, which has been widely used in the literature, but we cannot satisfy the requirements of Article 23.9.1.2 (ICZN 1999) to consider Millet's name a *nomen oblitum*. Therefore *Calliostoma baccatum* (Millet, 1865) must take priority over *Calliostoma tauromiliare* (Sacco, 1896).
Brébion (1964, p. 75) recorded this species from localities belonging to Assemblage I-III and commented on the great variability seen. In his description he commented that the base could be convex or flattened and the basal cords beaded or not. In the Le Pigeon Blanc population the base is always flat and the basal cords smooth. Indeed,

the Le Pigeon Blanc specimens are relatively constant in their apical angle, they have five primary spiral cords, of which the adapical cord below the suture is more strongly developed and the peripheral carina is composed of two close-set, smooth cords.

Distribution – Lower Miocene: Burdigalian, Italy (Sacco, 1896); Paratethys, Austria (Harzhauser & Landau, 2014). Middle Miocene: Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic, Tortonian, Messinian, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Calliostoma zizyphinum* (Linnaeus, 1758)**
Plate 9, fig. 3, 4

*1758	*Trochus zizyphinus* Linnaeus, p. 759.
1818	*Trochus laevigatus* J. Sowerby, p. 179, pl. 431, fig. 1.
1843	*Trochus laevigatus* Nyst, p. 379, pl. 36, fig. 2.
1843	*Trochus Sedgwicki* Nyst, p. 33, pl. 35, fig. 20.
1848	*Trochus zizyphinus* Linn. – Wood, p. 124, pl. 13, fig. 9a-c.
1848	*Trochus zizyphinus* var. *laevigatus* J. Sow. – Wood, p. 124, pl. 13, fig. 9d.
1878	*Trochus zizyphinus* L. – Nyst, pl. 6, fig. 25.
1878	*Trochus conulus* L. – Nyst, pl. 6, fig. 26 [*non Calliostoma conulus* (Linnaeus, 1758)].
1879	*Trochus zizyphinus* var. Linn. – Wood, p. 34, pl. 4, fig. 20.
1882	*Trochus zizyphinus* L. – Nyst, p. 99.
1882	*Trochus conulus* L. – Nyst, p. 101 [*non Calliostoma conulus* (Linnaeus, 1758)].
1918	*Calliostoma antwerpense* Cossmann, p. 289, pl. 9, figs 50, 51.
1923	*Trochus (Calliostoma) zizyphinus* (Linné) – Harmer, p. 708, pl. 57, figs 1, 2, 5.
1923	*Trochus (Calliostoma) zizyphinus* var. *laevigata* (J. Sowerby) – Harmer, p. 709, pl. 57, fig. 6.
1923	*Trochus (Calliostoma) zizyphinus* var. *dilatata* (Monterosato), fide B., D. & D. – Harmer, p. 710, pl. 57, fig. 3.
1923	*Trochus (Calliostoma) zizyphinus* var. *strangulata* Bucquoy, Datutzenberg et Dollfus – Harmer, p. 711, pl. 57, fig. 4.
1923	*Trochus (Calliostoma) conulus* (Linné) – Harmer, p. 735, pl. 58, fig. 6 [*non Calliostoma conulus* (Linnaeus, 1758)].
1954	*Calliostoma zizyphinum zizyphinum* (Linnaeus, 1758) – van Regteren Altena *et al*., p. 9, pl. 2, fig. 13b.
1957	*Calliostoma (Calliostoma) zizyphinum* Linné, 1758 – Glibert, p. 11, pl. 1, fig. 6.
1977	*Calliostoma zizyphinum* (Linnaeus, 1758) – Fretter & Graham, p. 74, figs 54-56.
1994	*Calliostoma (Calliostoma) zizyphinum* (Linné, 1758) – Giannuzzi-Savelli *et al*., p. 66, figs. 158-168.
1995	*Calliostoma (Calliostoma) zizyphinum* (Linnaeus, 1758) – Marquet, p. 64, pl. 3, fig. 2.
1998	*Calliostoma (Calliostoma) zizyphinum* (Linnaeus, 1758) – Marquet, p. 34, fig. 11.
2014	*Calliostoma zizyphinum* (Linné, 1758) – Pouwer & Wesselingh, p. 160, figs 31, 32.

Material and dimensions – Maximum height 11.8 mm (incomplete), width 10.8 mm. NHMW 2015/0133/0096 (1, Pl. 9, fi. 3)); LC (5 juveniles and fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – The few Le Pigeon Blanc specimens at hand are small, but agree with the many illustrations of the smoother sculptured forms of *Calliostoma zizyphinum* (Linnaeus, 1758) (*i.e*. Harmer, 1923, pl. 57, figs 1, 6, pl. 58, fig. 6; Giannuzzi-Savelli *et al*., 1994, fig. 163). It is similar to some forms of the middle Miocene *C. vibrayanum* (Dollfus & Dautzenberg, 1886) from the Loire Basin of France, but this species has a stronger peripheral keel and a smooth base. Some specimens of *C. conulus* are also similar, but *C. zizyphinum* has a wider apical angle and stronger beading on the early teleoconch whorls. We have not been able to find any fossil references for the species in the Mediterranean.

Distribution – Lower Pliocene: Atlantic, Coralline Crag, England (Wood, 1848, 1879; Harmer, 1923); Kattendijk Formation, Belgium (Marquet, 1998), NW France (this paper). Upper Pliocene: Atlantic, Red Crag, England (Wood, 1848; Harmer, 1923); Oorderen Sands, Belgium (Glibert, 1957). Pliocene (indeterminate): The Netherlands (van Regteren Altena *et al*., 1954; Pouwer & Wesselingh, 2014). Pleistocene: Atlantic, St Erth, England (Harmer, 1923). Present-day: Atlantic, North Sea to Canaries, Azores and into Mediterranean, rock bottoms between 8-300m (Fretter & Graham, 1977).

***Calliostoma* cf. *multistriatum* (Wood, 1886)**
Plate 9, fig. 5

cf. *1886	*Trochus multistriatus* Wood, *in* Kendall & Bell, p. 211.
cf. 1923	*Trochus* (*Calliostoma*) *multistriatus* (S.V. Wood) [*sic*] – Harmer, p. 727, pl. 59, fig. 7.

Material and dimensions – NHMW 2015/0133/0092 (1, Pl. 9, fig. 5), height 5.6 mm, maximum width 8.0 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Description – Shell small, trochiform, strongly depressed. Protoconch eroded. Teleoconch consisting of 4.5 strongly depressed, weakly convex whorls, with periphery at abapical suture. Suture linear, impressed. Spire whorls bearing seven flattened, narrow cords separated by grooves; the adapical two cords slightly wider. Early whorls finely beaded; beading weakens abapically, disappears on third teleoconch whorl. Last whorl strongly depressed, acutely angled at periphery, bearing seven cords; the seventh pe-

ripheral cord wider. Base flattened, imperforate, bearing 17 irregular concentric cords widening towards centre. Aperture tangential, sub-quadrangular; outer lip sharp. Columella smooth, weakly concave, leaning abaxially. Columellar callus somewhat thickened closing umbilicus.

Discussion – At first glance this strongly depressed shell resembles *Gibbula umbilicaris* (Linnaeus, 1758), but it differs in lacking a columellar denticle and having an imperforate base, characters that place it in the genus *Calliostoma* Swainson, 1840 rather than *Gibbula* Risso, 1826. Only one known species resembles this shell: *Calliostoma multistriatum* (Wood, *in* Kendall & Bell, 1886) from the Gelasian Pleistocene of St. Erth, England. Although Harmer (1923, p. 797) commented that the species was not rare at St. Erth, the only specimen illustrated (1923, pl. 59, fig. 7) differs from the French shell in having finer spiral sculpture. We await further material from Le Pigeon Blanc to ascertain the intraspecific variability.

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

***Calliostoma* sp.**
Plate 9, fig. 6

Material and dimensions – NHMW 2015/0133/0163 (1, Pl. 9, fig. 6), height 7.4 mm, maximum width 8.3 mm. Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Description – Shell small (incomplete; apical whorls preserved), with coeloconoid conical spire. Protoconch eroded. Four teleoconch whorls preserved; surface eroded on first two. Sculpture on third teleoconch whorl consisting of a strongly developed adapical cord, placed a short distance below suture, an even stronger abapical cord, placed immediately above suture, with two weaker cords intercalated, the adapical one strongest. Last whorl acutely angled at periphery, sculptured as above, abapical cord extremely elevated, rounded, obscurely bifid, forming carina. Base imperforate, flattened, bearing narrow cords and prominent, close-set prosocline growth lines.

Discussion – It is regrettable that we have insufficient material to formally describe this species, as the apical fragment at hand suggests a sculpture quite unlike that of any known European *Calliostoma* species. It shares some similarity with *Calliostoma vibrayanum* (Dollfus & Dautzenberg, 1886) from the middle Miocene Loire Basin of France, which also has four spiral cords per whorl with the cords bordering the suture more strongly developed, but even in the most strongly sculptured specimen illustrated by Glibert (1949, pl. 2, fig. 4d) the cords are nowhere near as strong as in the shell from Le Pigeon Blanc.

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

Family Solariellidae Powell, 1951
Genus *Microgaza* Dall, 1881

Type species (by monotypy) – *Callogaza* (*Microgaza*) *rotella* Dall, 1881, present-day, Barbados.

1881 *Microgaza* Dall, p. 50.

Note – We include in this genus a group of European Neogene fossil species often placed in the literature within the genus *Margarites* Gray, 1847. However, the type species of this genus, *M. diaphana* Gray, 1847 [*Margarites helicinus* (Phipps, 1774)] is a present-day circumboreal species and is quite unlike the shells here included in *Microgaza* Dall, 1881. The Caribbean type species of *Microgaza*, *M. rotella* (Dall, 1881) is closely similar to the group of European species here considered congeneric, especially the new species described below.

***Microgaza landreauensis* nov. sp.**
Plate 9, fig. 7

1964 *Margarites peneui* nov. sp. Brébion, p. 72, pl. 1, fig. 18 (*nomen nudum*).

Type material –Holotype MNHN.F.A57389 (Pl. 9, fig. 7), height 5.9 mm, maximum diameter 8.0 mm; paratype 1 NHMW 2015/0133/0101, height 5.5 mm, maximum diameter 7.1 mm; paratype 2 NHMW 2015/0133/0100, height 5.6 mm, maximum diameter 7.4 mm.

Other material – Maximum diameter 9.2 mm. NHMW 2015/0133/0102 (14); LC (50+). Type locality.

Etymology – Named after the type locality Le Landreau. *Microgaza* gender feminine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – An average-sized *Microgaza* species with relatively strong spiral sculpture on early teleoconch whorls, fine, close-set spiral threads on the last whorl, axial sculpture much reduced to growth lines, subsutural cord and peripheral keel absent, and a deep, wide umbilicus bearing spiral cords within.

Description – Shell small, fragile, low-trochiform, polished, with a depressed spire. Protoconch consisting of 1.25 smooth convex whorls, with large nucleus. Teleoconch consisting of approximately 4.5 moderately depressed convex whorls. Suture linear, impressed. Early teleoconch whorls bearing four narrow spiral cords, increasing in number and weakening abapically. Axial sculpture restricted to fine, prosocline growth lines, most prominent on early teleoconch whorls. Spire whorls bearing narrow subsutural platform, which becomes poorly

delimited on penultimate whorl. Last whorl strongly convex, subsutural platform obsolete, or almost so, rounded at periphery, bearing fine, close-set spiral threads. Aperture tangential, peristome almost complete, outer lip not thickened. Base convex, devoid of sculpture, except growth lines, weakly pleated at moderately angular umbilical margin. Umbilicus broad, deep, bearing spiral cords within.

Discussion – We were unable to locate Brébion's 'type' for *Margarites peneui nomen nudum*, said to be deposited in the Institut Catholique d'Angers (Angers). *Microgaza landreauensis* nov. sp. is most similar to *M. taurinensis* (Sacco, 1896) from the Burdigalian lower Miocene of Italy, but this species lacks spiral cords on the early teleoconch whorls, has a narrow, but well defined subsutural cord, absent in *M. landreauensis*, and has the periphery placed lower on the last whorl, giving the shell a somewhat different profile. The same differences separate the French species from *M.* cf. *taurinensis* in Landau *et al*. (2003, pl. 16, fig. 1) from the lower Piacenzian of Estepona, but this species also has a slightly narrower umbilicus that is sharp-edged. *Microgaza cuadrae* (Lévy & Bergeron, 1896) and *M. fischeri* (Lévy & Bergeron, 1896), also both from the Estepona assemblages, differ in having a pearled subsutural cord and a sharply angled periphery. *Microgaza pontileviensis* Cossmann, 1918 from the Langhian French Atlantic Loire Basin is smaller-shelled, has a well-delimited, narrow, beaded sutural ramp or cord that continues to the aperture, but otherwise the whorl surface is smooth, and a narrower umbilicus. *Margarites trochoideus* Wood, 1848 and *Eumargarita bellii* Harmer, 1923 from the lower Pliocene Coralline Crag of England (Wood, 1848; Harmer, 1923) and the Kattendijk Formation of Belgium (Marquet, 1998) are generally similar in shape and also have spiral sculpture on the spire whorls, but both lack a sutural ramp and have a rounded umbilical edge. We are unsure of the generic attribution of these species. They may also belong within *Microgaza*, although all the species included above have a sutural ramp or cord and a more or less angular umbilical edge.
Microgaza landreauensis was reported by Brébion, 1964) only from Le Pigeon Blanc.

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

Family Skeneidae Clark, 1851
Genus *Dikoleps* Høisaeter, 1968

Type species (by original designation) – *Margarita pusilla* Jeffreys, 1847 [= *Dikoleps nitens* (Philippi, 1844)], present-day, British Isles.

1968 *Dikoleps* Høisaeter, 1968, p. 47.

***Dikoleps cutleriana* (Clark, 1849)**
Plate 10, fig. 1

*1849 *Skenea Cutleriana* Clark, p. 424.
1977 *Skenea cutleriana* Clark, 1849 – Fretter & Graham, p. 86, figs 64, 65.
1984 *Dikoleps cutleriana* (Clark, 1849) – van Aartsen *et al*., p. 12, fig. 042.
1994 *Dikoleps cutleriana* (Clark, 1848) [*sic*] – Giannuzzi-Savelli *et al*., p. 106, fig. 353.
2006 *Dikoleps cutleriana* (Clark, 1848) [*sic*] – Marquet & Landau, p. 21, fig. 4/2a-g.

Material and dimensions – Maximum height 1.2 mm, maximum width 1.4 mm. NHMW 2015/0133/0185 (1), NHMW 2015/0133/0186 (1, Pl. 10, fig. 1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Somewhat variable in height, the specimens from Le Pigeon Blanc are very similar to that illustrated by Marquet & Landau (2006, fig. 4/2a-g) from the lower Pliocene of Doel, Belgium.

Distribution – Lower Pliocene: NW France (this paper); Luchtbal Sand, Belgium (Marquet & Landau, 2006). Present-day: Atlantic, SW England (Fretter & Graham, 1977) southwards into Mediterranean, Corsica (van Aartsen *et al*., 1984).

Superfamily Seguenzioidea Verrill, 1884
Family Seguenzioidea [unassigned]
Genus *Moelleriopsis* Bush, 1897

Type species (by monotypy) – *Moelleriopsis abyssicola* Bush, 1897, present-day, NE United States. Original spelling *Mölleriopsis*.

1897 *Moelleriopsis* Bush, p. 137.
1961 *Abyssogyra* Clarke, p. 352. Type species (by original designation): *Abyssogyra vemae* Clarke, 1961, present-day, southern Atlantic.

***Moelleriopsis messanensis* (Seguenza, 1876)**
Plate 10, figs 2, 3

*1876 *Cyclostrema messanensis* Seguenza, p. 188.
1986 *Cyclostrema normanni* Dautzenberg & Fischer, 1897 – Di Geronimo & Bellagamba, pl. 2, figs 3-5 [*non Moelleriopsis normani* (Dautzenberg & H. Fischer, 1897)].
1992 *Moelleriopsis messanensis* (Seguenza, 1876) – Warén, p. 174, figs 26D, 31B-D.
1994 *Moelleriopsis messanensis* (Seguenza, 1876) – Giannuzzi-Savelli *et al*., p. 108, fig. 361.

Material and dimensions – Maximum height 1.5 mm, maximum width 1.9 mm. NHMW 2015/0133/0182 (Pl. 10, fig. 2), NHMW 2015/0133/0183 (Pl. 10, fig. 3), NHMW 2015/0133/0184 (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire Atlantique department, NW France.

Discussion – Moelleriopsis messanensis (Seguenza, 1876) is characterised by having four cords or keels within the umbilicus, which separate it from the extant *Moelleriopsis normani* (Dautzenberg & H. Fischer, 1897), which is flatter and has only two spiral ribs in the umbilicus.
At Le Pigeon Blanc this species is common. Subadult specimens have well developed cords within the umbilicus. In larger gerontic specimens the umbilical keels weaken to become subobsolete in some specimens and the apertural quarter of the last whorls tends to become disjunct.
We have specimens at hand from the Assemblage I localities (Reneauleau, Brigné) as well as Assemblage III (Le Pigeon Blanc).
Moelleriopsis ruggierensis Tabanelli, 1991 from the Pliocene of Italy is a distinct species. Comparison with specimens from Ceparano, Italy (NHMW coll.) kindly sent to us by Cesare Tabanelli show the shell to be less depressed than *M. messanensis*, the suture is deeper, marked by a well-developed cord, the umbilical edge is sharper and the aperture relatively broader.

Distribution – Upper Miocene: Tortonian, NW France (NHMW coll.). Lower Pliocene: NW France (this paper). Pleistocene: central Mediterranean, Italy (Seguenza, 1876). Present-day: Atlantic, Bay of Biscay, western and central Mediterranean (Warén, 1992).

Discussion

In this paper we record three patelligastropod species, of which one is left in open nomenclature, representing one genus, and 28 vetigastropod species, of which two are left in open nomenclature, representing 11 genera (Fig. 2). Eleven species are described as new: *Emarginula brebioni* nov. sp., *Jujubinus armatus* nov. sp., *Jujubinus pigeonblancensis* nov. sp., *Jujubinus condevicnumensis* nov. sp., *Jujubinus ligeriensis* nov. sp., *Gibbula provosti* nov. sp., *Gibbula milleti* nov. sp., *Colliculus neraudeaui* nov. sp., ?*Tectus columbinus* nov. sp., *Calliostoma namnetense* nov. sp., *Microgaza landreauensis* nov. sp.
The Patellogastropoda are poorly represented in the Le Pigeon Blanc assemblage both in species and numbers of specimens, however, the presence of *Patella pellucida* Linnaeus, 1758, a cooler water species in the subtropical lower Pliocene of NW France, suggests that upwelling of cooler nutrient-rich waters may have been present.
Of the 28 vetigastropod species here recorded, eleven (39%) occur exclusively in northwestern French Zanclean deposits and are therefore highly restricted stratigraphically and geographically. Stratigraphically, six (21%) of the species found at Le Pigeon Blanc are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1949) and are also present in the Assemblage I (sensu Van Dingenen *et al*., 2015) of northwestern France [*Diodora graeca* (Linnaeus, 1758), *Emarginula dujardini* Dollfus & Dautzenberg, 1886, *Emarginula fissura* Linnaeus, 1758, *Clanculus (Clanculopsis) baccatus* (Defrance, 1824), *Paroxystele turoniensis* (Glibert, 1949); *Calliostoma baccatum* (Millet, 1865)]. Six species (21%) are also found in the North Sea Basin Pliocene [*Diodora graeca* (Linnaeus, 1758), *Emarginula fissura* Linnaeus, 1758, *Jujubinus striatus* (Linnaeus, 1758), *Gibbula tricarinifera* (Wood, 1842), *Calliostoma multigranum* (Wood, 1848), *Calliostoma zizyphinum* (Linnaeus, 1758)]. Six species (21%) are relatively cosmopolitan in the European Pliocene, found in the Atlantic and Mediterranean [*Diodora graeca* (Linnaeus, 1758), *Emarginula fissura* Linnaeus, 1758, *Emarginula octaviana* Coen, 1939, *Jujubinus striatus* (Linnaeus, 1758), *Gibbula magus* (Linnaeus, 1758), *Bolma rugosa* (Linné, 1767), *Calliostoma baccatum* (Millet, 1865)].
At genus level, most of the taxa are still found today off the coast of northwestern France. The genera *Clanculus* (*Clanculopsis*) Monterosato, 1880 and *Bolma* Risso, 1826 are still found in European waters, but with a more southern distribution, with their present-day northernmost occurences recorded along the west coast of Portugal. The genus *Paroxystele* Schultz, 1969 is now extinct, but was widespread in the Neogene of Europe. Again, this is the most northern record for the genus in the Neogene. The genus *Microgaza* Dall, 1881 is not found today in the Northeastern Atlantic, nor in the Mediterranean, but in the Caribbean. It seems to have been relatively widespread in the European Miocene and has been recorded from the lower upper Pliocene of Estepona (Landau *et al*., 2003). The biggest surprise is the possible presence of the genus *Tectus* de Montfort, 1810 in the Le Pigeon Blanc assemblage. *Tectus* is a thermophilic genus found today in Indo-Pacific waters. If this generic attribution is correct, this is the first post-lower Miocene European record of the genus, leaving a stratigraphic gap between the Burdigalian lower Miocene of the Aquitaine Basin of southwestern France and the Zanclean lower Pliocene of Le Pigeon Blanc. However, this is not the only turbinid genus with a relatively old geological record to turn up unexpectedly in the European Pliocene (see Landau & Lozouet, 2003).
Based on the gastropods revised in this paper, we find a relatively endemic assemblage in the Zanclean lower Pliocene of northwestern France, with small and equal influences from both northern and southern seas. The faunal composition suggests that average Sea Surface Temperatures may have been slightly warmer than they are at these latitudes today, possibly similar to those found off the southern Portuguese coasts today. This would fit with the palaeobiogeographic model suggested by Silva & Landau (2006), as the Le Pigeon Blanc region in northwestern France would lie either at the northernmost boundary of the Pliocene subtropical French-Iberian Province, or in the transition zone between this biogeographical province and the warm temperate Boreal-Celtic Province to the north. At present this is a preliminary hypothesis we hope to flesh out as the study of this assemblage progresses.

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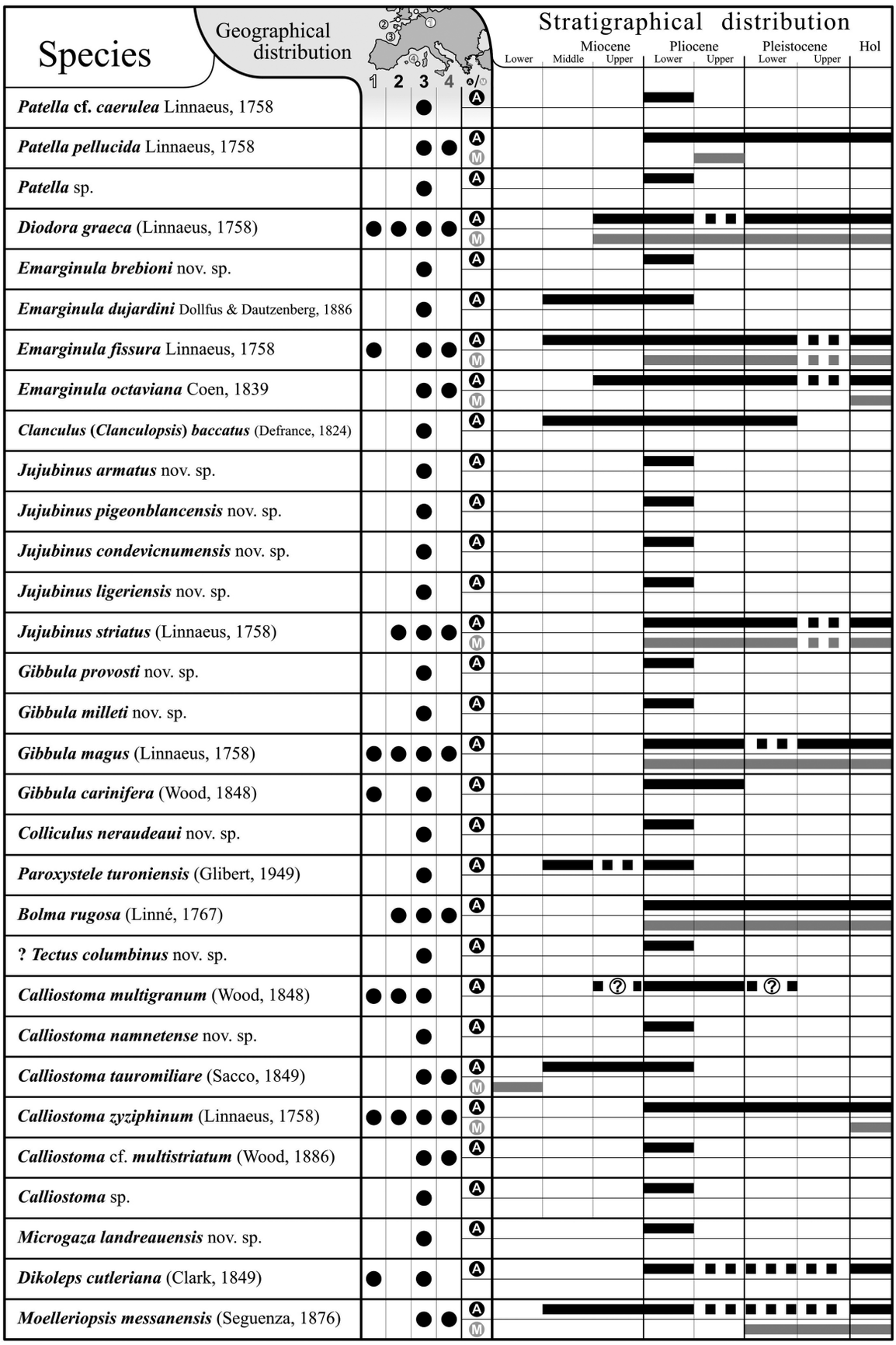

Figure 2. Geography, stratigraphy and distribution of species found in the Pliocene of Le Pigeon Blanc. For geographic distribution 1 = Mediterranean, 2 = NW France, 3 = Atlantic coasts British Isles, 4 = North Sea Basin. For stratigraphic distribution black signified Atlantic distribution (A), grey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

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Plate 1

1. *Patella* cf. *caerulea* Linnaeus, 1758, diameter 12.6 x 10.2 mm; height 2.8 mm (LC coll.).
2. *Patella pellucida* Linnaeus, 1758, NHMW 2015/0133/0403, maximum diameter 6.0 mm (incomplete).
3. *Patella* sp., NMHW2015/0133/0164, maximum diameter 23.6 mm.
4. *Patella* sp., NMHW2015/0133/0165, maximum diameter 29.7 mm.
5. *Diodora graeca* (Linnaeus, 1758), NHMW 2015/0133/0050, maximum diameter 15.3 mm, height 7.0 mm.
6. *Diodora graeca* (Linnaeus, 1758) form *apertura* Montagu, 1803, maximum diameter 25.0 mm, height 9.0 mm (LC coll.).
7. *Emarginula brebioni* nov. sp., holotype MNHN.F.A53407, maximum diameter 6.5 mm, height 3.1 mm; 6c frontal view to illustrate selenizone, Le Girondor, Boufféré, Vendée department, NW France. (photo Gaëlle Doitteau).
8. *Emarginula brebioni* nov. sp., paratype 10 NHMW 2015/0133/0054, maximum diameter 10.1 mm, height 6.5 mm; 7c shell rotated posteriorly to illustrate selenizone.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene unless stated.

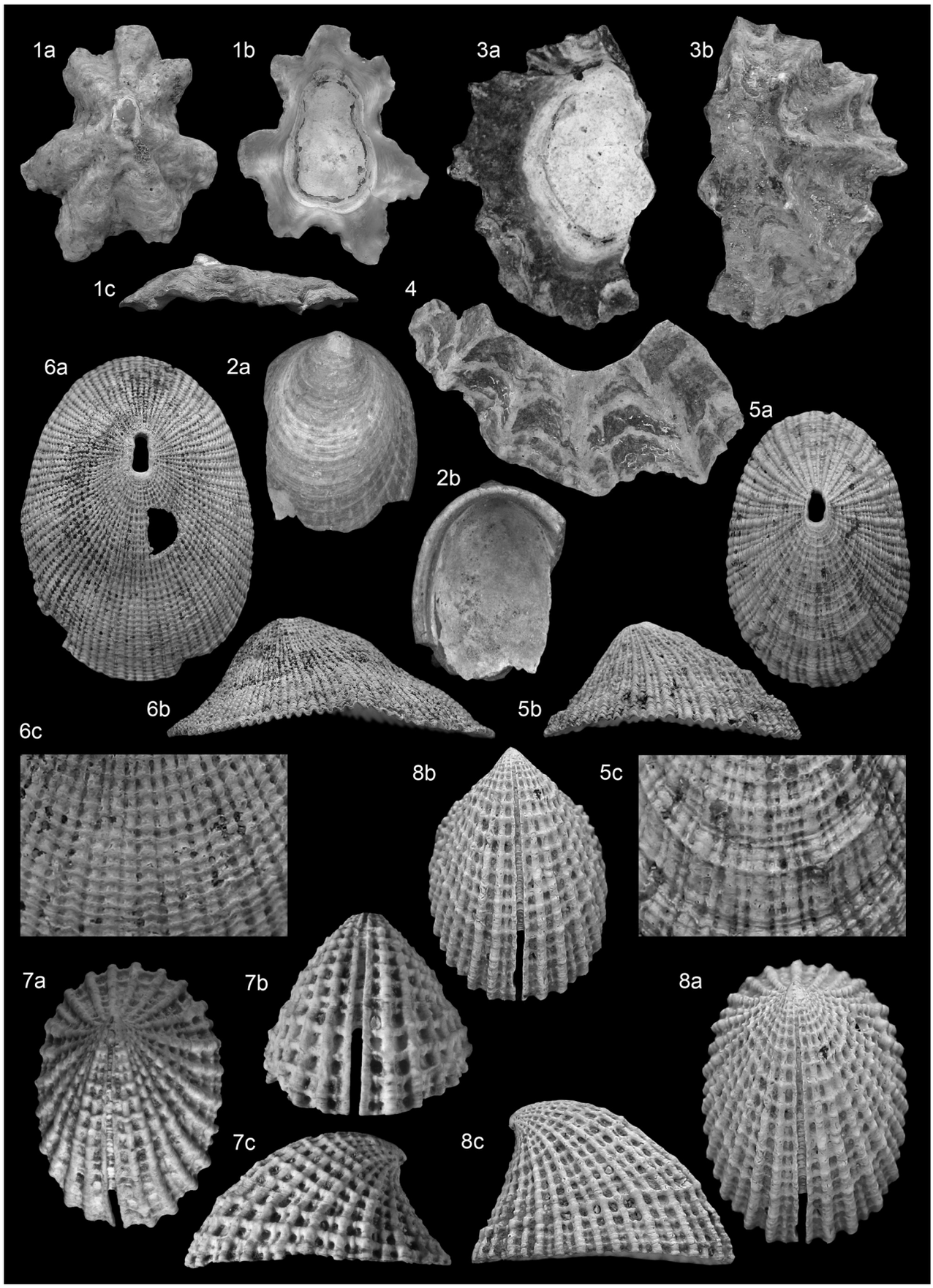

Plate 1

Plate 2

1. *Emarginula dujardini* Dollfus & Dautzenberg, 1886, NHMW 2015/0133/0166, diameter 18.3 mm x 12.6 mm, height 6.2 mm.
2. *Emarginula fissura* Linnaeus, 1758, NHMW 2015/0133/0053, maximum diameter 8.6 mm, height 5.8 mm; 2c shell rotated posteriorly to illustrate selenizone.
3. *Emarginula octaviana* Coen, 1839, NHMW 2015/0133/0167, diameter 12.0 mm x 8.0 mm, height 4.4 mm.
4. *Clanculus (Clanculopsis) baccatus* (Defrance, 1824), NHMW 2015/0133/0055, maximum diameter 8.0 mm, height 7.0 mm.
5. *Jujubinus armatus* nov. sp., holotype MNHN.F.A53413, maximum diameter 7.5 mm, height 10.3 mm (photo Gaëlle Doitteau; project E-Recolnat, MNHN, Paris).
6. *Jujubinus armatus* nov. sp., paratype 1 MNHN.F.A53414/1, maximum diameter 7.7 mm, height 10.4 mm (photo Gaëlle Doitteau; project E-Recolnat, MNHN, Paris).
7. *Jujubinus armatus* nov. sp., paratype 2 MNHN.F.A53414/2, maximum diameter 6.0 mm, height 7.2 mm (photo Gaëlle Doitteau; project E-Recolnat, MNHN, Paris).

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

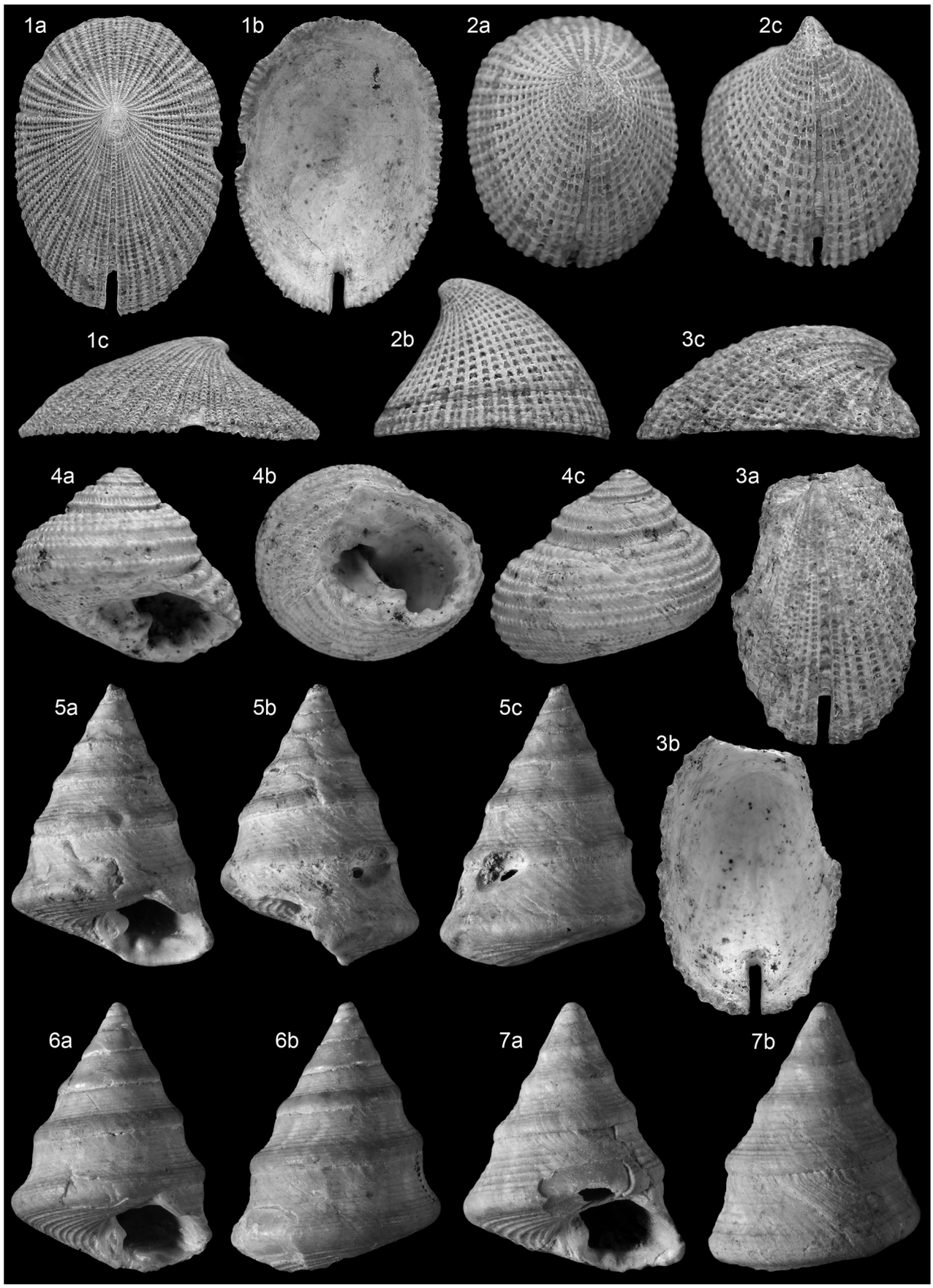

Plate 2

Plate 3

1. *Jujubinus armatus* nov. sp., paratype 1 NHMW 2015/0133/0057, maximum diameter 7.0 mm, height 9.7 mm.
2. *Jujubinus pigeonblancensis* nov. sp., holotype MNHN.F.A53409, height 7.1 mm, maximum width 6.4 mm (photo Gaëlle Doitteau).
3. *Jujubinus pigeonblancensis* nov. sp., paratype 1 MNHN.F.A53410, height 7.2 mm, maximum width 6.6 mm (photo Gaëlle Doitteau).
4. *Jujubinus pigeonblancensis* nov. sp., paratype 2 NHMW 2015/0133/0080, height 7.1 mm, maximum width 7.4 mm.
5. *Jujubinus condevicnumensis* nov. sp., paratype 2 NHMW 2015/0133/0085, maximum diameter 6.6 mm, height 6.8 mm.
6. *Jujubinus condevicnumensis* nov. sp., paratype 3 NHMW 2015/0133/0086, maximum diameter 5.5 mm, height 5.5 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

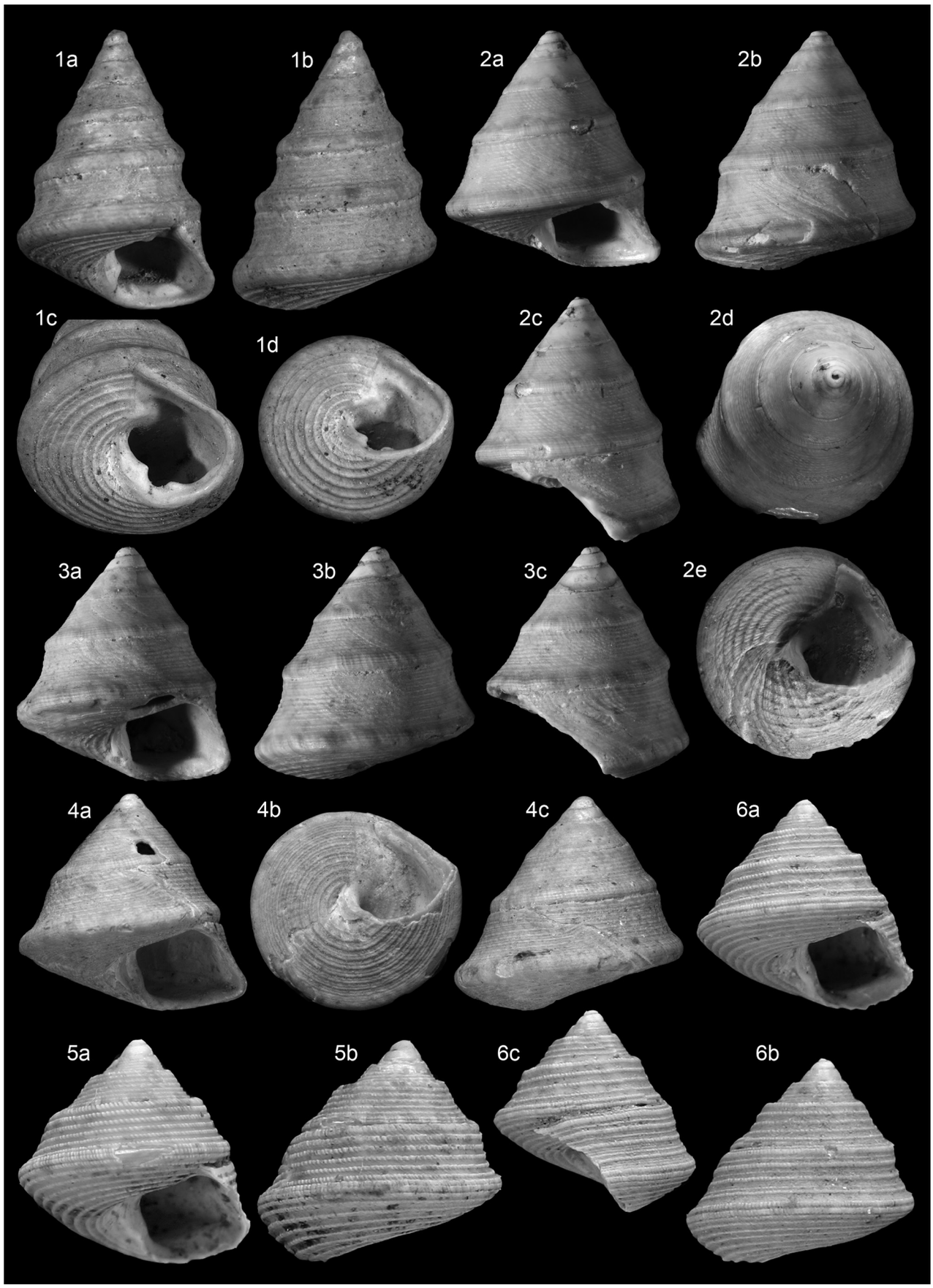

Plate 3

Plate 4

1. *Jujubinus condevicnumensis* nov. sp., holotype MNHN.F.A57386, maximum diameter 5.8 mm, height 6.3 mm.
2. *Jujubinus ligeriensis* nov. sp., holotype MNHN.F.A57387, maximum diameter 5.6 mm, height 6.0 mm.
3. *Jujubinus ligeriensis* nov. sp., paratype 1 NHMW 2015/0133/0062, maximum diameter 6.2 mm, height 7.1 mm.
4. *Jujubinus ligeriensis* nov. sp., paratype 2 NHMW 2015/0133/0064, maximum diameter 6.4 mm, height 7.4 mm.
5. *Jujubinus striatus* (Linnaeus, 1758), NHMW 2015/0133/0156, maximum diameter 6.7 mm, height 5.9 mm.
6. *Gibbula provosti* nov. sp., holotype MNHN.F.A53415, maximum diameter 8.7 mm, height 6.8 mm (photo Gaëlle Doitteau).

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

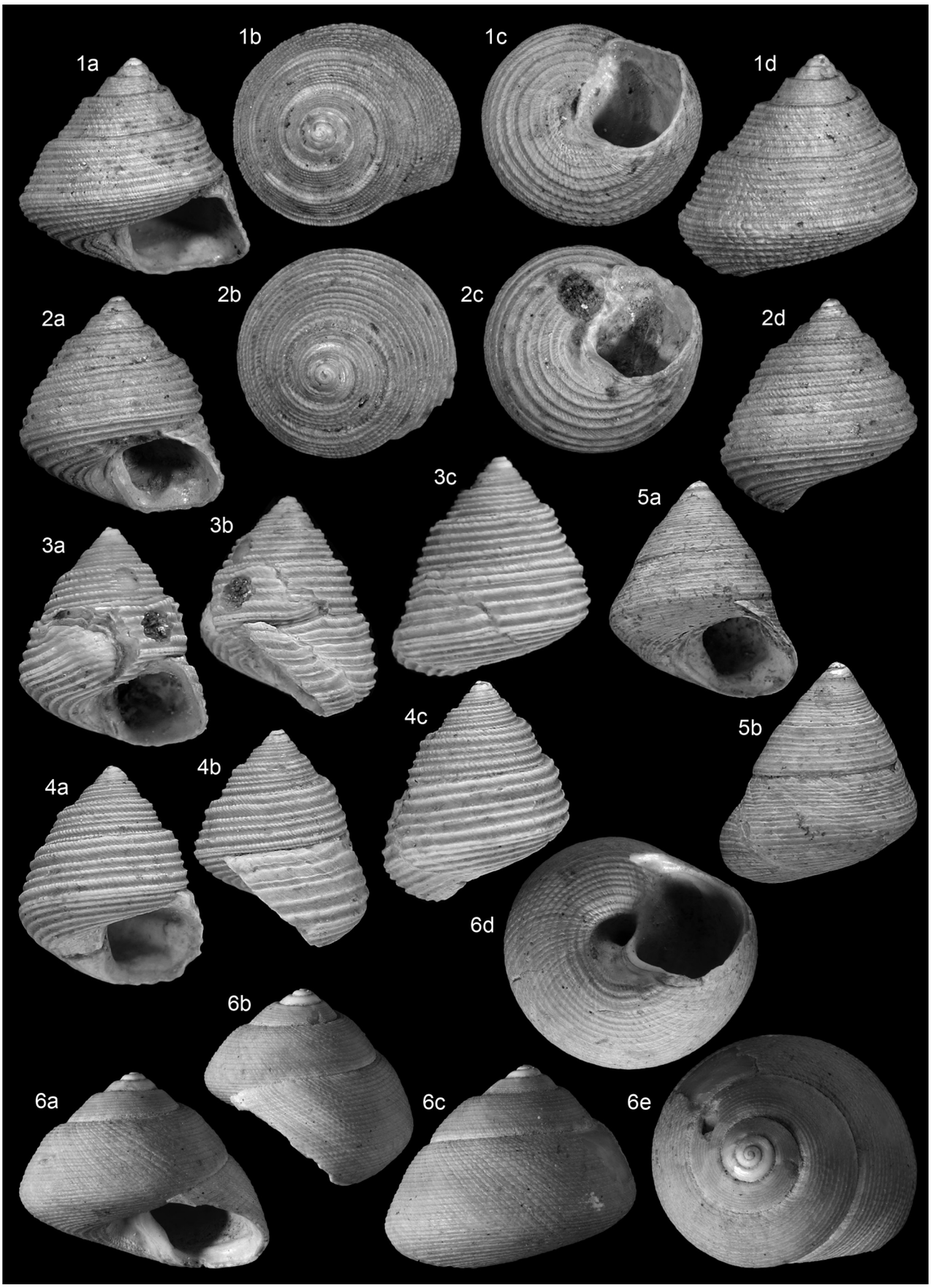

Plate 4

Plate 5

1. *Gibbula provosti* nov. sp., paratype 3 NHMW 2015/0133/0068, maximum diameter 7.3 mm, height 6.8 mm.
2. *Gibbula milleti* nov. sp., holotype MNHN.F.A57388, maximum diameter 6.8 mm, height 5.5 mm.
3. *Gibbula milleti* nov. sp., paratype 3 NHMW 2015/0133/0171, maximum diameter 6.8 mm, height 5.5 mm.
4. *Gibbula magus* (Linnaeus, 1758), NHMW 2015/0133/0065, maximum diameter 15.5 mm, height 15.3 mm.
5. *Gibbula magus* (Linnaeus, 1758), NHMW 2015/0133/0154, maximum diameter 12.2 mm, height 14.7 mm.
6. *Gibbula carinifera* (Wood, 1848), NHMW 2015/0133/0067, maximum diameter 6.0 mm, height 5.7 mm.
7. *Gibbula carinifera* (Wood, 1848), NHMW 2015/0133/0404, maximum diameter 9.4 mm, height 10.2 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

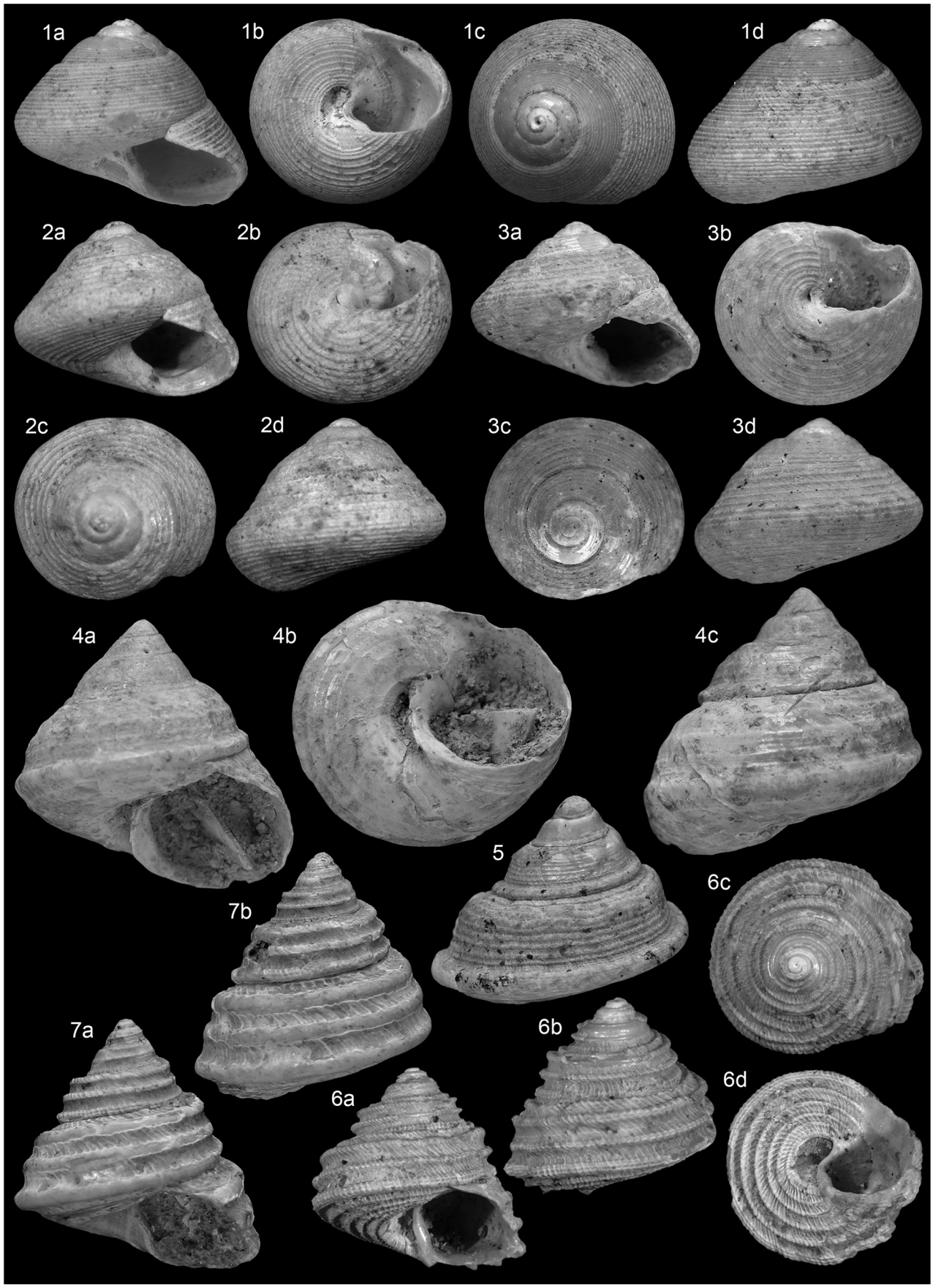

Plate 5

Plate 6

1. *Colliculus neraudeaui* nov.sp., holotype NHMW 2015/0133/0168, maximum diameter 10.2 mm, height 7.2 mm.
2. *Paroxystele turoniensis* (Glibert, 1949), NHMW 2015/0133/0169, height 18.1 mm, width 27.0 mm.
3. *Bolma rugosa* (Linné, 1767), NHMW 2015/0133/0170, height 44.6 mm, maximum diameter 55.6 mm.
4. *Calliostoma multigranum* (Wood, 1848), NHMW 2015/0133/0093, height 21.0 mm, maximum diameter 15.5 mm.
5. *Calliostoma multigranum* (Wood, 1848), NHMW 2015/0133/0094, height 10.8 mm, maximum diameter 9.0 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

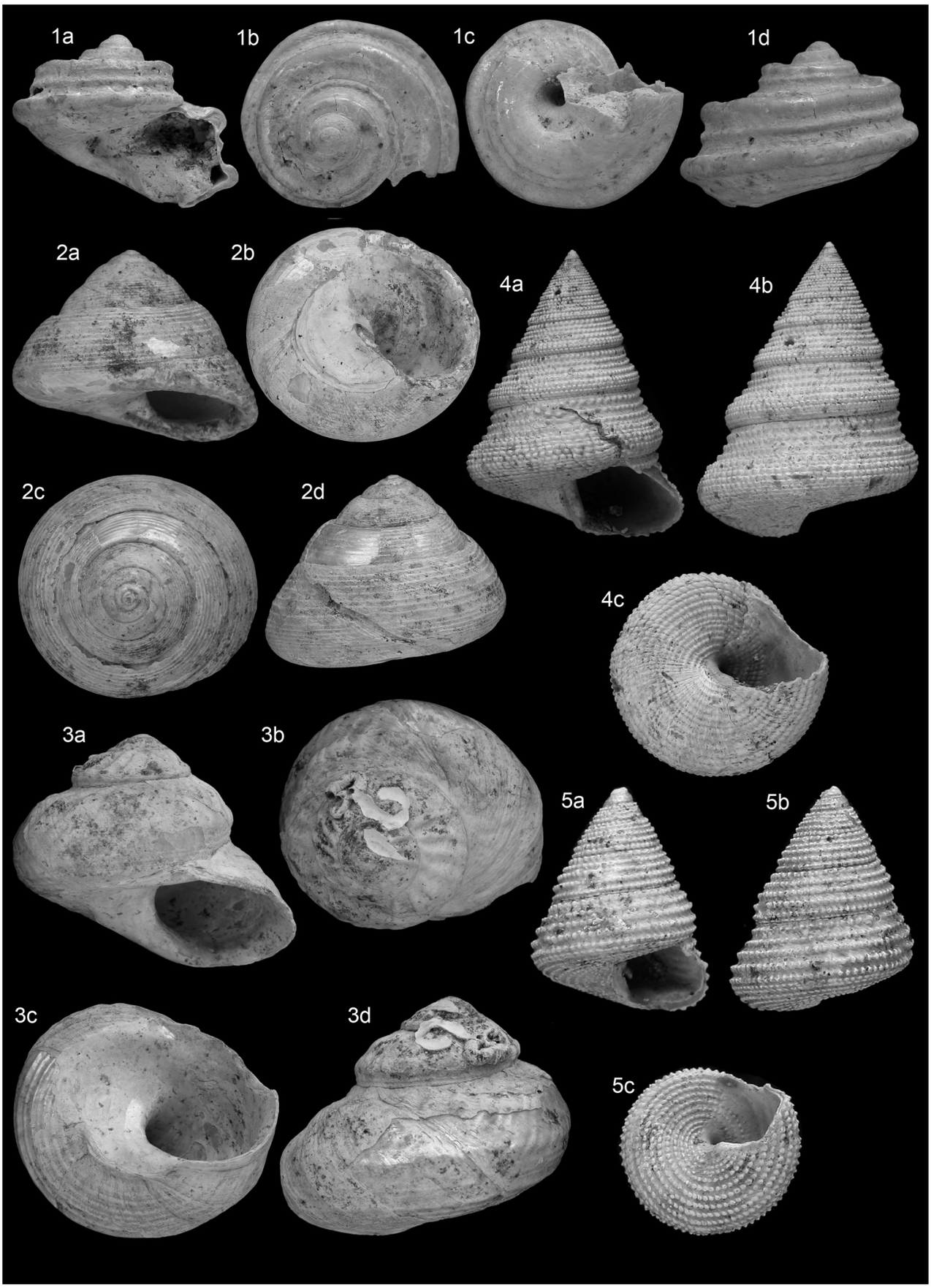

Plate 6

Plate 7

1. ?*Tectus columbinus* nov. sp., paratype 1 NHMW 2015/0133/0088, height 25.5 mm (incomplete), maximum width 23.4 mm.
2. ?*Tectus columbinus* nov. sp., paratype 2 NHMW 2015/0133/0089, height 29.0 mm (incomplete), maximum width 24.8 mm.
3. ?*Tectus columbinus* nov. sp., paratype 3 NHMW 2015/0133/0160, height 16.2 mm, maximum width 12.7 mm (juvenile).
4. ?*Tectus columbinus* nov. sp., holotype MHNN.P.020684, height 7.9 mm, maximum width 8.2 mm (photo Gérard Beaulieu; MHNN, Nantes).
5. ?*Tectus columbinus* nov. sp., FVD coll., height 27.3 mm, maximum width 24.1 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

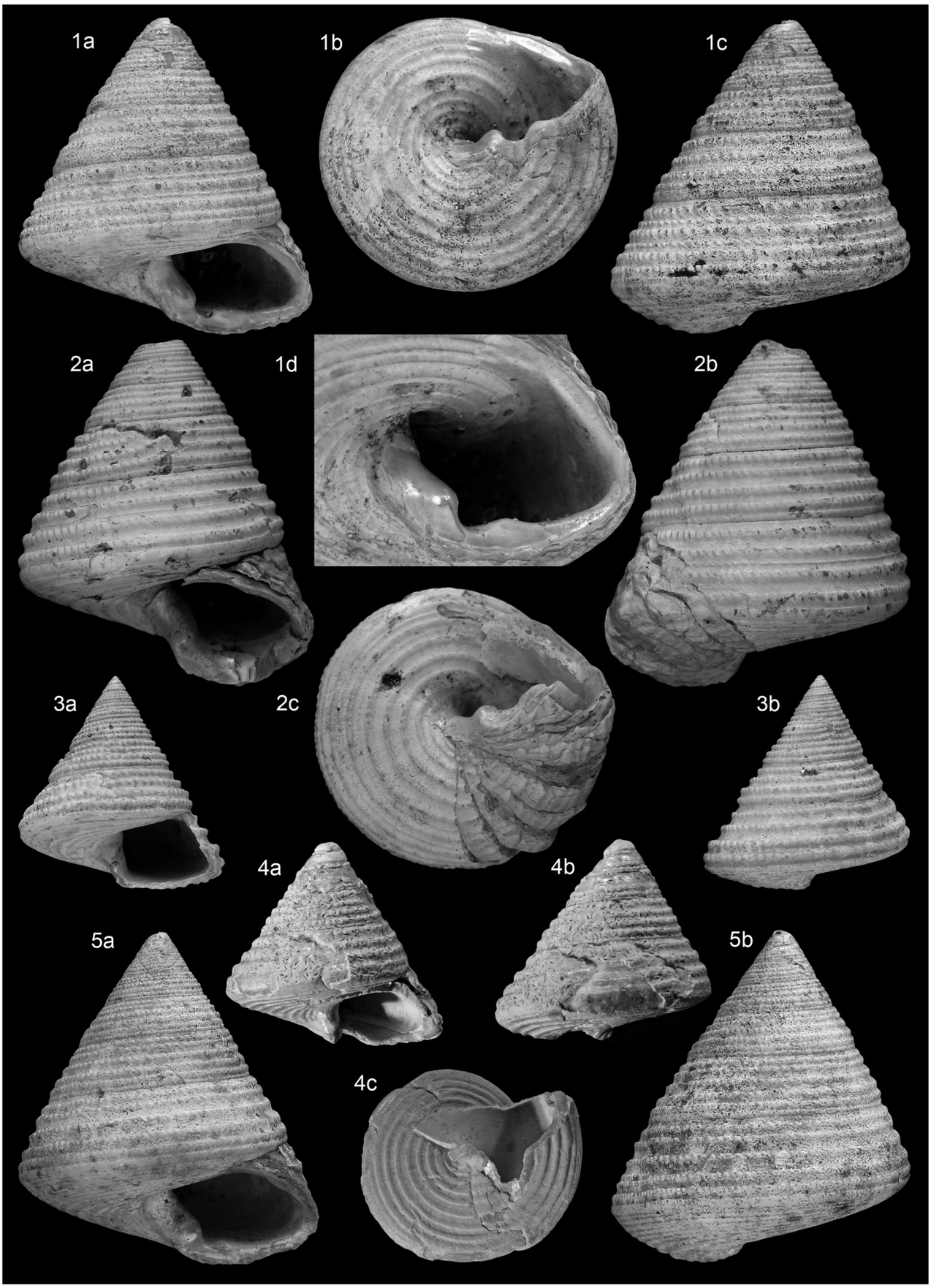

Plate 7

Plate 8

1. *Calliostoma namnetense* nov sp., holotype MNHN.F.A53411, height 18.9 mm, maximum width 16.8 mm (photo Gaëlle Doitteau; project E-Recolnat, MNHN, Paris).
2. *Calliostoma namnetense* nov sp., paratype 1 MNHN.F.A53412/1, height 11.6 mm, maximum width 11.0 mm (photo Gaëlle Doitteau; project E-Recolnat, MNHN, Paris).
3. *Calliostoma namnetense* nov sp., paratype 5 NHMW 2015/0133/0075, height 11.4 mm, maximum width 11.0 mm.
4. *Calliostoma namnetense* nov sp., paratype 7 NHMW 2015/0133/0090, height 11.4 mm, maximum width 11.0 mm.
5. *Calliostoma namnetense* nov sp., paratype 8 NHMW 2015/0133/0091, height 10.7 mm, maximum width 10.7 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

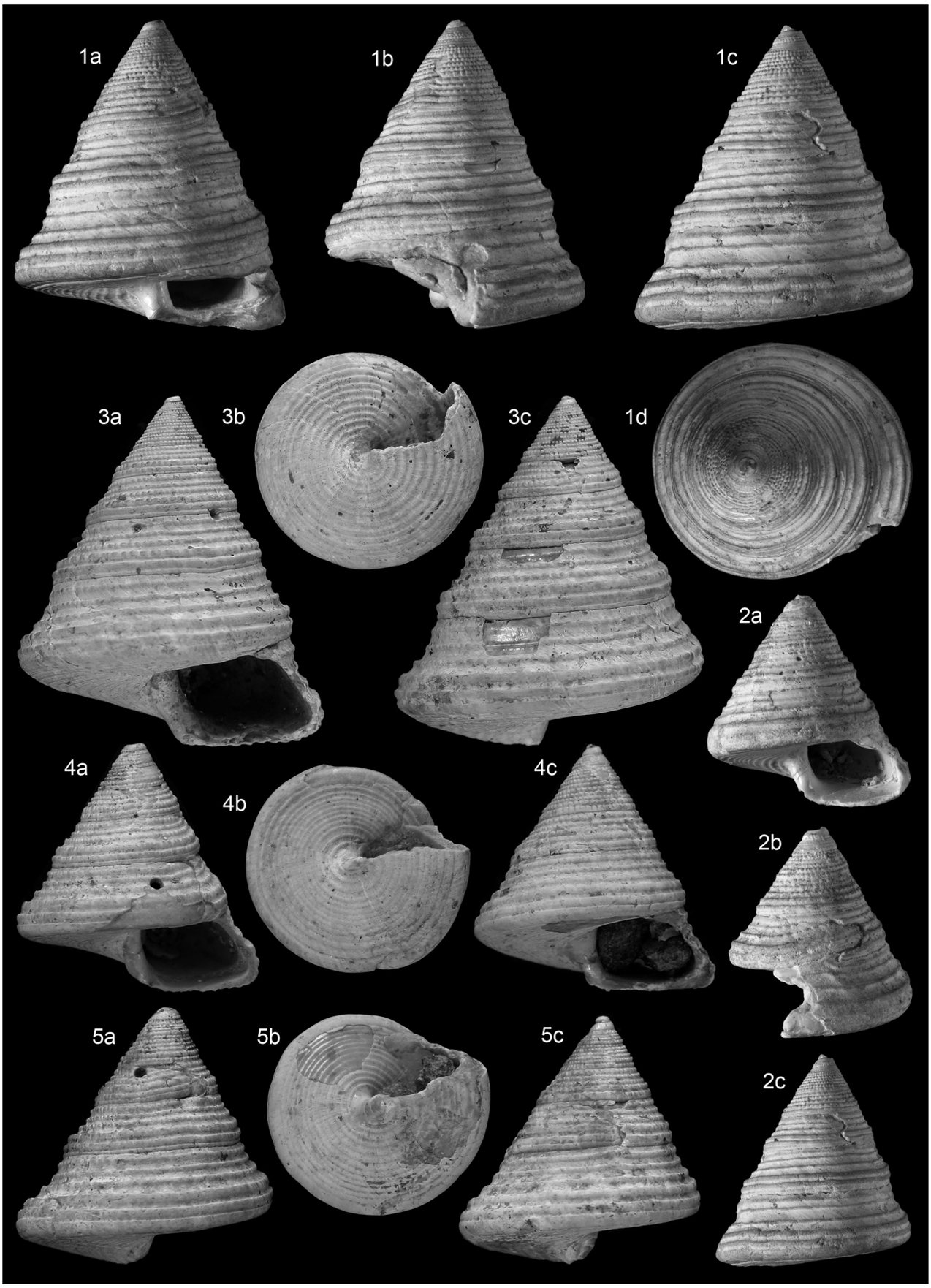

Plate 8

Plate 9

1. *Calliostoma baccatum* Millet (1865), NHMW 2015/0133/0161, height 13.9 mm, maximum width 11.5 mm.
2. *Calliostoma baccatum* (Millet, 1865), NHMW 2015/0133/0162, height 9.0 mm (incomplete), maximum width 9.0 mm.
3. *Calliostoma zizyphinum* (Linnaeus, 1758), NHMW 2015/0133/0096, height 11.8 mm, maximum width 10.8 mm.
4. *Calliostoma zizyphinum* (Linnaeus, 1758), LC coll., height 6.4 mm, maximum width 7.8 mm.
5. *Calliostoma* cf. *multistriatum* (Wood, 1886), NHMW 2015/0133/0092, height 5.6 mm, maximum width 8.0 mm.
6. *Calliostoma* sp., NHMW 2015/0133/0163, height 7.4 mm, maximum width 8.3 mm.
7. *Microgaza landreauensis* nov. sp., holotype MNHN.F.A57389, height 5.9 mm, maximum width 8.0 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

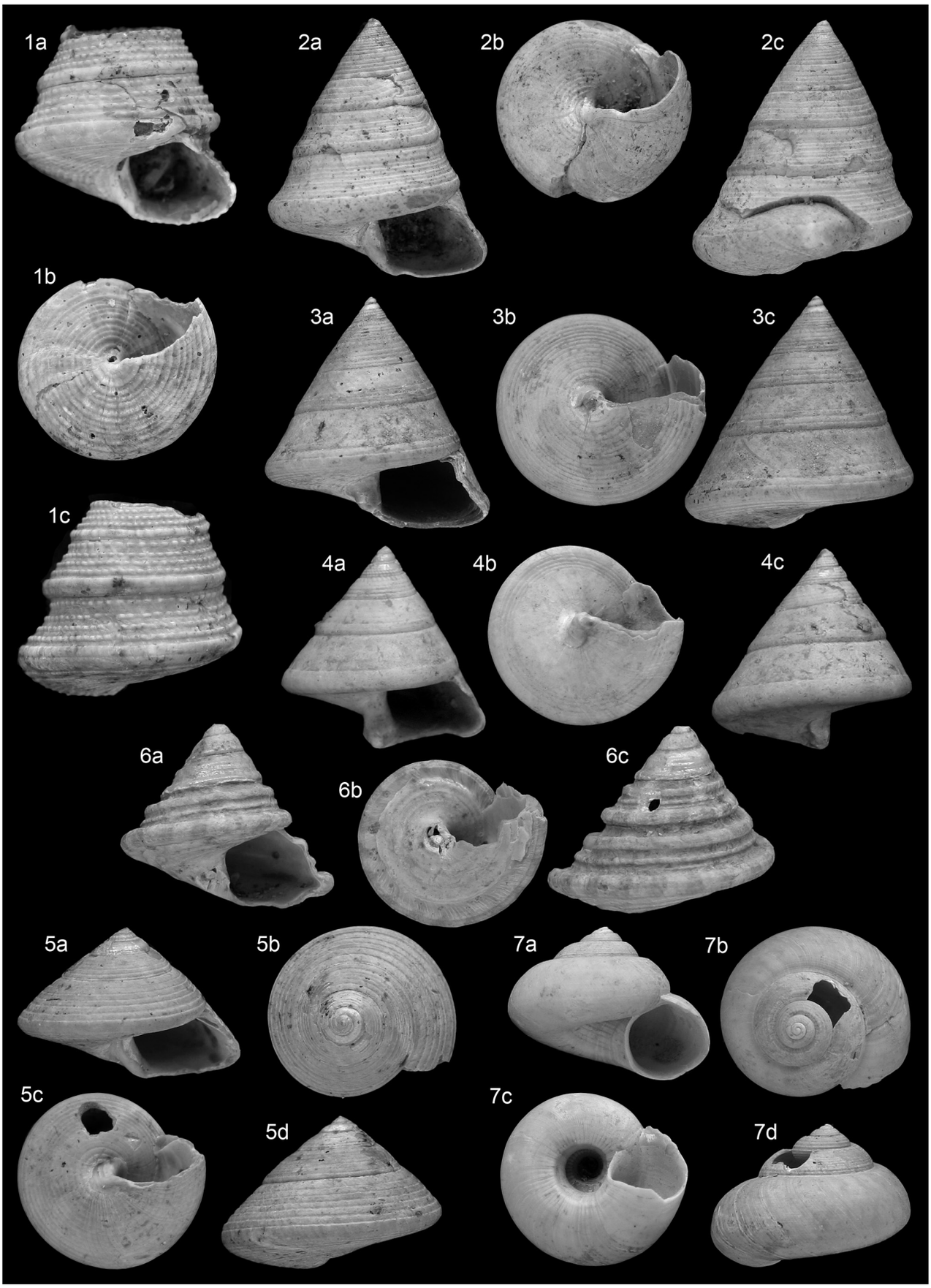

Plate 9

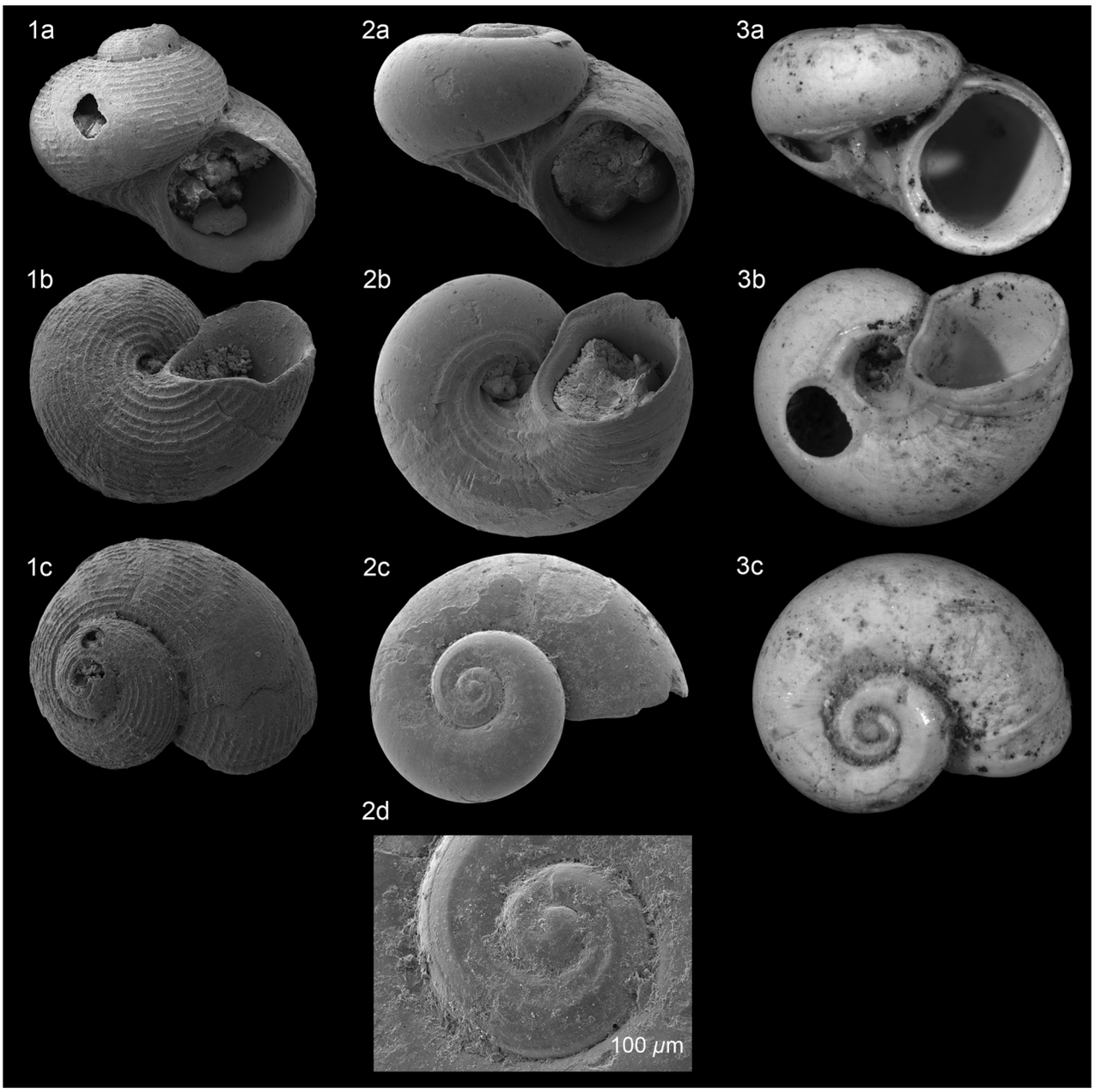

Plate 10

1. *Dikoleps cutleriana* (Clark, 1849), NHMW 2015/0133/0185, height 1.2 mm, maximum width 1.4 mm (SEM photograph).
2. *Moelleriopsis messanensis* (Seguenza, 1876), NHMW 2015/0133/0182, height 1.4 mm, maximum width 1.8 mm (SEM photograph).
3. *Moelleriopsis messanensis* (Seguenza, 1876), NHMW 2015/0133/0183, height 1.5 mm, maximum width 1.9 mm.

All: Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.