

The lower Pliocene gastropods of Le Pigeon Blanc (Loire-Atlantique, Northwest France), 4*. Neogastropoda (in part)

Frank Van Dingenen¹, Luc Ceulemans² & Bernard M. Landau^{3,4}

¹ *Cambeenboslaan A 11, B-2960 Brecht, Belgium; email: fvd@telenet.be*

² *Avenue Général Naessens de Loncin 1, B-1330 Rixensart, Belgium; email: luc.ceulem@skynet.be*

³ *Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, Netherlands; Instituto Dom Luiz da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal; and International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal; email: bernielandau@sapo.pt*

⁴ *Corresponding author*

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In this paper we review the Neogastropoda (in part) 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). Twenty-six species are recorded, of which three are new: *Euthria palumbina* nov. sp., *Bartschia (Agassitula) harasewychi* nov. sp., *Brocchinia pigeonblancensis* nov. sp. *Aplus aequicostatus* (Bellardi, 1877) is considered a junior subjective synonym of *Aplus scaber* (Millet, 1865). *Fusus (Aptyxis) rostratus ligerianus* Peyrot, 1938 is considered a junior subjective synonym of *Aptyxis omphale* (Millet, 1864). The data presented here concurs with that discussed in previous parts of this monograph, suggesting that 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, Neogastropoda, new taxa

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al.*, 2014, 2016a, b; Van Dingenen *et al.*, 2014, 2015, 2016): Gastropods of the order Neogastropoda (excluding Conoidea) 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). The Nassariidae of Assemblage III were revised in Van Dingenen *et al.* (2015), although a summary and update are included herein.

In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris recorded 20 species within the groups covered in this paper from Le Pigeon Blanc and other Assemblage III localities, some 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*.

Geological setting, Material and methods

(see Van Dingenen *et al.*, 2015: 75-79, figures 1, 2).

Abbreviations:

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

Systematic palaeontology

Order Neogastropoda Wenz, 1938
 Superfamily Buccinoidea Rafinesque, 1815
 Family Buccinidae Rafinesque, 1815
 Genus *Aplus* de Gregorio, 1885

Type species (by subsequent designation; Vokes, 1971) – *Murex plicatus* forma *serzus* de Gregorio, 1885, Neogene, Italy.

* For nr 3 in this series see *Vita Malacologica* 15: 35-55.

- 1826 *Anna* Risso, p. 214. Type species (by monotypy): *Anna massena* Risso, 1826, Pleistocene, France. *Anna massena* Risso, 1826 is a *nomen dubium* (see Brunetti & Della Bella, 2014).
1885 *Aplus* de Gregorio, p. 279.

Note – Brunetti & Della Bella (2014) argued that *Anna massena* Risso, 1826, is a *nomen dubium*, possibly a species of *Raphitoma* (family Raphitomidae), and so the genus *Anna* could not be used. The next available generic taxon for this group of shells is *Aplus* de Gregorio, 1885. De Gregorio (1885) did not designate a type species and included in his new genus *Aplus*, *Murex plicatus* ‘Brocchi’ (*i.e.*, *Murex plicatus* Gmelin, 1791, *sensu* Brocchi, 1814). Although Brunetti & Della Bella (2014) designated *Murex plicatus* forma *nilus* de Gregorio, 1885 as the type species, the type species of *Aplus* had already been designated by Vokes (1971, p. 83). WoRMS (Bouchet, 2015a) synonymised *Aplus* with *Pollia* (type species: *Buccinum undosum* Linnaeus, 1758). *Pollia undosa* is an Indo-Pacific species with quite a different shell form and unlikely to be monophyletic with the eastern Atlantic group here ascribed to *Aplus*. Similarly, the tropical American ‘*Anna*’ species also form a distinct group, *Ameranna* Landau & Vermeij, 2012. Until molecular data proves otherwise, we prefer to keep them distinct.

Aplus scaber (Millet, 1865)

Plate 1, figs 1-3

- 1854 *Fusus Scaber* Millet, p. 162 (*nomen nudum*).
1865 *Fusus scaber* Millet, p. 591.
1873 *Pollia aequicostata* Bellardi, p. 182, pl. 12, fig. 23.
1907 *Fusus scaber* Millet – Couffon, p. 185.
1964 *Cantharus (Pollia) exsculpta* Dujardin, 1837 – Brébion (*partim*), p. 428 [*non Aplus exsculptus* (Dujardin, 1837)].
1964 *Cantharus (Pollia) aequicostata* Bellardi, 1872 [*sic*] – Brébion, p. 429, pl. 10, figs 24, 25.
1981 *Pollia aequicostata* Bellardi, 1872 [*sic*] – Ferrero-Mortara *et al.*, p. 48, pl. 6, fig. 8.
2014 *Aplus aequicostatus* (Bellardi, 1877) – Brunetti & Della Bella, p. 18, figs 5A-F.

Material and dimensions – Maximum height 14.6 mm. NHMW 2015/0133/0369-71 (3: Pl. 1, figs 1-3 respectively), NHMW 2015/0133/0372 (32), LC (40), FVD (35). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Brunetti & Della Bella (2014) reviewed the Italian Pliocene *Aplus* species. The size, shape, sculpture and protoconch character of the Le Pigeon Blanc specimens are most like that of *Aplus aequicostatus* (Bellardi, 1873). The protoconch of the French material consists of about 2.5 convex whorls, with a medium-sized nucleus. The protoconch shape is a little variable, inflated and somewhat uncoiled in some specimens. There is also con-

siderable variability in the shell profile seen in the series illustrated here, with broader and more slender specimens present. For comparison with congeners see Brunetti & Della Bella (2014).

Brébion (1964, p. 429) noted that *Fusus scaber* Millet was a synonym of *A. inaequicostatus*. He probably did not use Millet’s name, correctly considering *Fusus scaber* Millet, 1854 to be a *nomen nudum*. However, the name was later validated by the following description: ‘*Fusus scaber*, Millet. *Coq. petite, un peu allongée, ventrue inférieurement; composée de six à sept tours de spire garnis de côtes étroites, saillantes qui se rendent ainsi jusqu’à la suture; ces côtes sont couvertes de stries serrées, rudes, si ce n’est la partie supérieure de chaque tour qui n’en présente aucune. Ouverture presque ovale, à canal très-court, et quelques légers plis se font remarquer sur la partie intérieure du bord droit, qui présente en dehors un fort bourrelet. Longueur: 10-11 millimètres; diamètre: 4-5 millimètres. Sc, Th. (1865, p. 591)’. We cannot apply Article 23.9.1.2 (ICZN 1999) to consider Millet’s name a *nomen oblitum* as Couffon (1907, p. 185) used the name as a valid taxon. Therefore, *A. inaequicostatus* (Bellardi, 1873) is a junior subjective synonym of *Aplus scaber* (Millet, 1865).*

Millet (1865, p. 591) recorded this species from Assemblage I localities of Sceaux d’Anjou and Thorigné, Brébion (1964, p. 428) added St-Michel. Brébion also recorded *Cantharus (Pollia) exsculpta* Dujardin, 1837 from Le Pigeon Blanc. We have not found any specimens of *Aplus exsculptus* at Le Pigeon Blanc, and the record probably refers to *A. inaequicostatus*.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene: Italy (Brunetti & Della Bella, 2014).

Genus *Euthria* Gray, 1850

Type species (by subsequent designation; Petit, 2012) – *Murex corneus* Linnaeus, 1758, present-day, Mediterranean.

1850 *Euthria* Gray, p. 67

Note – Hadorn & Fraussen (1999) synonymised *Siphonofusus* Drivas & Jay 1990 with *Euthria* Gray, 1850. *Siphonofusus* species are slender, with a longer siphonal canal than usual for *Euthria* and live in deep water. Moreover, they are from Japan and unlikely to be monophyletic with *Euthria*, as envisaged here, which seems to be a European group. We are unconvinced that any of the Indo-Pacific species described (*i.e.* Fraussen & Hadorn, 2003) are monophyletic with the eastern Atlantic species. We therefore provisionally exclude *Siphonofusus* from the generic synonymy until we have more molecular data on the group.

***Euthria palumbina* nov. sp.**

Plate 1, figs 4-6

1964 *Buccinulum (Euthria) lecointrei* Brébion, p. 420, pl. 10, figs 15-16 (*nomen nudum*).

Type material – Holotype NHMW 2015/0133/0363 (Pl. 1, fig. 4), height 38.6 mm; paratype 1 NHMW 2015/0133/0364 (Pl. 1, fig. 5), height 25.8 mm; paratype 2 NHMW 2015/0133/0366, height 24.0 mm (Pl. 1, fig. 6); paratype 3 MNHN.F.A57934, height 24.2 mm; paratype 4 MNHN.F.A57935, height 21.7 mm; paratype 5 MNHN.F.A57935, height 22.6 mm.

Other material – Maximum height 39.2 mm. NHMW 2015/0133/0365 (25), LC (50+), FVD (50+).

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

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – An *Euthria* species of small size, relatively slender fusiform in shape, with a protoconch consisting of two whorls, teleoconch sculptured by 9-10 rounded ribs that weaken on penultimate whorl and become obsolete, or almost so, on last whorl, very weak spiral sculpture of alternate strength, an ovate aperture thickened by labial varix, denticulate within, the parietal tooth strongest, and a moderately long siphonal canal, 19% of total height.

Description – Shell small to small for genus, solid, relatively slender fusiform. Protoconch consisting of two convex whorls, with medium-sized nucleus (dp = 1.0 mm; hp = 1.1 mm; dn = 270 μm). Protoconch boundary sharp. Teleoconch of six convex whorls, with periphery just below mid-whorl. Sculpture of 9-10 elevated, prosocline, rounded ribs, broadening towards abapical suture, roughly equal in width to their interspaces, crossed by very numerous fine cords of primary and secondary strength. Last whorl weakly inflated, with narrow, slightly concave subsutural ramp, shoulder high, rounded, whorl constricted at base, axial sculpture strongest at shoulder, weakening to subobsolete over base, spiral sculpture strengthening over base. Aperture ovate, anal canal marked by adapical notch, siphonal canal of moderate length, 19% of total height, open, narrow, slightly posteriorly recurved. Outer lip thickened by labial varix, sinuous in profile, edge bevelled, bearing a row of small rounded denticles along entire lip height, placed at inner edge of bevelled portion. Columella evenly excavated, bearing row of irregular tubercles along entire length, with stronger parietal tubercles adapically; tubercles subobsolete mid-columella in some specimens. Columellar

callus thin, adherent, sharply delimited, poorly expanded. Siphonal fasciole rounded, narrow.

Discussion – *Euthria palumbina* nov. sp. is fairly typical for the genus as understood here (see note under generic assignment above), although rather small shelled compared to some of its congeners. The species is common in the Le Pigeon Blanc assemblage and there is little variability. *Euthria adunca* (Bronn, 1831) from the Pliocene Mediterranean is larger shelled, the shoulder is slightly more angular, the axial ribs are wider, the spiral cords stronger and the siphonal canal is longer. *Euthria submarginata* (d’Orbigny, 1852) from the middle Miocene of the Loire Basin is even smaller, squatter, thinner shelled, with more numerous axial ribs (12) and stronger and less numerous spiral cords, the primary cords forming elongated tubercles where they cross the ribs. *Euthria varicigera* Peyrot, 1928 from the middle Miocene Aquitaine Basin of France has less convex spire whorls, more numerous axial ribs (15), stronger primary spiral sculpture and a more elongate last whorl. *Euthria pseudomarginata* Peyrot, 1928 from the lower Miocene Burdigalian Aquitaine Basin is smaller shelled than *E. palumbina* and like the previous species also has more numerous axial ribs (15) and stronger spiral sculpture than *E. palumbina*. *Euthria verrucifera* Bellardi, 1873 from the upper Miocene of Italy is similar in shape to *E. palumbina*, but differs in having broader axial ribs and stronger spiral sculpture.

Brébion (1964, p. 421) recorded this species from the middle Miocene Loire Basin (Mirebeau), Assemblage I localities (Renauleau, Sceaux-d’Anjou, Thorigné, St-Michel), Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Le Girondor, Palluau) and Assemblage IV (Gourbesville).

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

***Euthria turonensis* Peyrot, 1938**

Plate 1, fig. 7

*1938 *Euthria adunca* var. *turonensis* Peyrot, p. 230, pl. 4, figs 11, 16, 19.

1952a *Euthria adunca turonensis* Peyrot, 1938 – Glibert, p. 324, pl. 9, fig. 4.

?1964 *Buccinulum (Euthria) regulare* Brébion, p. 423, pl. 10, fig. 19 (*nomen nudum*).

Material and dimensions – Height 19.3 mm. NHMW 2015/0133/0368 (1: Pl. 1, fig. 7). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Revised description – Shell small, solid, slender fusiform. Protoconch not preserved. Teleoconch of five weakly but

regularly convex whorls, shoulder and subsutural ramp poorly delimited by weak angulation, with periphery just below mid-whorl. Sculpture of elevated, orthocone, rounded ribs, extending between sutures, broadening slightly towards abapical suture, half the width of their interspaces; 9 on first whorl, 17 on last whorl, crossed by numerous spiral cords of primary to tertiary strength. Last whorl relatively elongate, regularly rounded, constricted at base, axial sculpture strongest mid-whorl, weakening over base. Aperture ovate, anal canal marked by adapical groove, siphonal canal moderate length, open, narrow, slightly posteriorly recurved. Outer lip thickened by labial varix, edge bevelled, bearing a row of elongated denticles along entire lip length, placed at inner edge of bevelled portion, extending as lirae within aperture. Columella evenly excavated, bearing two small abapical tubercles, one mid-aperture, one parietal. Columellar callus adherent, sharply delimited, narrow. Siphonal fasciole rounded, narrow.

Discussion – *Euthria turonensis* Peyrot, 1938, which seems to be exceedingly rare at Le Pigeon Blanc, differs from *Euthria palumbina* nov. sp. in being more slender-shelled, the whorls are more weakly, but regularly convex rather than subangular, it lacks a well-defined subsutural ramp, the axial ribs are more numerous and the spiral cords stronger and less numerous. Moreover, the denticles placed within the outer lip are more numerous and extend into the aperture as lirae rather than being restricted to the inner edge of the bevelled outer lip.

We consider it conspecific with the specimens illustrated by Glibert (1952a, pl. 9, fig. 4) as *Euthria adunca turonensis* Peyrot, 1938. The series illustrated by Glibert shows some variability in the strength of the shoulder cord; his fig 4a is rather broader-shelled, with a stronger shoulder cord, like the specimen illustrated by Peyrot (1938, pl. 4, figs 11, 16, 19), whereas Glibert's fig. 4c is more elongated, with a weak shoulder, similar to the specimen from Le Pigeon Blanc. As pointed out by Glibert (1952a, p. 325) the north western French forms differ from the Pliocene Mediterranean *E. adunca* (Bronn, 1831) in being much smaller sized and in having more numerous axial ribs (15-17 vs. 10-11).

It also fits well with the description of a shell illustrated by Brébion (1964) as *Buccinulum (Euthria) regulare* (*nomen nudum*) from the older upper Miocene Assemblage I locality of St-Michel: 'Long. 14mm, larg. 7mm. Forme étroite à spire formée de 4 à 5 tours ornés d'une douzaine de côtes s'étendant sur toute leur hauteur et de 7 à 8 cordons spiraux plus étroit égaux à leurs intervalles, plus fins et serrées vers l'arrière des tours, l'ensemble étant très régulier. Base entièrement couverte de cordons; labre peu épaissi, muni d'une dizaine de denticules; bord columellaire avec 2 denticules en avant et une faible dent pariétale; canal court (1964, p. 423)'. Brébion drew attention to the narrow shell shape, regular sculpture, with the ribs extending between the sutures and the two tubercles on the abapical portion of the columella. The only differences between the Le Pigeon Blanc shell and that from St-Michel is that the former has a greater number

of axial ribs on the last whorl (17, vs. 12) and more numerous denticles within the outer lip (16 vs. 12). Brébion (1964) wrote that this shell differed from *E. turonensis* 'par la taille plus faible, la petitesse du canal, l'absence de bourrelet'. However, as discussed above, these differences are not consistent.

Unfortunately, the single shell available from Le Pigeon Blanc gives us no information on the intraspecific variability.

Distribution – Middle Miocene (Langhian): Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1952a). ?Upper Miocene: Atlantic (Tortonian): north western France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (this paper).

Family Colubrariidae Dall, 1904

Genus *Bartschia* Rehder, 1943

Type species (by original designation) – *Bartschia significans* Rehder, 1943, present-day, Florida, USA.

1943 *Bartschia* Rehder, p. 199.

Subgenus *Agassitula* Olsson & Bayer, 1972

Type species (by original designation) – *Metula agassizi* Clench & Aguayo, 1941, present-day, Cuba.

1972 *Agassitula* Olsson & Bayer, p. 917.

***Bartschia (Agassitula) harasewychi* nov. sp.**

Plate 1, fig. 8; Plate 2, fig. 11

1964 *Buccinulum (Euthria) aenigmaticum* Brébion, p. 425, pl. 10, fig. 22 (*nomen nudum*).

Type material – Holotype: NHMW 2015/0133/0367 (Pl. 1, fig. 8), height 27.9 mm, width 10.3 mm; paratype 1 NHMW 2015/0133/0426 (Pl. 2, fig. 11), height 20.4 mm, width 7.4 mm.

Other material – LC (3 fragments).

Etymology – Named after M. G. (Jerry) Harasewych, Research Zoologist at the Smithsonian Institution, Washington, DC, USA, in recognition of his many contributions to American malacology and particularly his work on the family Colubrariidae. *Bartschia* gender feminine.

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A *Bartschia (Agassitula)* species of medium size, with a tall spire, covered by finely reticulated sculpture, in which the axial component is slightly dominant,

a moderately inflated and broad last whorl, 56% of total height, modestly thickened outer lip, finely denticulate within and a short siphonal canal, 7% of total height.

Description – Shell of medium size and thickness, fusiform, with elevated, conical spire. Protoconch not preserved. Teleoconch of 6.5 evenly convex whorls, lacking shoulder, separated by shallow adpressed suture. Sharp protoconch-teleoconch boundary preserved, marked by the onset of five spiral cords and narrow, close-set axial ribs, 19 on first whorl, crossed by narrow, close-set equal spiral cords, increasing in number abapically, ten on penultimate whorl, forming dense, horizontally elongated cancellated pattern, with axial sculpture predominant. Single spiral thread intercalated in some interspaces on penultimate whorl. A sudden change in sculpture on second half of the penultimate whorl is probably due to damage during life. Last whorl 56% of total height, moderately inflated (width/ height 0.66), unsculptured, with irregular surface, crossed by coarse growth lines. Aperture ovate, anal canal relatively shallow and broad, siphonal canal short, open, dorsally reflected. Outer lip thickened by modest varix, with bevelled edge, bearing a row of 11 short, subequal denticles along inner edge. Siphonal canal of moderately short, 7% of total height, open, weakly recurved. Columella smooth. Columellar and parietal callus moderately thickened, adherent, poorly delimited. Siphonal fasciole poorly developed, rounded.

Discussion – Although many of the colubrariid genera/subgenera related to *Metula* H. Adams & A. Adams, 1853 have now been synonymised with it (WoRMS; Bouchet, 2015b), we follow Harasewych (2014) in recognising *Bartschia* Rehder, 1943 as a separate genus. *Bartschia* species differ from *Metula* in having proportionally broader shells, with more evenly rounded whorls, a shorter, wider aperture with more pronounced denticles within the outer lip and slightly coarser sculpture with spiral cords predominant. The subgenus *Agassitula* Olsson & Bayer, 1972, differs from *Bartschia* in having more elongated shells, in which the spire is half or more of the total shell height and a longer siphonal canal (Harasewych, 2014, p. 92). The genera/subgenera *Agassitula* and *Bartschia* share a similar stratigraphical and geographical distribution and are not recognised by all (*i.e.* WoRMS; Bouchet, 2015c). The specimens from Le Pigeon Blanc fit well within the generic description of *Bartschia* (*Agassitula*), except possibly in that the axial sculpture is slight dominant. The holotype (Pl. 1, fig. 8) from France seems to have suffered some injury during life, possibly a crab attack, from which it survived, but lost its sculpture on whorls formed subsequent to the injury. The paratype (Pl. 2, fig. 11) did not suffer injury and shows no change in sculpture on the last whorl. However, it is not chosen as the holotype as it is not fully grown and lacks the adult apertural dentition.

Whilst the genus *Metula* is recognised in the European Neogene, as far as we are aware, this is the first record for the subgenus *Bartschia* (*Agassitula*), or indeed *Bartschia*, in Europe. Today the genus is tropical American. The

type species, *Bartschia* (*A.*) *agassizi* Clench & Aguayo, 1941 and *Bartschia* (*A.*) *peartae* Harasewych, 2014 from the present-day Caribbean are both immediately separated from the French species by their finer sculpture. *Bartschia* (*A.*) *guppyi* Olsson & Bayer, 1972, also from the present-day Caribbean and *B. (A.) limonensis* (Olsson, 1922) from the lower Pleistocene Moin Formation of Costa Rica both have closer-set sculpture, with tubercles developed at the sculptural intersections, giving the surface a beaded rather than cancellated appearance.

Brébion (1964, p. 426) recorded this species from the upper Miocene Tortonian Assemblage I localities (Thorigné, Contigné). Unfortunately, we have been unable to locate any of Brébion's material reported as being in 'musée d'Angers'. In this paper we extend the stratigraphic range for the species to the lower Pliocene Zanclean Assemblage III.

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

Family Columbellidae Swainson, 1840

Genus *Mitrella* Risso, 1826

Type species (by subsequent designation; Cox, 1927) – *M. flaminea* Risso, 1826 (= *Murex scriptus* Linnaeus, 1758), present-day, Mediterranean.

1826 *Mitrella* Risso, p. 247.

Note – The genus *Mitrella* Risso, 1826 as used here is interpreted rather widely and is unlikely to be monophyletic. We are unaware of any molecular studies on mitrellid gastropods, and await these, hoping that they will shed some light on relationships. Until then we do not think it useful to give a generic synonymy.

Mitrella erythrostoma (Bellardi, 1848)

Plate 1, fig. 9

- *1848 *Columbella erythrostoma* Bellardi, Bonelli m.s., p. 9, pl. 1, figs 4-5.
- 1890 *Columbella (Mitrella) erythrostoma* Bon. – Sacco, p. 40, pl. 2, fig. 40.
- 1904 *Mitrella erythrostoma* (Bon.) var. *compressula* Sacco, p. 93, pl. 19, figs 51-52.
- 1938 *Columbella (Alia) ligeriana* Peyrot, p. 204, pl. 4, figs 45, 46.
- 1952a *Columbella (Alia) erythrostoma* Bonelli, 1825 – Glibert, p. 320, pl. 8, fig. 5.
- 1975 *Mitrella erythrostoma* var. *compressula* Sacco – Fekih, p. 126, pl. 37, fig. 16.
- 1981 *Columbella (Mitrella) erythrostoma* Bellardi, 1848, Bonelli m.s. – Ferrero-Mortara *et al.*, p. 183, pl. 57, fig. 12.
- 2011 *Mitrella erythrostoma* (Bellardi, 1848) – Landau *et al.*, p. 28, pl. 13, fig. 19.

Material and dimensions – Maximum height 22.7 mm. NHMW 2015/0133/0373 (1: Pl. 1, fig. 9), LC (5), FVD (2). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Mitrella erythrostoma* (Bellardi, 1848) is a relatively large-shelled mitrellid, characterised by its weakly convex spire whorls, its moderately inflated last whorl, elongated aperture, with the outer lip pinched inwards just above mid-height, bearing teeth along its entire inner edge, more strongly developed on the pinched section, its poorly callused inner lip and short siphonal canal. Some specimens have a shorter spire, which gave rise to Sacco's (1904) variety *compressula*. The specimen from Le Pigeon Blanc has a slightly taller spire than usual for the species, but the last whorl characters are identical. We would agree with Glibert (1952a) in synonymising the French middle Miocene specimens from the Loire Basin described by Peyrot (1938) as *Columbella (Alia) ligeriana*.

The only species somewhat similar is the Mediterranean Pliocene *Mitrella turgidula* (Brocchi, 1814), which also has a pinched outer lip, but it is easily separated from *M. erythrostoma* by its broader, regularly conical, more pointed spire, shallower suture and broad last whorl, which is more strongly constricted at the base.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1952a). Upper Miocene: Proto-Mediterranean, Italy (Glibert, 1952a). Lower Pliocene: Atlantic, NW France (this paper); Guadalquivir Basin, Spain (Landau *et al.*, 2011); central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (BL unpublished data); central Mediterranean, Italy (Bellardi, 1848; Sacco, 1904).

***Mitrella bruggeni* van Aartsen, Menkhorst & Gittenberger, 1984**

Plate 1, fig. 10

- 1981 *Pyrene broderipi* (G.B. Sowerby I, 1844) – Sabelli & Spada, unnumbered page 2, figs 7a-c. (*non* G.B. Sowerby I, 1844).
- 1984 *Mitrella maldonadoi* Luque, p. 13 (*nomen nudum*).
- *1984 *Mitrella bruggeni* van Aartsen, Menkhorst & Gittenberger, p. 77, fig. 176a.
- 1987 *Mitrella maldonadoi* Luque, 1984 – Luque, p. 231, pl. 1, figs 3-5.
- 2003 *Mitrella bruggeni* van Aartsen, Menkhorst & Gittenberger – Giannuzzi-Savelli *et al.*, p. 254, figs 613-622.

Material and dimensions – Maximum height 11.9 mm. NHMW 2015/0133/0378 (1: Pl. 1, fig. 10), LC (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – A few specimens from Le Pigeon Blanc

are ascribed to the present-day species *Mitrella bruggeni* van Aartsen, Menkhorst & Gittenberger, 1984. It is one of the few shells from Le Pigeon Blanc with colour pattern preserved, showing spiral rows of spots. This type of pattern is present in several present-day European *Mitrella* species, of which *M. bruggeni* is one. *Mitrella gervillii* (Payraudeau, 1826) is another, but differs in being more slender, with slightly more convex spire whorls and usually with more numerous teeth within the outer lip. *Mitrella broderipi* (G.B. Sowerby II, 1844) is another western Mediterranean species with spotted colour pattern, but differs in being smaller, squatter, with slightly more convex whorls and a less constricted base. Lastly, *M. svelta* Kobelt, 1889 (= *Columbella lanceolata* Locard, 1886; *non* G.B. Sowerby I, 1832a) is the largest and most slender of the group, with a taller, more straight-sided spire than any of the preceding species. As far as we are aware, this is the first fossil record for the species. A more northern distribution during the lower Pliocene than found today is consistent with many other thermophilic elements in the Assemblage III fauna.

Distribution – Lower Pliocene: Atlantic, NW France (this paper). Present-day, western Mediterranean, Canaries, Madeira (van Aartsen, Menkhorst & Gittenberger, 1984).

***Mitrella vialensis* (Sacco, 1890)**

Plate 2, figs 1, 2

- *1890 *Columbella (Clinurella) vialensis* Sacco, p. 46, pl. 2, fig. 53.
- 1964 *Mitrella (Atilia) inedita* Bellardi, 1890 – Brébion (*partim*: Pigeon Blanc records), p. 127, pl. 9, fig. 28 (only) [*non Mitrella inedita* (Sacco, 1890)].
- 1981 *Columbella (Clinurella) vialensis* Sacco in Bellardi, 1890 – Ferrero-Mortara *et al.*, p. 183, pl. 57, fig. 12.
- 2002 *Mitrella vialensis* (Sacco in Bellardi, 1890) – Chirli, p. 13, pl. 7, figs 3-8.
- 2010 *Mitrella minima* (Sacco, 1890) – Sosso & Dell'Angelo, p. 59 unnumbered fig. top left (*non* Sacco, 1890).

Material and dimensions – Maximum height 11.8 mm. NHMW 2015/0133/0374 (1: Pl. 2, fig. 1), NHMW 2015/0133/0375 (1: 9.0 mm), NHMW 2015/0133/0376 (Pl. 2, fig. 1); NHMW 2015/0133/0377 (50+), LC (50), FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Mitrella vialensis* (Sacco, 1890) is characterised by its tall, slender, non-scalate, coeloconoid spire, weakly rounded spire whorls, relatively low last whorl, which is strongly constricted at the base and the presence of denticles within the outer lip. No protoconch description of Italian specimens is available, but the specimens from Le Pigeon Blanc have a tall multispiral protoconch of about 3-3.5 smooth convex whorls (Pl. 2, fig. 2). Italian specimens at hand (NHMW coll.) have a multispiral

protoconch similar to that of the French specimens. The only possible difference between the two populations is that in the Italian specimens the spiral cords on the base are slightly stronger and cover more of the lower half of the last whorl than they do in the shells from Le Pigeon Blanc. However, we consider this difference of minor significance.

Mitrella vialensis belongs to a group of closely similar species including *Mitrella borsoni* (Bellardi, 1848), which is widespread in the middle and upper Miocene Atlantic and Mediterranean Sea (Landau *et al.*, 2013). This species differs from *M. vialensis* in having a more scalate spire and a less constricted base. *Mitrella minima* (Sacco, 1890), also from the Pliocene of Italy, is very similar to *M. vialensis* but smaller, more constricted at the base and has a smooth inner lip without denticles. The strength of the denticles is rather variable in *M. vialensis* and *M. minima* may be a subadult specimen as the syntype illustrated by Ferrero Mortara *et al.*, (1981, pl. 57, fig. 10) lacks the thickened labial varix typical of the genus. Either way, the specimen illustrated by Sosso & Dell'Angelo (2010, p. 59) as *M. minima* has strong labial dentition and should be ascribed to ++*M. vialensis*. *Mitrella scalaris* (Sacco, 1890) from the middle Miocene of Italy, is of similar size and shape, but differs in having an outer lip that is more flared and somewhat alate adapically.

Brébion (1964, p. 401) recorded, but did not figure, *M. borsoni* from numerous Assemblage I, III and IV localities, but not Le Pigeon Blanc. Until we review the Assemblage I localities we cannot be certain to which of this closely similar group of species the reference refers to. He did figure one shell from Le Pigeon Blanc under the name *Mitrella (Atilia) inedita* Bellardi, 1890 (1964, pl. 9, fig. 28), which we have included in the synonymy of *M. vialensis*. *Mitrella inedita* (Sacco, 1890) from the upper Miocene of Italy is also similar, but differs in having a regularly conical rather than coelocoid spire and the base is less constricted resulting in a broader siphonal canal, which is also slightly shorter than in *M. vialensis* and less posteriorly reflected.

Distribution – Lower Pliocene: Atlantic, NW France (this paper); central Mediterranean, Italy (Sacco, 1890; Chirli, 2002). Upper Pliocene: central Mediterranean, Italy (Sosso & Dell'Angelo, 2010).

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

Type species (by subsequent designation, Tate, 1868) – *Columbella scalarina* G.B. Sowerby I, 1832, present-day, Panamic Pacific.

1853 *Anachis* H. Adams & A. Adams, p. 184.

Note – This European Neogene group of tall-spined, slender columbellids with cancellate sculpture have been placed by all authors in the genus *Anachis* H. Adams & A. Adams, 1853. The Panamic Pacific type species, *Co-*

lumbella scalarina G.B. Sowerby I, 1832 is quite different with predominantly axial sculpture and a solid, inflated last whorl that is large in relation to the spire. We doubt that the two groups are monophyletic. Unfortunately the European group has no modern representatives, so their relationship cannot be tested using molecular phylogenetics. The shell shape of this group is far closer to the tropical American Atlantic genus *Suturoglypta* Radwin, 1968, but this also has strongly predominant axial sculpture. We hesitate to erect a genus for this group as some European Neogene species such as *Anachis hoernesii* (Mayer, 1869) and *A. haueri* (Hoernes & Auinger, 1880) seem to have intermediate features.

***Anachis milleti* nov. sp.**

Text-fig. 1/1-4, Plate 2, fig. 3

1964 *Anachis fannyae* (Dollfus mss.) – Brébion, p. 410, pl. 10, figs 5, 6 (*nomen nudum*).

Type material – Holotype: MNHN.F.A57685 (Text-fig. 1/1), height 6.8 mm, width 2.6 mm; paratype 1 NHMW 2016/0103/0063 (Text-fig. 1/2), height 5.8 mm, width 2.6 mm; paratype 2 MNHN.F.A57686, height 6.8 mm, width 2.7 mm; paratype 3 NHMW 2016/0103/0064, height 7.2 mm, width 2.9 mm; St-Clément-de-la-Place. Paratype 4 MNHN.F.A57656 (pl. 10, fig. 5 of Brébion, 1964; herein Text fig. 1/3), height 5.6 mm, Sceaux-d'Anjou (Maine-et-Loire, France).

Other material – St-Clément-de-la-Place: maximum height 7.2 mm. NHMW 2016/0103/0065 (40), LC (50+), FVD (50+). Sceaux d'Anjou: maximum height 7.0 mm. NHMW 2016/0103/0066 (50+), LC (50+), FVD (50+). Le Pigeon Blanc: maximum height 11.3 mm. NHMW 2015/0133/0379 (1: Pl. 2, fig. 3), NHMW 2015/0133/0380 (5). Palluau (Vendée, France): MNHN.F.A57657 (pl. 10, fig. 6 Brébion, 1964; herein Text-fig. 1/4), MNHN.F.A57658 (4)

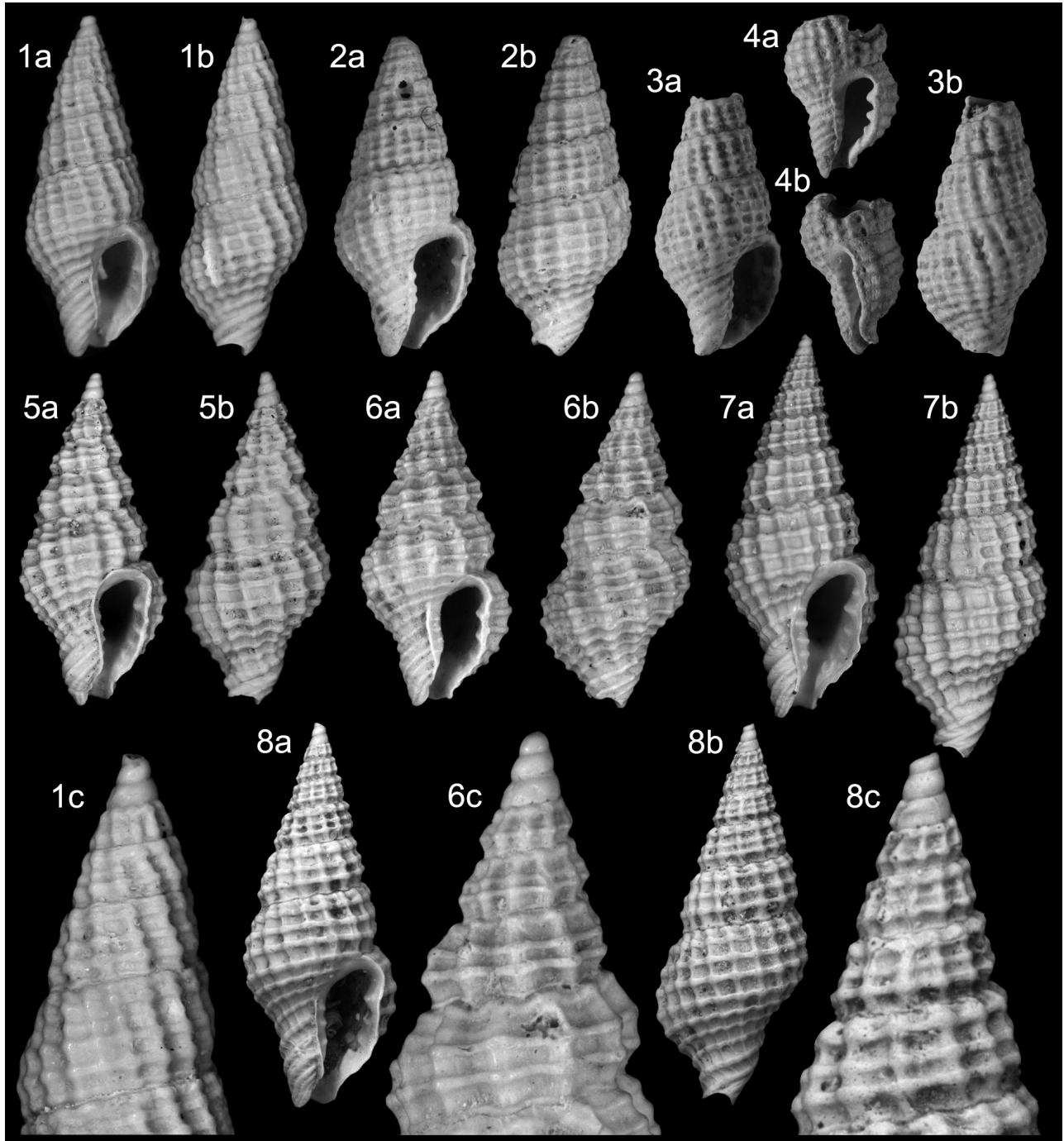
Etymology – Named after Pierre-Amié Millet de la Turtaudière, (1783-1873), Secrétaire Général de la Société d'Agriculture d'Angers, in recognition of his pioneering work on the palaeontology of Maine-et-Loire. *Anachis* gender feminine.

Locus typicus – Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – An *Anachis* species of small size, with a slender fusiform shell shape, a tall spire and weakly inflated last whorl, bearing moderately dense and fine reticulated sculpture with axial and spiral elements of roughly equal in strength, forming small tubercles at the intersections, and a tall multispiral protoconch.

Description – Shell small, slender fusiform. Protoconch multispiral, two smooth convex whorls preserved. Teleo-



Text-figure 1. Assemblage I *Anachis* species: 1-4. *Anachis milleti* nov. sp.; 1: **holotype**, MNHN.F.A57685, height 6.8 mm; 2: **paratype 1**, NHMW 2016/0103/0063, height 5.8 mm; 3: **paratype 4**, MNHN.F.A57656, height 5.6 mm (photo Jocelyn Falconnet; MNHN); 4: MNHN.F.A57657 (photo Jocelyn Falconnet; MNHN); 5-6. *Anachis hordacea* (Millet, 1865). 5: NHMW 2016/0103/0072, height 6.9 mm; 6: NHMW 2016/0103/0073, height 6.0 mm; 7-8. *Anachis collyrata* (Millet, 1865); 7: NHMW 2016/0103/0067, height 9.0 mm; 8: NHMW 2016/0103/0068, height 11.7 mm.

Figures 1-2, 5-8 from Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France; Figure 3 from Sceaux-d'Anjou, Maine-et-Loire, France; Figure 4 from Palluau, Vendée, France. All Tortonian, upper Miocene.

conch of 5.5 straight-sided to weakly convex whorls, with periphery at or just above abapical suture. Suture shallow. Sculpture on first teleoconch whorl of two narrow, raised spiral cords placed adjacent to sutures. On second whorl a third cord develops below adapical cord,

with a further cord added below adapical cord on subsequent whorls. Axial sculpture of prosocline ribs, 15-16 on penultimate whorl, equal in strength to spiral cords, forming moderately dense reticulated surface sculpture. Small tubercles develop at sculptural intersections. Last

whorl weakly inflated, not shouldered, with periphery just below mid-whorl, roundly constricted at base, bearing ten spiral cords and 18-19 ribs that weaken over base. Aperture small, ovate, outer lip strongly thickened by labial varix bearing 4-5 denticles within, adapical two denticles more strongly developed. Siphonal canal open, of moderate length, narrow, posteriorly recurved. Columella straight, bearing four stout folds. Columellar callus thickened, narrow, sharply delimited, parietal portion poorly developed. Siphonal fasciole flattened, not delimited from base, bearing spiral cords.

Discussion – Although *Anachis milleti* nov. sp. occurs in the lower Pliocene Assemblage III locality of Le Pigeon Blanc, it is far more abundant in the upper Miocene Assemblage I deposits. We therefore take the opportunity to describe this species, but nominate St-Clément-de-la-Place for the type stratum and locality.

This group of *Anachis* species with tall spires and reticulated sculpture are well represented in the French Atlantic Miocene. *Anachis degrangei* Dollfus in Degrange-Touzin, 1894 from the middle Miocene Aquitaine and Loire basins of France is the most similar to *A. milleti* in its tall slender shape and relatively weakly inflated last whorl, but this species has fewer ribs and cords and the two subsutural cords are more strongly developed, forming a subsutural collar, resulting in a somewhat scalate appearance to the spire. This subsutural collar is even more strongly developed in *A. clathrata* (Dujardin, 1837), which is lower spired than the preceding species and has predominantly axial sculpture. This group is well represented in the NW French Assemblage I localities, where two further species occur: *A. collyrata* (Millet, 1865) (Text-fig. 1/7-8) and *A. hordacea* (Millet, 1865) (Text-fig. 1/5-6), both of which differ from *A. milleti* in having less dense reticulated sculpture, with fewer ribs and cords on the spire whorls. Like in *A. milleti*, in *A. collyrata* further cords develop below the adapical cord on the spire whorls, whereas in *A. hordacea* the abapical cord develops first, followed by the middle cord and adapical cord last. These species will be discussed further in the relevant paper.

Anachis milleti is far less common in the Le Pigeon Blanc assemblage than it is in the Assemblage I localities. However, the few specimens available are all about half as large again as the largest from Assemblage I. The small size of the Assemblage I species is a theme we will visit repeatedly during this series of papers.

Brébion (1964, p. 411) recorded *A. milleti* (as *A. fannyae*) from the middle Miocene Loire Basin (Manthelan), Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné, Le Temple du Cerisier), Assemblage III (Le Pigeon Blanc, Palluau, La Gauvinière).

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

Family Fascioliidae Gray, 1853
Subfamily Fusiniinae Wrigley, 1927
Genus *Aptyxis* Troschel, 1868

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

1868 *Aptyxis* Troschel, p. 61, 64.

1882 *Aptyxis* Bucquoy *et al.*, p. 16, 35. Incorrect subsequent spelling.

***Aptyxis omphale* (Millet, 1864)**

Plate 2, figs 4, 5

1854 *Fusus Rostratus* Sismonda [*sic*] – Millet, p. 162 (*non Fusus rostratus* Olivi, 1792; *non* Solander, 1766 = *Fusinus sanctaluciae* (von Salis-Marschlin, 1793).

1854 *Fusus Omphale* Millet, p. 162 (*nomen nudum*).

1854 *Fusus Vicinus* Millet, p. 162 (*nomen nudum*).

1854 *Fusus Ventricosus* Millet, p. 162 (*nomen nudum*).

*1864 *Fusus omphale* Millet, p. 674.

1865 *Fusus vicinus* Millet, p. 590.

1865 *Fusus ventricosus* Millet, p. 590 (*non* Lesson, 1842; Menke, 1843 and others).

1938 *Fusus (Aptixis [sic]) rostratus* var. *ligeriana* Peyrot, p. 233, pl. 4, figs 13, 14.

1938 *Fusus (Aptixis [sic]) rostratus* var. *simplicior* Peyrot, p. 234.

1938 *Fusus (Aptixis [sic]) turonensis* Peyrot, p. 235, pl. 4, figs 28, 34 (not fig. 16 as stated in text; *lapsus*).

1952a *Fusus (Aptyxis) rostratus ligerianus* Peyrot, 1938 – Glibert, p. 349, pl. 11, fig. 3.

1964 *Fusinus (Aptyxis) ligerianus* Peyrot, 1938 – Brébion, p. 478.

Material and dimensions – Maximum height 23.1 mm. NHMW 2015/0133/0381 (1: Pl. 2, fig. 4), NHMW 2015/0133/0382 (Pl. 2, fig. 5), NHMW 2015/0133/0383 (12), LC (20), FVD (15). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The enormous shell variability found in this species was discussed at length by Glibert (1952a), who synonymised the various forms described by Peyrot (1938). The specimens from Le Pigeon Blanc are small compared to some of those found in the middle Miocene Loire Basin, similar to the smaller specimens illustrated by Glibert (1952a, pl. 11, figs 3c, 3e). Like in the older Miocene Loire Basin population, the shell width and the strength of the shoulder cord, making the whorls rounded or slightly angular, is variable. The protoconch is paucispiral, composed of about 1.5 whorls, with a large bulbous nucleus (Pl. 2, fig. 5). However, Millet (1854) listed several of the forms described by Peyrot (1938) under the names *Fusus rostratus* Sismonda, *F. omphale* Millet, *F. vicinus* Millet and *F. ventricosus* Millet. Millet's (1854) epithets are all *nomina nuda* (Landau *et al.*, 2016b), but *F. omphale* was validated in 1864 by the fol-

lowing description: ‘*Coq. allongée, fusiforme, composée de sept à huit tours de spire, le dernier terminé en une longue queue; tous garnis de côtes saillantes, couvertes, comme tout le reste de la coquille, de stries élevées, alternant en grosseur. Cette coquille atteint 6 centimètres et demi de longueur, et 2 centimètres et plus de diamètre* (1864, p. 678)’, which applies to this species. It would have been beneficial to retain Peyrot’s (1938) name, 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 *Fusus (Aptyxis) rostratus ligerianus* Peyrot, 1938 must be considered a junior subjective synonym of *Fusus omphale* Millet, 1864.

Brébion (1964, p. 479) recorded this species from Assemblage I localities (Renauleau, Sceaux d’Anjou, Thorigné, St-Clément-de-la-Place, Contigné, St-Michel, Chalonnnes, Beaulieu), Assemblage II (Apigné, Moulin de Carcé), Assemblage III (Le Pigeon Blanc, La Dixmérie), and Assemblage IV (Gourbesville).

Distribution – Middle Miocene: Atlantic (Langhian) Loire Basin, France (Glibert, 1952a). Upper Miocene: Atlantic (Tortonian and Messinian): north western France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

Genus *Carinofusus* Ceulemans, Landau & Van Dingenen, 2014

Type species (by monotypy) – *Clavella neogenica* Cossmann, 1901, Pliocene, north western France.

2014 *Carinofusus* Ceulemans, Landau & Van Dingenen, p. 25.

***Carinofusus neogenicus* (Cossmann, 1901)**

Plate 2, fig. 6

*1901 *Clavella neogenica* Cossmann, p. 21.

2014 *Carinofusus neogenicus* (Cossmann, 1901) – Ceulemans *et al.*, p. 26, pl. 1 figs 1-4, pl. 2, figs 1-4 (*cum syn*).

Material and dimensions – NHMW 2014/0288/0001 (Pl. 2, fig. 6), height 87.2 mm, width 31.2 mm; NHMW 2014/0288/0002, height 101.5 mm, width 32.2 mm; NHMW 2014/0288/0003, height 54.9 mm, width 27.0 mm; NHMW 2014/0288/0004 incomplete juvenile, height 24.4 mm; NHMW 2014/0288/0005, outer lip and spire fragment of large adult, height: 72.5 mm (fragment; reconstructed height at least 110 mm); NHMW 2014/0288/0006 (9 juveniles + adult fragments); FVD (2 incomplete adults + 63 subadult/juvenile); LC (45 subadult/juvenile); MNHN.F.A51235 (Brébion 1964, pl. 12, fig. 6) and MNHN.F.A51236 (Brébion 1964, pl. 12, fig. 7), specimens from MNHN’s collection. Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique de-

partment, NW France.

Discussion – This remarkable fusinid cannot be confused with any other shell. It is the largest shell found at Le Pigeon Blanc, characterised by sharply carinate later whorls and axial sculpture restricted to the early teleoconch whorls. Whilst juvenile specimens are not uncommon, adult shells are extremely difficult to find. For full discussion see Ceulemans *et al.* (2014).

Distribution – Lower Pliocene: Atlantic, NW France (Cossmann, 1901; Brébion, 1964; Ceulemans *et al.*, 2014).

Subfamily Peristerniinae Tryon, 1880

Genus *Polygona* Schumacher, 1817

Type species (by monotypy) – *Polygona fusiformis* Schumacher, 1817, present-day, Caribbean.

1817 *Polygona* Schumacher, p. 241.

***Polygona bellardii* (Michelotti, 1847)**

Plate 2, fig. 7

*1847 *Turbinella Bellardii* Michelotti, p. 264, pl. 8, fig. 2.

1884 *Latirus Bellardii* (Michtti.) – Bellardi, p. 24, pl. 1, fig. 19.

1935 *Lathyrus (Ascolathyrus) Bellardii* (Michtti) – Montanaro, p. 66, pl. 5, figs 7, 8.

1964 *Latirus bellardii* Michelotti, 1847 – Brébion, 473, pl. 12, figs 3, 4.

Material and dimensions – Maximum height 29.6 mm. NHMW 2015/0133/0384 (1: Pl. 2, fig. 7), NHMW 2015/0133/0385 (30), LC (50+), FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Following Vermeij & Snyder’s (2006) recent revision of the *Latirus*-group, we place this species in the genus *Polygona* Schumacher, 1817. It fits well within the *Polygona angulata* group of Vermeij & Snyder (2006) characterised by shells with a stepped spire, a distinct shoulder angulation, nodose axial ribs, an adapical sinus present on the outer lip, the outer lip convex in the central portion and lirae within the outer lip usually beaded, but smooth in some small species. *Polygona bellardii* (Michelotti, 1847) is one of the smaller species included in this genus, and very similar in size, shape and sculpture to some of the extant western Atlantic species such as *P. lactea* (Matthews-Cascon, Matthews & Rocha, 1991). The outer lip appears smooth in the Le Pigeon Blanc specimen illustrated, but it is weakly lirate within, the lirae stopping a short distance before the lip margin.

We would agree with Brébion that we cannot separate the shells from Le Pigeon Blanc from that illustrated by Bellardi (1884, pl. 1, fig. 19) as *Latirus bellardii* (Michtti.). There is some intraspecific variation in the French

shells; in some specimens the axial ribs broaden and are more widely spaced on the last whorl, becoming subobsolete on the last half whorl. The protoconch is paucispiral consisting of 1.5 smooth whorls with a bulbous nucleus (Pl. 2, fig. 7c). *Polygona spinifera* (Bellardi, 1884), also from the upper Miocene Tortonian of Italy is closely similar to *P. bellardii*, but has a slightly wider shell and develops small spines on the tubercles at the whorl periphery. This might just be a variety of *P. bellardii*, but we provisionally keep them distinct as we have not seen any spiny specimens in the Le Pigeon Blanc assemblage.

Brébion (1964, p. 474) recorded this species from Assemblage III (Le Pigeon Blanc, La Dixmérie, Palluau), and Assemblage IV (Gourbesville).

Distribution – Upper Miocene: Proto-Mediterranean (Tortonian): central Mediterranean, Italy (Michelotti, 1847; Bellardi, 1884; Montanaro, 1935). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: NW France (Brébion, 1964).

Family Nassariidae Iredale 1916 (1835)
Subfamily Nassariidae Iredale 1916 (1835)
Genus *Tritia* Risso, 1826

Type species (by subsequent designation, Gray, 1847) – *Buccinum reticulatum* Linnaeus, 1758, present-day, Europe.

- 1799 *Nassa* Lamarck, 1799. Type species (by monotypy): *Buccinum mutabile* Linnaeus, 1758, present-day, Mediterranean. Junior homonym of *Nassa* Röding, 1798.
- 1826 *Tritia* Risso, p. 172.
- 1826 *Cyclope* Risso, p. 169. Type species (by monotypy): *Cyclope neritoidea* Risso, 1826 (substitute name for *Buccinum neriteum* Linnaeus, 1758), present-day, Mediterranean.
- 1840 *Cyclonassa* Swainson, p. 300. Type species (by monotypy): *Buccinum neriteum* Linnaeus, 1758, present-day, Mediterranean. Junior objective synonym of *Cyclope*, with the same type species.
- 1847 *Hinia* Leach in Gray, p. 269. Type species (by subsequent designation, Cossmann, 1901): *Buccinum reticulatum* Linnaeus, 1758, present-day, Mediterranean.
- 1853 *Telasco* H. Adams & A. Adams, p. 119. Type species (by subsequent designation: Bucquoy *et al.*, 1882): *Buccinum variabile* Philippi, 1836, present-day, Mediterranean.
- 1853 *Uzita* H. Adams & A. Adams, p. 120. Type species (by subsequent designation, Cossmann, 1901): *Buccinum miga* Bruguière, 1789, present-day, West Africa.
- 1853 *Neritula* H. Adams & A. Adams, p. 122. Type species (by subsequent designation, Cernohorsky, 1984): *Buccinum neriteum* Linnaeus, 1758, present-day, Mediterranean.

- 1853 *Amycla* H. Adams & A. Adams, p. 186. Type species (by subsequent designation: Bucquoy *et al.*, 1882): *Buccinum corniculum* Olivi, 1792, present-day, Mediterranean.
- 1912 *Gussonea* Monterosato, p. 295. Type species (by original designation): *Buccinum tinei* Maravigna, 1840, present-day, Mediterranean.
- 1918 *Amyclina* Iredale, p. 28, 31. Type species (by original designation): *Buccinum corniculum* Olivi, 1792, present-day, Mediterranean. Unnecessary substitute name for *Amycla* H. Adams & A. Adams, 1853.
- 1920 *Hannonia* Pallary, p. 36. Type species (by monotypy): *Nassa tingitana* Pallary, 1901, present-day, Mediterranean.
- 1929 *Naytiopsis* Thiele, p. 324. Type species (by monotypy): *Buccinum granum* Lamarck, 1822, present-day, Mediterranean.
- 1929 *Proneritula* Thiele, p. 324. Type species (by monotypy): *Cyclope westerlundii* Brusina, 1900 [= *Tritia neritea* (Linnaeus, 1758)], present-day, Mediterranean.

Note – We draw attention to an important paper by Galindo *et al.* (2016) on nassariid phylogeny, which showed that shell characters fail to accurately define supraspecific taxa within Nassariinae. They suggested that all the European and West African species should be placed under *Tritia* Risso, 1826 (type species *Buccinum reticulatum* Linnaeus, 1758, present-day, Europe), although surprisingly some southern Australian and New Zealand species also fit within the *Tritia* molecular clade. They also recognised the genus *Naytia* H. & A. Adams in West Africa (type species *Strombus glabratus* G.B. Sowerby II, 1842, present-day, West Africa). The western Atlantic and eastern Pacific species should be placed in *Phrontis* H. & A. Adams, 1853 (type species *Buccinum tiarula* Kiener, 1841, present-day, Pacific coast of America). The genus *Nassarius* Duméril, 1805 (type species *Buccinum arcularia* Linnaeus, 1758, present-day, Indo-Pacific) was considered strictly Indo-Pacific, together with the genus *Reticunassa* Iredale, 1936 (type species, *Nassa paupera* Gould, 1850, present-day, Indo-Pacific). Therefore, all the species described and discussed by Van Dingenen *et al.* (2015) under the genus *Nassarius* should be re-assigned to *Tritia*.

Van Dingenen *et al.* (2015) described and recorded 11 nassariid species from Le Pigeon Blanc:

- Tritia brebioni* (Van Dingenen, Ceulemans, Landau & Silva, 2015)
Tritia crebresulcata (Bellardi, 1882)
Tritia landreauensis (Van Dingenen, Ceulemans, Landau & Silva, 2015)
Tritia merlei (Van Dingenen, Ceulemans, Landau & Silva, 2015)
Tritia spectabilis vandewouweri (Glibert, 1959)
Tritia pacaudi (Van Dingenen, Ceulemans, Landau & Silva, 2015)
Tritia palumbis (Van Dingenen, Ceulemans, Landau &

Silva, 2015)

Tritia columbina (Van Dingenen, Ceulemans, Landau & Silva, 2015)

Tritia turpis (Van Dingenen, Ceulemans, Landau & Silva, 2015)

Tritia turonensis (Deshayes, 1844)

Tritia sp. A.

To this list we add two further nassariid species:

***Tritia gibbosula pliopergibbosa* (Sacco, 1904)**

Plate 2, fig. 8

*1904 *Nassa* (*Arcularia*) *gibbosula* var. *pliopergibbosa* – Sacco, p. 63, pl. 15, figs 34-35.

non 1964 *Arcularia gibbosula* Linné, 1766 [*sic*] – Brébion, p. 434, pl. 10, figs 32, 33 [*non Nassarius gibbosulus* (Linnaeus, 1758) = *Tritia gendryi* (Van Dingenen, Ceulemans, Landau & Silva, 2015)].

2009 *Nassarius gibbosulus pliopergibbosus* (Sacco, 1904) – Landau *et al.*, p. 60, pl. 12, figs 11-12, pl. 22, fig. 2 (*cum syn.*).

Material and dimensions – Height 12.4 mm. NHMW 2015/0133/0410 (1: Pl. 2, fig. 8). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Tritia gibbosula pliopergibbosa* (Sacco, 1904) differs from the present-day Mediterranean and adjacent Atlantic *Tritia gibbosula* (Linnaeus, 1758) in the proportions of their shells. The fossil shells are less tall than the present-day shells, but of similar diameter. This gives the shell a squatter, more quadrate appearance, especially the last whorl. In the fossil shells the mean ratio of the diameter against height of the shell is 75%, whereas in the Recent shells it is only 69%. For further discussion see Landau *et al.* (2009).

This species is represented in the Le Pigeon Blanc assemblage by a single, well preserved shell. It is typical in size and shape for the species. Brébion's (1964, p. 434) records for *Arcularia gibbosula* in the Assemblage IV localities of north western France represent *Tritia gendryi* (Van Dingenen, Ceulemans, Landau & Silva, 2015). This species is much larger than *T. gibbosula* or *T. g. pliopergibbosa*, it has subobsolete axial folds on the dorsum, but no distinct dorsal gibbosity, the venter is rounded and not depressed or dimpled as in *T. gibbosula* or *T. g. pliopergibbosa*, and the parietal tooth is more strongly developed, below which the columella is more deeply excavated in the mid-portion.

Distribution – Middle Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1925). Late Miocene: Atlantic, Cabela, southern Portugal (NHMW coll.); Proto-Mediterranean, Italy (Bellardi, 1882; Montanaro, 1939; Venzo & Pelosio, 1963). Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, Spain (González-Delgado, 1989; Landau *et al.*, 2011); western Mediterranean,

north-east Spain (Martinell, 1982; Gili, 1991), southern France (Martinell & Domènech, 1986; Gili, 1991); central Mediterranean, Italy (Bellardi, 1882; Chirli, 1988, 2000), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2009), Alpes Maritimes (Chirli & Richard, 2008); central Mediterranean, Italy (Bellardi, 1882; Malatesta, 1974; Cavallo & Repetto, 1992). Pliocene indet.: central Mediterranean, Italy (Sacco, 1904).

***Tritia nitida* (Jeffreys, 1867)**

Plate 2, fig. 9

*1867 *Nassa nitida* Jeffreys, p. 349.

2009 *Nassarius nitidus* (Jeffreys, 1867) – Landau *et al.*, p. 31, pl. 6, figs 3-5 (*cum syn.*).

Material and dimensions – Height 10.2 mm. NHMW 2015/0133/0411 (1: Pl. 2, fig. 9). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Rolán & Luque (1994) showed that *T. reticulata* (Linnaeus, 1758) and *T. nitida* (Jeffreys, 1867) were separable on shell, soft parts and egg capsule morphology. The shell of *T. nitida* differs in having a somewhat scalate spire and fewer axial ribs (11-19 in *T. nitida* vs. 16-23 in *T. reticulata*). The mid-apertural denticles are often more strongly developed in *T. reticulata*, and *T. nitida* has a protoconch with less than two whorls, *T. reticulata* more than two. The single shell from Le Pigeon Blanc is squat with only nine strongly elevated axial ribs, but probably belongs within the range of variability of *T. nitida*. Unfortunately, the protoconch is not preserved in the French fossil shell. *Tritia antiqua* (Bellardi, 1882) also belongs within the *T. reticulata* species complex. It is closely similar to *T. nitida* (Jeffreys, 1867), but differs in having a squatter shell than *T. nitida*, and having strong tubercles on the columella, which extend along the whole length of the inner lip. Tubercles on the columella are sometimes more numerous, but not as strongly developed in either *T. nitida* or *T. reticulata*. The shell from Le Pigeon Blanc has two small abapical columellar tubercles and a slightly stronger parietal tubercle, all far weaker than those seen in *T. antiqua*.

Distribution – Lower Pliocene: western Mediterranean, north-eastern Spain (Martinell, 1982; Gili, 1991); central Mediterranean, Italy (Bellardi, 1882; Chirli, 2000), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, NW France (this paper), Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona, southern Spain (Landau *et al.*, 2009), Alpes Maritimes (Chirli & Richard, 2008); central Mediterranean, Italy (Bellardi, 1882; Ruggieri *et al.*, 1959). Pleistocene: Atlantic, United Kingdom (Harmer, 1916); central Mediterranean, Italy (Cerulli-Irelli, 1911). Recent: Atlantic, Mediterranean (Rolán & Luque, 1994).

Superfamily Muricoidea Rafinesque, 1815
 Family Mitridae Swainson, 1829
 Subfamily Mitrinae Swainson, 1829
 Genus *Mitra* Lamarck, 1798

Type species (by tautonymy) – *Voluta mitra* Linnaeus, 1758, present-day, Indo-Pacific.

- 1798 *Mitra* Lamarck, p. 369.
 1798 *Mitra* Röding, p. 135. Type species (by subsequent designation, Winckworth, 1945): *Voluta episcopalis* Linnaeus, 1758, present-day, Indo-Pacific. Homonym and junior objective synonym of *Mitra* Lamarck, 1798.
 1815 *Mitraria* Rafinesque, p. 145. Invalid: established as a substitute name for *Mitra* Lamarck, 1798 without diagnosis or included species.
 1853 *Chrysame* H. Adams & A. Adams, p. 171. Type species (by subsequent designation, Cox, 1927): *Mitra coronata* Lamarck, 1811, present-day, West Pacific.
 1900 *Fuscomitra* Pallary, p. 263. Type species (by subsequent designation, Cox, 1936): *Mitra fusca* Pallary, 1900 (= *M. cornea* Lamarck, 1811), present-day, Mediterranean.
 1917 *Episcomitra* Monterosato, p. 26. Type species (by monotypy): *Mitra zonata* Marryat, 1818, present-day, Mediterranean.

Note – Landau *et al.* (2011, 2013) argued that the the European Neogene '*Mitra*' species of the *M. fusiformis* group and present-day Mediterranean species should be placed in separate genus [*Episcomitra* Monterosato, 1917; 2011: *Fuscomitra* Pallary, 1900; 2013]. Apart from the unbarbed outer lip, the European species tend to have spiral sculpture restricted to the base on the last whorl, whereas many of the Pacific *Mitra* species have a totally spirally striate teleoconch.

The molecular phylogeny presented by Fedosov *et al.* (2015) included one Mediterranean species *Mitra cornicula* (Linnaeus, 1758) and found it was nestled amongst the core Mitridae (2015, p. 347, fig. 3). Therefore the shell features highlighted by Landau *et al.* (2011, 2013), seem not to be of generic value. Similarly, Landau *et al.* (2016a) separated the American tropical eastern Pacific species and placed them in the genus *Atrimitra* Dall, 1918. *Atrimitra* is also synonymised with *Mitra* by WoRMS (Rosenberg, 2015). In view of the above, this might well be true, however, no eastern Pacific species were included in the molecular phylogeny of Fedosov and until proven we exclude *Atrimitra* from the synonymy of *Mitra*.

The European fossil *Mitra* species are in need of review. There has been no critical review of the Miocene-Pliocene Mediterranean species following the standard works on the family by Bellardi (1887a, b, 1888). Cernohorsky (1976) suggested that many of Bellardi's species were synonyms, but neither performed a critical review, nor formally synonymised Bellardi's taxa. Chirli (2002) figured numerous Italian Pliocene species attributing them to Bellardi's species, but his text adds little comparative

data and is mainly limited to a repeat of Bellardi's Latin descriptions accompanied by a new description in Italian. The mitriid material from the lower Pliocene Assemblage III locality of Le Pigeon Blanc is usually incomplete and invariably has the apex abraded and the protoconch missing. We recognise three species in the assemblage. They all have spiral sculpture on early teleoconch whorls, they all have almost flat-sided to weakly concave spire whorls and they all lack spiral sculpture over the base. We have compared them to similar described forms, but note that the identifications must be considered provisional until the family is reviewed. It is also possible that further species lurk amongst the broken mitriid material at hand.

***Mitra* sp. 1**

Plate 2, fig. 10

Material and dimensions – Maximum height 27.2 mm. NHMW 2015/0133/0395 (1: Pl. 2, fig. 10); NHMW 2015/0133/0421 (3), LC (3), FVD (1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell small for genus, slender fusiform. Apex abraded in all specimens. Teleoconch of six almost flat-sided relatively tall whorls separated by superficial, markedly oblique linear suture. Early teleoconch whorls bearing 6-7 narrow flattened cords separated by punctate grooves; cords weaken abapically and disappear on third whorl. Last whorl slender, 60% of total height, hardly constricted at base, devoid of spiral sculpture over base. Aperture elongate, narrow, 40% of total height, outer lip simple, siphonal canal moderate length, weakly recurved. Columella with four oblique folds, weakening abapically. Columellar callus sharply delimited, poorly expanded, forming narrow callus rim, thickened abapically, forming medial border of narrow, shallow umbilical slit.

Discussion – *Mitra* sp. 1 has a slender fusiform shell shape, with almost flat-sided spire whorls, separated by a shallow oblique suture. It is closely similar to *Mitra infundibulum* Bellardi, 1887, described from the upper Miocene of Italy. These shell features led Bellardi (1887a, p. 12) to erect a '*6^a Serie*' for this species alone. Despite the similarity in shell shape, *M. infundibulum* was described as having five columellar folds (Bellardi, 1887a, p. 12), whereas all the French fossil specimens at hand have four.

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

***Mitra gravis* Bellardi, 1887**

Plate 3, figs 1-3

- *1887a *Mitra gravis* Bellardi, p. 11, pl. 1, fig. 6.
 1964 *Mitra gravis* Bellardi, 1887 – Brébion, p. 501, pl. 12, figs 31, 32.

Material and dimensions – Maximum height 28.4 mm. NHMW 2015/0133/0417 (1: Pl. 3, fig. 1); NHMW 2015/0133/0418 (1: Pl. 3, fig. 2); NHMW 2015/0133/0419 (1: Pl. 3, fig. 3); NHMW 2015/0133/0420 (15), LC (50+), FVD (18). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell small to medium-sized for genus, fusiform with tall conical spire. Apex abraded in all specimens. Teleoconch of 6-7 weakly convex whorls separated by impressed linear suture. Early teleoconch whorls bearing seven narrow flattened cords separated by punctate grooves; cords weaken abapically and disappear on third whorl. Last whorl weakly inflated, 60% of total height, hardly constricted at base, devoid of spiral sculpture over base. Aperture elongate, narrow, 38% of total height, outer lip simple, siphonal canal short. Columella with four oblique folds, weakening abapically. Columellar callus sharply delimited, poorly expanded, forming narrow callus rim, thickened abapically closing umbilicus completely in most specimens.

Discussion – We would agree with Brébion (1964, p. 501) in considering this species closely similar to *Mitra gravis* Bellardi, 1887 described from the upper Miocene of Italy. These mitrids form part of Bellardi's (1887a, p. 14) '5^a Serie', characterised by their relatively long spire in relation to the last whorl, giving them a somewhat turriculate rather than fusiform contour, cords on the early whorl and absence of them over the base, four columellar folds and a short siphonal canal. Of the species included in this group by Bellardi, the Le Pigeon Blanc shells are most like *M. gravis*, and although we have not seen this species and it was not re-illustrated by Ferrero Mortara *et al.* (1981) nor Davoli (2000), we provisionally consider them conspecific.

Distribution – Upper Miocene: Proto-Mediterranean (Tortonian), Italy (Bellardi, 1887a). Lower Pliocene: Atlantic, NW France (Brébion, 1964).

***Mitra cf. atava* Bellardi, 1887**

Plate 3, figs 4-5

- cf. *1887a *Mitra atava* Bellardi, p. 15, pl. 1, fig. 12.
 cf. 1981 *Mitra atava* Bellardi, 1887 – Ferrero Mortara *et al.*, p. 147, pl. 41, fig. 3.

Material and dimensions – Maximum height 51.4 mm. NHMW 2015/0133/0393 (1: Pl 3, fig. 4), NHMW 2015/0133/0394 (7), LC (9), FVD (3). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell medium-sized for genus, broad fusiform with conical spire. Apex abraded in all specimens. Teleoconch of 6-7 convex whorls separated by impressed linear suture. Early teleoconch whorls bearing narrow flattened cords, difficult to quantify due to

abrasion, separated by punctate grooves; cords weaken abapically and disappear on third whorl. Last whorl moderately inflated, 64% of total height, weakly constricted at base, devoid of spiral sculpture over base. Aperture elongate, narrow, 43% of total height, outer lip simple, siphonal canal moderate length, weakly recurved and twisted. Columella with five oblique folds, weakening abapically. Columellar callus sharply delimited, poorly expanded, forming narrow callus rim, thickened abapically, forming medial border of narrow, shallow umbilical slit.

Discussion – This species seems to belong to Bellardi's (1887a, p. 14) '8^a Serie', characterised by their regularly fusiform shape, the presence of cords on the early whorl and absence of them over the base in most species, five columellar folds and the siphonal canal slightly twisted to the left. Bellardi used *Mitra turricula* De Cristofori & Jan as reference species for the group, which differs from *Mitra atava* Bellardi, 1887 in having teleoconch whorls strongly shouldered just below the suture. Some of the other species included in this group are closely similar to *M. atava* and, like the rest of the group, need to be revised. This is the largest of the Le Pigeon Blanc mitrids and also bears some resemblance to *Mitra fusiformis* (Brocchi, 1814), which has 5-6 columellar folds, but the latter differs in having shouldered whorls and the early spire whorls lack spiral sculpture.

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

Family Cystiscidae Stimpson, 1865

Subfamily Persiculinae G. A. Covert & H. K. Covert, 1995

Genus *Gibberula* Swainson, 1840

Type species (by monotypy) – *G. zonata* Swainson, 1840 (= *Volvaria oryza* Lamarck, 1822), present-day, eastern Atlantic.

- 1840 *Gibberula* Swainson, p. 323.
 1875 *Granula* Jousseume, p. 167. Type species (by subsequent designation; Coan, 1965): *Marginella bensoni* Reeve, 1865, present-day, South Africa.
 1951 *Kogomea* Habe in Kuroda, p. 103. Type species (by original designation): *Erato novemprovincialis* Yokoyama, 1928, Pleistocene, Japan.
 1957 *Epiginella* Laseron, p. 279. Type species (by original designation): *E. ablita* Laseron, 1957, present-day, Australia.
 1957 *Phyloginella* Laseron, p. 280. Type species (by original designation): *P. compressa* Laseron, 1957, present-day, Coral Sea.
 1962 *Diluculum* Barnard, p. 14. Type species (by original designation): *D. inopinatum* Barnard, 1962, present-day, South Africa.

***Gibberula miliaria* (Linnaeus, 1758)**

Plate 3, fig. 6

- *1758 *Voluta miliaria* Linnaeus, p. 730.
- 1952a *Persicula* (*Gibberula*) *miliaria* Linné, 1766 – Glibert, p. 369, pl. 12, fig. 8.
- 1964 *Gibberula miliaria* Linné – Brébion, p. 533.
- 1987 *Gibberula miliaria* (Linné, 1758) – Gofas, p. 125, figs 14-16, pl. 1, fig. d-d'.
- 2003 *Gibberula miliaria* (Linné, 1758) – Giannuzzi-Savelli *et al.*, p. 276, figs 699-704.

Material and dimensions – Maximum height 7.5 mm. NHMW 2015/0133/0396 (1: Pl. 3, fig. 6), NHMW 2015/0133/0397 (8), LC (12), FVD (5). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Two *Gibberula* species occur in the Le Pigeon Blanc assemblage, the larger of the two is ascribed to *Gibberula miliaria* (Linnaeus, 1758). The spire is low in most specimens, the outer lip denticulate in all, and the columella bears 5-6 folds, weakening apically. It is similar to the Pliocene Mediterranean *G. proxima* Landau, La Perna & Silva, 2006 from the Estepona Basin, Spain, but the latter is broader-shelled, with the shoulder placed higher, *G. miliaria* is more slender and regularly cylindrical in shape, and the labial varix is thicker, especially abapically in *G. proxima*.

Gibberula miliaria was also recorded by Glibert (1952a) from the middle Miocene Loire Basin and by Brébion (1964) in the Assemblage I, II and IV deposits in north-western France (Brébion, 1964). These records will be discussed in a subsequent paper. Interestingly, the presence of this species in the Pliocene Mediterranean and Iberian coast has not been confirmed in the recent literature (Chirli, 2002; Landau *et al.*, 2006b; Silva *et al.*, 2011). We have not included older references, which need to be confirmed.

Silva *et al.* (2011) discussed the biogeographical implications of the European shallow marine marginelliform gastropods and considered them a relatively thermophilic group. They demonstrated the increase in generic and specific diversity with a decrease in latitude (southwards), and the southwards shift in diversity since Pliocene time (2011, tables 1, 2, figure 7). The Le Pigeon Blanc marginellid assemblage suggests that *Gibberula* is the most tolerant to cooler waters, as it is the only genus present in the lower Pliocene of north western France and we are not aware of any Pliocene records of marginellids further north. It is also interesting that the two species found here; *G. miliaria* and *G. philippii* (Monterosato, 1878) are now extant in the Mediterranean, whereas the Pliocene cohort of species (Chirli, 2002; Landau *et al.*, 2006b; Silva *et al.*, 2011) are extinct. Landau *et al.* (2006b) and Silva *et al.* (2011) traced the diverse origins of the Pliocene Mediterranean marginellid assemblage and recognised a strong West African influence to the fauna. It is possible that the cooling of SST (sea surface temperature) since the Pliocene resulted in the extinction

of the more thermophilic West African influenced cohort of species, which were then replaced by more temperature tolerant northern forms.

Brébion (1964, p. 503) recorded this species from Assemblage I localities (Renauleau, Thorigné, Sceaux d'Anjou, St-Clément-de-la-Place, St-Michel, Beaulieu), Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Le Girondor), and Assemblage IV (Gourbesville). In the distribution we have only included the Assemblage III records. The others will be discussed in subsequent papers.

Distribution – Lower Pliocene: Atlantic, NW France (Brébion, 1964). Present-day: Mediterranean and adjacent Atlantic (Gofas, 1987).

***Gibberula philippii* (Monterosato, 1878)**

Plate 3, fig. 7

- *1878 *Marginella philippi* [sic] Monterosato, p. 109. (*nom. nov. pro Marginella minuta* Philippi, 1844 non Pfeiffer, 1840 = *Gibberula pfeifferi* Faber, 2004; non *Marginella minima* Gray, 1826).
- 1964 *Gibberula philippi* [sic] Monterosato, 1878 – Brébion, p. 534, pl. 13, figs 15-17.
- 1987 *Gibberula philippii* (Monterosato, 1878) – Gofas, p. 129, figs 18-20, pl. 2, figs b-e.
- 2003 *Gibberula philippii* (Monterosato, 1878) – Giannuzzi-Savelli *et al.*, p. 276, figs 713-714.

Material and dimensions – Maximum height 3.5 mm. NHMW 2015/0133/0398 (1: Pl. 3, fig. 7), NHMW 2015/0133/0399 (20), LC (50+), FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – The smaller of the two *Gibberula* species found at Le Pigeon Blanc we attribute to *Gibberula philippii* (Monterosato, 1878). The French fossil specimens agree with the description and figures given by Gofas (1987) for the species, except that the denticulation at the inner edge of the outer lip is variable: well developed in some specimens, absent in others. Interestingly, the presence of this species in the Pliocene Mediterranean and Iberian coast has not been confirmed in the recent literature (Chirli, 2002; Landau *et al.*, 2006b; Silva *et al.*, 2011), for further discussion see under *G. miliaria* (above). We have not included older references, which need to be confirmed.

Brébion (1964, p. 503) recorded this species from the middle Miocene Loire Basin (La Beurelière), Assemblage I localities (Thorigné, St-Clément-de-la-Place, St-Michel), Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Palluau), and Assemblage IV (Gourbesville). In the distribution we have only included the Assemblage III records. The others will be discussed in subsequent papers.

Distribution – Lower Pliocene: Atlantic, NW France

(Brébion, 1964). Present-day: Mediterranean and adjacent Atlantic (Gofas, 1987).

Superfamily Olivoidea Latreille, 1825

Family Olividae Latreille, 1825

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

Type species (by subsequent designation, Cossmann, 1899) – *Ancillaria tankervillei* Swainson, 1825, present-day, Caribbean.

1853 *Amalda* H. Adams & A. Adams, p. 148.

Amalda glandiformis* (Lamarck, 1810) morphotype *elongata

Plate 3, fig. 8

- *1810 *Ancillaria glandiformis* Lamarck, p. 305.
- 1964 *Ancilla (Baryspira) glandiformis* Lamarck, 1810 – Brébion, p. 482.
- 2006 *Amalda glandiformis* (Lamarck, 1810) morphotype *elongata* – Landau & Silva, p. 6, pl. 1, figs 1-8 (*cum syn.*).
- 2013 *Amalda glandiformis* (Lamarck, 1810) – Landau *et al.*, p. 222, pl. 32, figs 9, 10, pl. 68, fig. 4, pl. 80, fig. 6.

Material and dimensions – Maximum height 51.2 mm. NHMW 2015/0133/0386 (1: Pl. 3, fig. 8), NHMW 2015/0133/0387 (12), LC (25), FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was discussed in detail by Landau & Silva (2006) and Landau *et al.* (2013). The *elongata* morphotype of *Amalda glandiformis* (Lamarck, 1810) is characterised by its tall narrow spire and thin callus. Specimens of the form *elongata* are very similar to *Amalda obsoleta* (Brocchi, 1814), generally fusiform in shape, with a tall narrow spire and thin spire and parietal calluses, but are separated based on the width of the ancillid band, which is much wider in *A. obsoleta* than in *A. glandiformis* forma *elongata*. As discussed by Landau & Silva (2006), all the Pliocene Iberian Atlantic reports for the genus *Amalda* correspond to *A. glandiformis* morphotype *elongata*, although not always identified as such. Cox (1941) erected the name *Ancilla marinhensis* for the Portuguese Pliocene form, without justifying the separation, apart from saying they were different from the French and Italian Miocene specimens. Brébion (1971, p. 130) synonymised the Portuguese shells with *Amalda glandiformis*. Zbyszewski (1959), on the other hand considered them *A. obsoleta*. All these shells fall within the range of *A. glandiformis* forma *elongata* as defined by Glibert (1952a). The same is true in the Le Pigeon Blanc assemblage. *Amalda glandiformis* forma *elongata* is the only form of the species found in the north-western French Assemblage III localities. Moreover, it is the dom-

inant medium-sized gastropod found in Le Pigeon Blanc, with hundreds of specimens present.

The presence of *Amalda* in vast numbers in the Le Pigeon Blanc assemblage is interesting. Landau & Silva (2006) pointed out that today *Amalda* is a temperate genus and that it occurs in tropical and subtropical zones only in places where there is upwelling of cooler, nutrient-rich waters. They suggested that in the fossil assemblages, the presence of large numbers of *Amalda*, in assemblages of tropical or subtropical character, was an indicator of upwelling. Thus, the great number of *Amalda* found in the Le Pigeon Blanc assemblage, that is subtropical in character, suggests upwelling in the area. This hypothesis is further supported by the presence of *Patella pellucida* Linnaeus, 1758 (Ceulemans *et al.*, 2016, p. 53). *Patella pellucida* is a north-western Atlantic shallow water grazing gastropod typically living and feeding on laminarian algae (Silva *et al.*, 2006). 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. Therefore, the presence of *P. pellucida* in Le Pigeon Blanc suggests laminarian algae surviving in subtropical waters, and hence the presence of upwelling.

Brébion (1964, p. 483) recorded *A. glandiformis* morphotype *elongata* from Assemblage I localities (Thorigné, St-Michel), Assemblage II (Apigné, Lillion), and Assemblage III (Corcoué-sur-Logne, Les Cléons, Le Pigeon Blanc, Le Gironдор, La Gauvinière, La Dixmérie, Palluau).

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1952a); Aquitanian Basin, France (Glibert, 1960); Paratethys, Hungary (Strausz, 1966), Bulgaria (Kojumdzieva & Strachimirov, 1960); Proto-Mediterranean: Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic, Cabela, Portugal (Pereira da Costa, 1867), NW France (Glibert, 1960; Brébion, 1964); Proto-Mediterranean: Italy (Sacco, 1904; Davoli, 1989). Lower Pliocene: Atlantic, Guadalquivir Basin (González-Delgado, 1992; Landau *et al.*, 2011). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Cox, 1941; Zbyszewski, 1959; Brébion, 1971; Silva, 2001, 2002), Bou Regreg Basin, NW Morocco (Glibert, 1960); western Mediterranean: Estepona Basin (Landau & Silva, 2006).

Subfamily Scaphellinae Gray, 1857

Genus *Euroscaphella* Van Dingenen, Ceulemans & Landau, 2014

Type species (by original designation) – *Voluta lamberti* J. Sowerby, 1816, North Sea Basin, Pliocene, England.

2014 *Euroscaphella* Van Dingenen, Ceulemans, & Landau, p. 104.

***Euroscaphella namnetensis* Van Dingenen, Ceulemans, & Landau, 2014**

Plate 3, fig. 9

- 1908 *Voluta Lamberti* Sow. – Dumas, p.121.
 1964 *Scaphella lamberti* (Sowerby, 1816) – Brébion, p. 517, pl. 13, fig. 2 [*non Euroscaphella lamberti* (J. Sowerby, 1816)].
 1989 *Scaphella lamberti* (Sowerby, 1816) – Lauriat-Rage *et al.*, p. 131, pl. 8, fig. 19 [*non Euroscaphella lamberti* (J. de C. Sowerby, 1816)].
 *2014 *Euroscaphella namnetensis* Van Dingenen, Ceulemans, & Landau, p. 104, pl. 1, figs 1-10.

Material and dimensions – Holotype NHMW 2014/0287/0001 (Pl. 3, fig. 9), length 82.3 mm, width 30.2 mm, protoconch diameter 5.2 mm; paratype 1 NHMW 2014/0287/0002, length 96.6 mm, width 31.3 mm (incomplete: outer lip damaged); paratype 2 NHMW 2014/0287/0003, length 84.3 mm, width 27.4 mm (incomplete: outer lip damaged); paratype 3 NHMW 2014/0287/0004, length 63.3 mm, width 23.6 mm (subadult: outer lip damaged); paratype 4 NHMW 2014/0287/0005, length 46.9 mm, width 17.4 mm (juvenile), NHMW 2014/0287/0006 (11 juveniles); FVD (4 + 50+ subadult and juveniles); LC (3 + 45 subadult and juveniles), Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – *Euroscaphella namnetensis* Van Dingenen, Ceulemans, & Landau, 2014 is characterised by its small size for the genus, its solid, fusiform shell, strongly flattened protoconch, short spire, with whorls rapidly increasing in height, in having a slender, weakly shouldered last whorl, an outer lip with a well-developed palatal callus, and a short siphonal canal. It is most similar to the slightly older *E. miocenica* Fischer & Tournouër, 1879 from the middle Miocene Langhian of the Loire Basin, which also has a relatively solid shell and a well-developed palatal callus. It differs, however, in being smaller in size, in having a more slender last whorl, which is less shouldered than in *E. miocenica* and in having the base of the last whorl hardly constricted, and therefore the siphonal fasciole is not well-developed, as it is in *E. miocenica*. For further discussion see Van Dingenen *et al.* (2014).

Distribution – Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2014).

Superfamily Cancellarioidea Forbes & Hanley, 1851
 Family Cancellariidae Forbes & Hanley, 1851
 Subfamily Cancellariinae Forbes & Hanley, 1851
 Genus *Bivetiella* Wenz, 1943

Type species (by original designation of *Bivetia* Jousseume, 1887b) – *Cancellaria similis* G. B. Sowerby I, 1833, present-day, north western Africa.

- 1943 *Bivetiella* Wenz, p. 1356. Replacement name for

Bivetia Jousseume, 1887b, p. 193, *non* 1887a, p. 163.

- 1949 *Bivetiella* Marks, p. 456. Type species (by original designation): *Cancellaria similis* G. B. Sowerby I, 1833, present-day, north western Africa. Junior objective synonym and junior homonym of *Bivetiella* Wenz, 1943.

***Bivetiella cancellata* (Linné, 1767)**

Plate 4, fig. 1

- *1767 *Voluta cancellata* Linné, p. 1191.
 2006a *Cancellaria (Bivetiella) cancellata* (Linnaeus, 1767) – Landau *et al.*, p. 63, pl. 1, figs 1, 2 (*cum syn.*).
 2007 *Bivetiella cancellata* (Linnaeus, 1767) – Verhecken, p. 295, figs 11, 13-18, 21A, 22, 23A, 24A, 25.
 2010 *Cancellaria cancellata* (Linnaeus, 1767) – Sosso & Dell'Angelo, p. 43, unnumbered fig. p. 59 3rd row middle.
 2011 *Bivetiella cancellata* (Linnaeus, 1767) – Brunetti *et al.*, p. 88, figs 1C-G, 2A-C.

Material and dimensions – Maximum height 10.5 mm (incomplete juvenile). LC (2 juveniles, most complete; Pl. 4, fig. 1). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species was fully discussed by Landau *et al.* (2006a) and Brunetti *et al.* (2011). It seems to be very uncommon in the Le Pigeon Blanc assemblage, where it is represented by a few juvenile specimens. *Bivetiella cancellata* (Linné, 1767) today is found along the coast of West Africa and into the Mediterranean, but not the southern Atlantic Iberian coast. This record in the lower Pliocene of north western France again demonstrates a range contraction for the species due to cooling since Pliocene time.

Distribution – Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, Spain (González-Delgado, 1992; Landau *et al.*, 2011); Morocco (Lecointre, 1952; González-Delgado *et al.*, 1999); western Mediterranean, northern Spain (Almera & Bofill, 1884; Martinell, 1979); Roussillon, France (Fontannes, 1882); central Mediterranean, Italy (Chirli, 2002; Brunetti *et al.*, 2011); Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001), Estepona Basin, Spain (Vera-Peláez *et al.*, 1995; Landau *et al.*, 2006a); central Mediterranean, Italy (Sacco, 1894; Glibert, 1960; Caretto, 1963; Malatesta, 1974; Pavia, 1975; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Brunetti *et al.*, 2011). Pleistocene: western Mediterranean, Morocco (Lecointre, 1952), Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1911; Glibert, 1960; Malatesta, 1960). Present-day: West Africa, Morocco-Angola, Canary, São Tomé and Príncipe islands, western Mediterranean, Alboran Sea (Verhecken, 2007).

Genus *Brocchinia* Jousseume, 1887

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

1887b *Brocchinia* Jousseume, p. 221.

***Brocchinia pigeonblancensis* nov. sp.**

Plate 4, figs 2-4

1964 *Narona (Brocchinia) mitraeformis* Brocchi, 1814 – Brébion (*partim*), p. 531, pl. 13, figs 12, 13 (non *Voluta mitraeformis* Brocchi, 1814, non Lamarck, 1811 = *Brocchinia tauroparva* Sacco, 1894) (Assemblage III records only).

Type material – Holotype MNHN.F.A57681, height 12.0 mm (specimen illustrated by Brébion, 1964, pl. 13, figs 12, 13; herein Pl. 3, fig. 2); paratype 1 NHMW 2015/0133/0388 (Pl. 3, fig. 3), height 11.1 mm; paratype 2 NHMW 2015/0133/0414, height 12.2 mm; paratype 3 NHMW 2015/0133/0415, height 10.5 mm; paratype 4 NHMW 2015/0133/0416, height 10.4 mm; paratype 5 NHMW 2015/0133/0389 (juvenile; Pl. 3, fig. 4).

Other material – Maximum height 12.3 mm. NHMW 2015/0133/0390 (50+); LC (50+), FVD (50+). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

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

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

Stratum typicum – Zanclean, lower Pliocene.

Diagnosis – A *Brocchinia* species of medium size for genus, with a paucispiral protoconch composed of 1.5-1.75 whorls, a tall, slender spire, sculpture consisting of eight broad rounded axial ribs, somewhat nodular mid-whorl, weakening abapically, obsolete, or almost so, on last whorl, weak spiral sculpture, and a thin, somewhat flared outer lip, lirate within.

Description – Shell of medium size for genus, of medium thickness, fusiform, elongated, with an elevated conical spire. Protoconch of 1.5-1.75 relatively tall, smooth whorls, with an impressed suture, nucleus medium-sized. Junction with teleoconch sharply delimited by prosocline scar. Teleoconch of four shouldered whorls, with steep, concave subsutural ramp, separated by weakly impressed linear suture. Spiral sculpture weak, begins at transition zone, consisting of five narrow spiral cords, narrower than their interspaces, Abapically number of cords increases to 9-10 on penultimate whorl. Axial sculpture starts on first teleoconch whorl, consisting of eight broad, prosocline, rounded ribs, obsolete on

subsutural ramp, nodular at shoulder, weakening again towards abapical suture. Last whorl about 60% total height. Sculpture on last whorl variable, in most specimens axial ribs strong mid-whorl, in some ribs weaken on last whorl, subobsolete towards outer lip. Aperture ovate, about 40% of total height. Outer lip not thickened, regularly convex, somewhat flared, lirate within. Siphonal canal open, short, wide. Columella bearing two oblique folds of equal strength. Parietal callus thin, sharply delimited, closely adherent and hardly expanded. Umbilicus closed.

Discussion – The taxonomy of the European Neogene *Brocchinia* species becomes ever more complex. Malatesta (1974) noted *Voluta mitraeformis* Brocchi, 1814 to be a junior primary homonym of *Voluta mitraeformis* Lamarck, 1811 and suggested *Cancellaria pusilla* H. Adams, 1869 as a replacement name, although he considered the Recent and Neogene populations to be separable and stated that the name *Cancellaria cerithiopsis* Almera & Bofill, 1887 [*sic*] was available for the fossil specimens. Petit (1986b) pointed out that *Cancellaria pusilla* H. Adams, 1869 was not available, being a junior primary homonym of *Cancellaria pusilla* G.B. Sowerby I, 1832 and that *C. cerithiopsis* dates from 1898, not 1887. Petit (1986a) suggested *Brocchinia parvula parvula* (Beyrich, 1856) for the populations from the Miocene North Sea Basin and Paratethys and *Brocchinia parvula tauroparva* Sacco, 1894 for the Italian Miocene to Pliocene shells. Davoli (1982, 1995) argued that Brocchi's name was available as Brocchi pointed out that his species belonged to Lamarck's genus *Cancellaria* and should be retained in order to guarantee a stable nomenclature. On p. 645 Brocchi clearly proposed the species '*Voluta mitraeformis*', although in the text under the description he does say '*Questa Voluta ha la forma di una Mitra di Lamarck, ma appartiene non per tanto al genere Cancellaria di questo naturalista*'. Under the ICZN rules this is of no significance. Its original introduction as *Voluta mitraeformis* makes it a junior primary homonym and thus unavailable. Landau *et al.* (2006a) pointed out that the genus was represented in the European Neogene by a group of related, but distinct species. They highlighted the importance of the protoconch morphology and showed that the north western French upper Miocene-Pleistocene forms were not conspecific with those found in the Mediterranean. Brunetti *et al.* (2011) reviewed the Italian Pliocene species. These authors rejected Petit's (1986a) conclusion that *Brocchinia parvula tauroparva* was typical of the Pliocene Italian forms, as Sacco (1894) based this subspecies on middle Miocene specimens, which Brunetti *et al.* (2011, p. 120) said were different, without clearly stating what these differences were. These authors argued that the first available name for the Pliocene form was *B. mitraeformis depressiplicata* Sacco, 1894. However, they recognised three species in the Italian Pliocene: *B. depressiplicata*, *B. subanodosa* Sacco, 1894 and *B. crassinodosa* Sacco, 1894. Apart from teleoconch sculptural details separating these three species, they differ in the number of protoconch whorls, having 2.0: 2.75: 2.5

whorls respectively.

The revision by Brunetti *et al.* (2011) confirms the statement made by Landau *et al.* (2006a) that the north western French *Brocchinia* species were not conspecific with those found in the Italian Pliocene. When this statement was made, the junior author (BL) was comparing material from the Assemblage I locality of Sceaux d'Anjou. This is the material described by Millet (1854, p. 160) as *Cancellaria auriculoides*. However, on examination of the plentiful material at hand from Assemblage I localities of Sceaux d'Anjou, Renauleau and St-Clément-de-la-Place (NHMW coll.), the Le Pigeon Blanc specimens differ in being slightly larger, but thinner shelled, with a higher spire and in having the axial ribs much broader and somewhat nodular mid-whorl. In most specimens of *Brocchinia pigeonblancensis* nov. sp. the axial ribs continue relatively strongly at least onto the first half of the last whorl, whereas in *B. auriculoides* the axial ribs weaken much earlier on the second or third teleoconch whorl. The spiral sculpture is weak in both species, but even more so in *B. pigeonblancensis*. We note that there might be a second *Brocchinia* species in the Assemblage I material, which will be explored in a separate paper. Cossmann (1899, p. 20) described *B. rissioaeformis* from the Upper Pliocene-Pleistocene Assemblage IV locality of Gourbesville. The holotype is poorly preserved, but the specimen illustrated by Brébion (1964, p. 532, pl. 13, fig. 14) from the type locality shows a rather small (height 7 mm), squat species, with a protoconch composed of two whorls, about 12 spiral cords and no axial sculpture.

Harmer (1918, p. 396, pl. 39, figs 40, 41) described and illustrated specimens of *Brocchinia* from the Coralline and Red Craggs of eastern England. Unfortunately he did not describe the protoconch type. However, two specimens at hand from the lower Pliocene Coralline Crag of Gedgrave (NHMW coll.) have a paucispiral protoconch similar to the shells from Le Pigeon Blanc, but the English specimens are larger and more solid than the French shells, the spiral sculpture is coarser, the axial sculpture is weaker so that the last whorl is devoid of ribs, and the aperture is more dilated, with stronger lirations within the outer lip. We provisionally consider them distinct.

In the Italian Pliocene *B. pigeonblancensis* is most like *B. depressiplicata*, but differs in having a paucispiral protoconch of only 1.5-1.75 whorls instead of two and in having fewer axial ribs (8 vs. 10-11), which are broader and more prominent mid-whorl, giving the whorls a shouldered appearance. *Brocchinia crassinodosa* Sacco, 1894, apart from having a multispiral protoconch composed of 2.5 whorls, has even fewer (7 vs. 8), more elevated ribs than *B. pigeonblancensis*, which extend between the sutures, as this species does not have a distinct subsutural ramp.

In the extant faunas the eastern Atlantic *Brocchinia clenchi* Petit, 1986, found off Portugal, Selvagem Grande, Canary Islands, Azores, and Western Sahara (Verhecken, 2007), also has a paucispiral protoconch of 1.5 whorls, but differs in having fewer, wider spaced spiral cords and weaker axial ribs.

In summary, in the Pliocene three species occur in the

Mediterranean: *B. depressiplicata*, *B. subanodosa* Sacco, 1894 and *B. crassinodosa* Sacco, 1894, one species occurs in lower Pliocene of north western France: *B. pigeonblancensis* and a further, probably undescribed, species in the Pliocene North Sea Basin of England. One species occurs in the upper Pliocene-Pleistocene of north western France: *B. rissioaeformis*. Today the genus has a more restricted distribution in the Atlantic, found only south of central Portugal.

Brébion (1964, p. 532) recorded *Narona (Brocchinia) mitraeformis* from numerous assemblages in north western France, but in view of the discussion above we consider only the Assemblage III (Le Pigeon Blanc, Palluau) records as *B. pigeonblancensis*.

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

Genus *Trigonostoma* Blainville, 1827

Type species (by monotypy) – *Delphinula trigonostoma* Lamarck, 1822 [= *Trigonostoma scalare* (Gmelin, 1791)], present-day, Indo-Pacific.

1827 *Trigonostoma* Blainville, p. 652.

Trigonostoma umbilicare (Brocchi, 1814)

Plate 4, fig. 5

- *1814 *Voluta umbilicaris* Brocchi, p. 312, pl. 3, figs 10-11.
- non 1874 *Cancellaria umbilicaris* ? Brocchi – Wood, p. 182, addendum plate, fig. 10. (*non Voluta umbilicaris* Brocchi) (= *Trigonostoma bellardii* De Stefani & Pantanell, 1879).
- non 1878 *Cancellaria umbilicaris* Brocch. – Nyst, pl. 1, fig. 5, pl. 28, fig. 8. (*non Voluta umbilicaris* Brocchi) (= *Trigonostoma bellardii* De Stefani & Pantanell, 1879).
- non 1882 *Cancellaria umbilicaris* Brocchi – Nyst, p. 8. (*non Voluta umbilicaris* Brocchi) (= *Trigonostoma bellardii* De Stefani & Pantanell, 1879).
- non 1916 *Trigonostoma umbilicare* (Brocchi) – Harmer, p. 400, pl. 40, figs 3, 4. (*non Voluta umbilicaris* Brocchi) (= *Trigonostoma bellardii* De Stefani & Pantanell, 1879).
- 2006a *Trigonostoma (Trigonostoma) umbilicare* (Brocchi, 1814) – Landau *et al.*, p. 68, pl. 3, fig. 1 (*cum syn.*).
- 2009 *Trigonostoma umbilicare* (Brocchi, 1814) – Brunetti *et al.*, p. 112, figs 16A-D.
- 2011 *Trigonostoma umbilicare* (Brocchi, 1814) – Landau *et al.*, p. 30, pl. 15, fig. 12.

Material and dimensions – Height 34.3 mm. NHMW 2015/0133/0413 (1 incomplete; Pl. 4, fig. 5), LC (1 incomplete, 5 fragments). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – This species is represented by two large incomplete specimens from Le Pigeon Blanc. Only part of the spire and the outer lip are preserved, but they are typical for this rather large *Trigonostoma* species, which until now was known only from the Pliocene Mediterranean and adjacent Atlantic. This is the most northern Pliocene record for the species. The North Sea Basin records of *T. umbilicare* (Wood, 1874; Nyst, 1878, 1882; Harmer, 1916) represent *T. bellardii* De Stefani & Pantanelli, 1879.

Distribution – Lower Pliocene: Atlantic, NW France (this paper), Guadalquivir Basin, Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Sacco, 1894; Chirli, 2002; Brunetti *et al.*, 2009). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Vera-Peláez *et al.*, 1995; Landau *et al.*, 2006a); central Mediterranean, Italy (Sacco, 1894; Glibert, 1960; Cavallo & Repetto, 1992).

***Trigonostoma* sp.**

Plate 4, fig. 6

Material and dimensions – Height 16.2 mm, width 10.5 mm. NHMW 2015/0133/0412 (1; Pl. 4, fig. 6). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell small to medium sized, solid, fusiform with scalate spire. Protoconch dome-shaped, consists of three convex whorls. Teleoconch of four barrel-shaped whorls, with moderately broad, flattened, concave sutural gutter. Suture superficial, undulating. Axial sculpture consisting of eight relatively broad, elevated, rounded, prosocline ribs, forming broad nodes at shoulder. Ribs cross sutural gutter, narrowing towards adapical suture, dividing gutter into large pits. Spiral sculpture overrides axial ribs, consists of six narrow primary cords below shoulder, with secondary and tertiary threads intercalated in interspaces on later whorls. Spiral sculpture most evident where it crosses ribs, subobsolete between ribs on later whorls. Last whorl moderately inflated, with deeply concave sutural gutter, convex below shoulder, with ten primary spiral cords, basal cord delimiting deep, moderately wide umbilicus, smooth within, except inconspicuous growth lines. Aperture subtrigonal, approximately 40% of the total height, Outer lip thickened by labial varix, lirate within, with small siphonal spout abapically. Columella shallowly excavated, bearing three oblique columellar folds, weakening abapically. Columellar callus thickened, erect, forming medial border of umbilicus, parietal callus sharply delimited, thickened, weakly expanded.

Discussion – One well preserved specimen of a *Trigonostoma* Blainville, 1827 species may represent an undescribed species. It is most similar to Pliocene Atlantic and Mediterranean and *T. bellardii* De Stefani & Pantanelli, 1879, but most specimens of this species have more numerous axial ribs, which are narrower, less elevated and spinous at the shoulder, the spiral sculpture, although

also weak, is stronger than in the shell from Le Pigeon Blanc and does not weaken in the interspaces between the ribs as it does in the French shell, and the umbilicus is wider. *Trigonostoma parvotriangula* Sacco, 1894 from the Pliocene Mediterranean has similar axial sculpture composed of broad elevated ribs that form tubercles at the shoulder, but this species has a broader shell shape and a much wider umbilicus, which bears sculpture within. We await further material to better characterise this species.

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

Subfamily Admetinae Troschel, 1865

Genus *Pseudobabylonella* Brunetti, Della Bella, Forli & Vecchi, 2009

Type species (by original designation) – *Cancellaria minima* Reeve, 1856, present-day, West Africa.

2009 *Pseudobabylonella* Brunetti, Della Bella, Forli & Vecchi, p. 65.

***Pseudobabylonella fusiformis* (Cantraine, 1835)**

Plate 4, fig. 7

- *1835 *Cancellaria fusiformis* Cantraine, p. 391.
- 2006a *Babylonella fusiformis* (Cantraine, 1835) – Landau *et al.*, p. 86, pl. 9, figs 1-4 (*cum syn.*).
- 2008 *Babylonella costillifera* [*sic*] (Sowerby, 1818) – Chirli & Richard, p. 53, pl. 10, fig. 7.
- 2009 *Pseudobabylonella fusiformis* (Cantraine, 1835) – Brunetti *et al.*, p. 66, figs 7B-L, 8A-D.
- 2009 *Pseudobabylonella subangulosa* (Wood, 1848) – Brunetti *et al.*, p. 69, figs 9A-F, 12B.
- 2009 *Pseudobabylonella applicata* Brunetti *et al.*, p. 70, figs 10C-H, 11A-E, 12A.
- 2010 *Pseudobabylonella applicata* Brunetti, Della Bella, Forli & Vecchi, 2009 – Sosso & Dell'Angelo, p. 43, p. 60 unnumbered fig. top row right.
- 2010 *Pseudobabylonella fusiformis* (Cantraine, 1835) – Sosso & Dell'Angelo, p. 43, p. 60 unnumbered fig. middle row left.

Material and dimensions – Height 8.7 mm. NHMW 2015/0133/0391 (1; Pl. 4, fig. 7), LC (4). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Discussion – Landau *et al.* (2006a) and Verhecken (2007) highlighted how uncomfortably *Cancellaria fusiformis* Cantraine, 1835 and *Cancellaria minima* Reeve, 1856 fitted within the cancellariid generic groups recognised at the time. Brunetti *et al.* (2009) erected a new supraspecific taxon for these species: *Pseudobabylonella*, a solution with which we agree. The most outstanding character of the genus is the fine cancellate sculpture covering the protoconch.

In the same paper these authors revised the representatives of their new genus in the Plio/Pleistocene of Italy and recognised three species: *P. fusiformis*, *P. subangulosa* (Wood, 1848) and *P. applicata* Brunetti, Della Bella, Forli & Vecchi, 2009 differing in shell profile and sculptural detail. The variability of these species is tabulated in their paper (Brunetti *et al.*, 2009, p. 78).

In our opinion the authors are over-splitting. The reasons for this conclusion are: 1) All three have exactly the same protoconch. 2) All three have the same stratigraphic distribution (Brunetti *et al.*, 2009, p. 79, tab. 3). 3) All three species are widely distributed geographically, based on the synonymy given by the authors (*i.e.* all three species occur in the North Sea Basin and Mediterranean (the record of *B. fusiformis subangulosa* (Wood) given by Marquet (1998) is included in the synonymy of both *P. fusiformis* and *P. subangulata* with a question mark). 4) In their description, *P. applicata* has five cords on the sub-sutural ramp and six cords from the shoulder to the abapical suture (2009, p. 73). The authors do not distinguish primary from secondary cords. The development of secondary spiral sculpture in many cancellariids is variable, and it is clear that their figs 11A-E have four primary cords below the shoulder (including shoulder cord), with a secondary thread developed in some of the interspaces (compare their figs 11A, B vs. C, D). This is even more clearly demonstrated by the two specimens illustrated by Landau *et al.* (2006a, pl. 9, figs 2, 3) from the upper Pliocene Estepona Basin of Spain, which were both synonymised with *P. applicata* by Brunetti *et al.* (2009). 5) The present-day West African representative of the genus *B. minima* (Reeve, 1856) differs in having a paucispiral protoconch. The interspecific variability was illustrated by Verhecken (2007, p. 293, figs 9A-F). The variability in shell profile and sculpture mirrors that seen in its Neogene ancestor *P. fusiformis*. Brunetti *et al.* (2009, p. 66) countered this argument by saying that these figures probably represented various different species.

If we consider the shell characters of the specimen from Le Pigeon Blanc, the elongated, slender shell profile is that of *P. applicata*, however, the whorls are regularly rounded, as the shoulder cord is not outstanding. On the penultimate whorl there are four primary cords from the shoulder, with a single secondary thread intercalated in the interspaces. This would fit within the diagnostic criteria for *P. applicata*. However, there are 16 axial ribs, which is considerably more than the 10-12 recognised by Brunetti *et al.* (2009, p. 78) for *P. applicata*. The protoconch is identical to that of the rest of the group (Pl. 4, fig. 7c).

At present we do not find it useful to erect yet another specific taxon within *Pseudobabylonella* for the Le Pigeon Blanc specimens. We prefer to consider *P. fusiformis* a stratigraphically and geologically widespread species characterised by its multispiral protoconch covered in cancellate microsculpture and teleoconch with cancellate sculpture composed of a variable number of axial and spiral elements. This is probably the predecessor of the present-day *B. minima*, which has a similarly sculptured paucispiral protoconch and variable teleoconch sculp-

ture. If future genetic testing of *B. minima* should show it to represent a species complex rather than a single taxon, the above discussion could be reviewed.

Distribution – Middle Miocene: North Sea Basin, Germany (Kautsky, 1925; Glibert, 1960; Anderson, 1964; Wienrich, 2001), Denmark (Ravn, 1907; Sorgenfrei, 1958; Rasmussen, 1956, 1968), Netherlands (Glibert, 1960; Nord-sieck, 1972; Janssen, 1984a & b), Belgium (Glibert, 1952b); Atlantic, Aquitaine Basin, France (Cossmann, 1899; Peyrot, 1928). Upper Miocene: Proto-Mediterranean, Italy (Sacco, 1894; Davoli, 1982, 1995). Lower Pliocene: Atlantic: NW France (this paper); North Sea basin, England (Wood, 1848; Harmer, 1916), Belgium (Marquet, 1997, 1998); central Mediterranean, Italy (Sacco, 1894; Pavia, 1975; Chirli, 2002; Brunetti *et al.*, 2009). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2006a), Alpes Maritimes (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1894; Cavallo & Repetto, 1992; Brunetti *et al.*, 2009; Sosso & Dell'Angelo, 2010).

Pseudobabylonella? sp.

Plate 4, fig. 8

1964 *Narona (Sveltia) elongata* Brébion, p. 528, p. 13, fig. 8 (*nomen nudum*).

Material and dimensions – Height 11.3 mm. NHMW 2015/0133/0392 (1: Pl. 4, fig. 8). Le Pigeon Blanc, Le Landreau, Nantes area, Loire-Atlantique department, NW France.

Description – Shell small, moderately fragile, slender fusiform. Protoconch and early teleoconch whorls missing. Five relatively tall, regularly convex teleoconch whorls preserved. Sculpture of narrow orthocone axial ribs, 15 on penultimate whorl, crossed by seven narrow spiral cords, slightly narrower and more crowded on sub-sutural ramp, shoulder cord slightly stronger, subequal below shoulder. Last whorl elongate with 18 axial ribs, secondary spiral threads intercalated between primaries mid-whorl, base weakly constricted. Aperture ovate, outer lip damaged, smooth within. Columella weakly excavated, bearing two narrow oblique folds. Columella callus hardly developed, poorly delimited; parietal callus not developed.

Discussion – This is undoubtedly the same species described by Brébion (1964, p. 528, p. 13, fig. 8) as *Narona (Sveltia) elongata* Brébion (*nomen nudum*). However, we are uncertain of the generic placement. Species included in the genus *Sveltia* Jousseume, 1887 are larger, more solid, and have a better developed inner lip callus. The slender, rather delicate shell, and weak inner lip callus are reminiscent of *Pseudobabylonella* Brunetti, Della Bella, Forli & Vecchi, 2009, but we would need to see a protoconch for the characteristic reticulated microsculpture to be certain. We await more material to better characterise this species.

Brébion (1964, p. 528) recorded it from Assemblage III (Le Pigeon Blanc) only.

Discussion

In this paper we record 26 neogastropod species, of which four are left in open nomenclature, representing 17 genera. Three species are described as new: *Euthria palumbina* nov. sp., *Bartschia* (*Agassitula*) *harasewychi* nov. sp. and *Brocchinia pigeonblancensis* nov. sp. Just under half of the species (46%) occur exclusively in north western French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. Stratigraphically (see Text-fig. 2), eight (30%) of the species found at Le Pigeon Blanc are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1949). Six (23%) are also present in the Assemblage I (sensu Van Dingenen *et al.*, 2015) of north western France. Fourteen (53%) are also recorded in the Miocene to present-day Mediterranean and only one species is shared with the North Sea Basin and one with the Atlantic coasts of the British Isles.

As with previous parts of this series (Ceulemans *et al.*, 2016; Van Dingenen *et al.*, 2016), an important number of genera such as *Aplus*, *Euthria*, *Aptyxis*, *Bivetiella* and *Trigonostoma* are still found in European waters, but with a more southern distribution, again suggesting that average Sea Surface Temperatures were higher than they are at these latitudes today, possibly similar to those found off the southern Portuguese coasts at present time.

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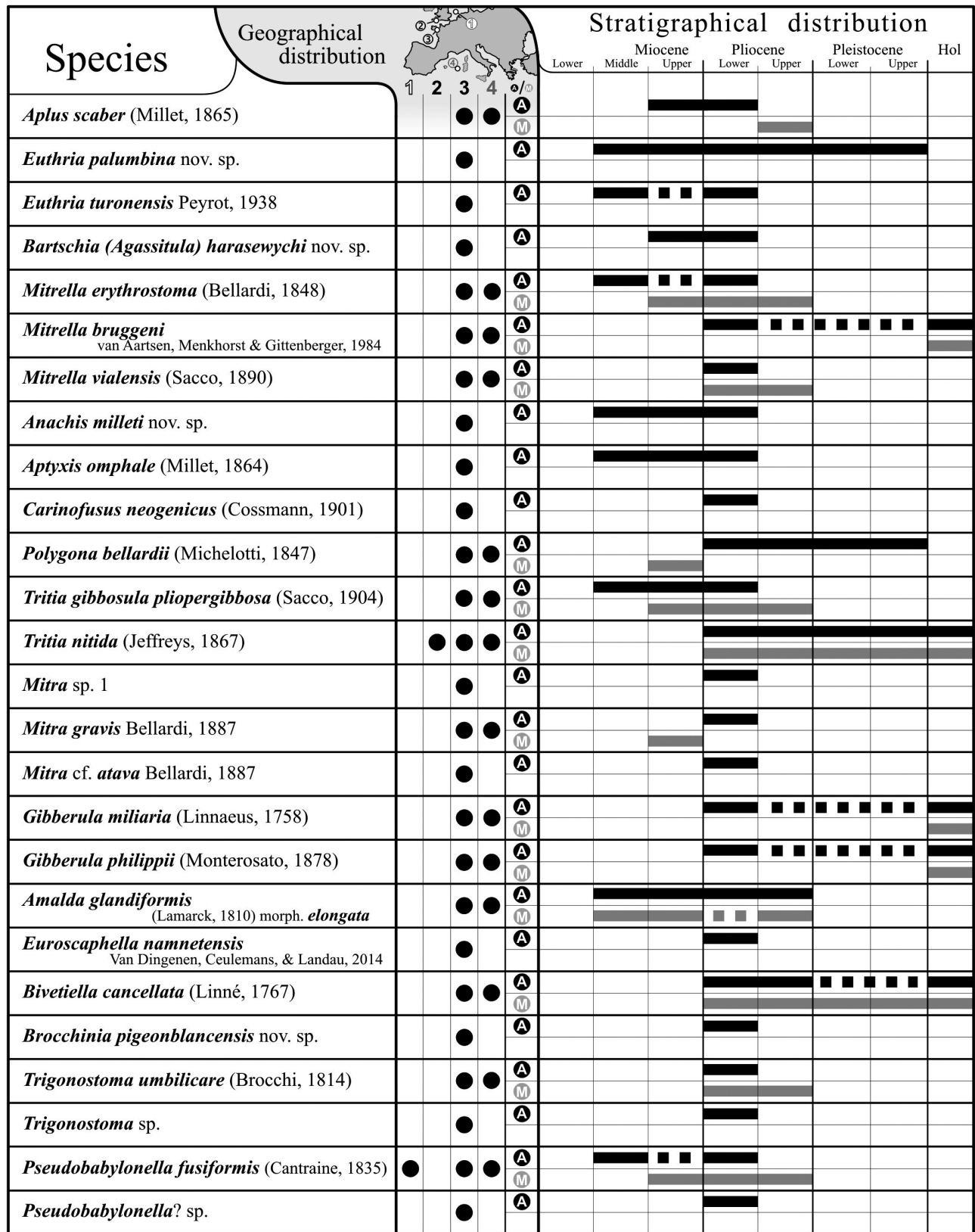
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Text-figure 2. Geography, stratigraphy and distribution of species found in the Pliocene of Le Pigeon Blanc. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution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

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Plate 1

1. *Aplus scaber* (Millet, 1865), NHMW 2015/0133/0369, height 13.8 mm.
2. *Aplus scaber* (Millet, 1865), NHMW 2015/0133/0370, height 11.7 mm.
3. *Aplus scaber* (Millet, 1865), NHMW 2015/0133/0371, height 13.0 mm.
4. *Euthria palumbis* nov. sp., **holotype** NHMW 2015/0133/0363, height 38.6 mm.
5. *Euthria palumbis* nov. sp., **paratype 1** NHMW 2015/0133/0364, height 25.8 mm.
6. *Euthria palumbis* nov. sp., **paratype 2** NHMW 2015/0133/0365, detail of protoconch.
7. *Euthria turonensis* Peyrot, 1938, NHMW 2015/0133/0368, height 19.3 mm.
8. *Bartschia (Agassitula) harasewycki* nov. sp., **holotype** NHMW 2015/0133/0367, height 27.9 mm.
9. *Mitrella erythrostoma* (Bellardi, 1848), NHMW 2015/0133/0373, height 22.7 mm.
10. *Mitrella bruggeni* van Aartsen, Menkhorst & Gittenberger, 1984, NHMW 2015/0133/0378, height 11.9 mm.

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

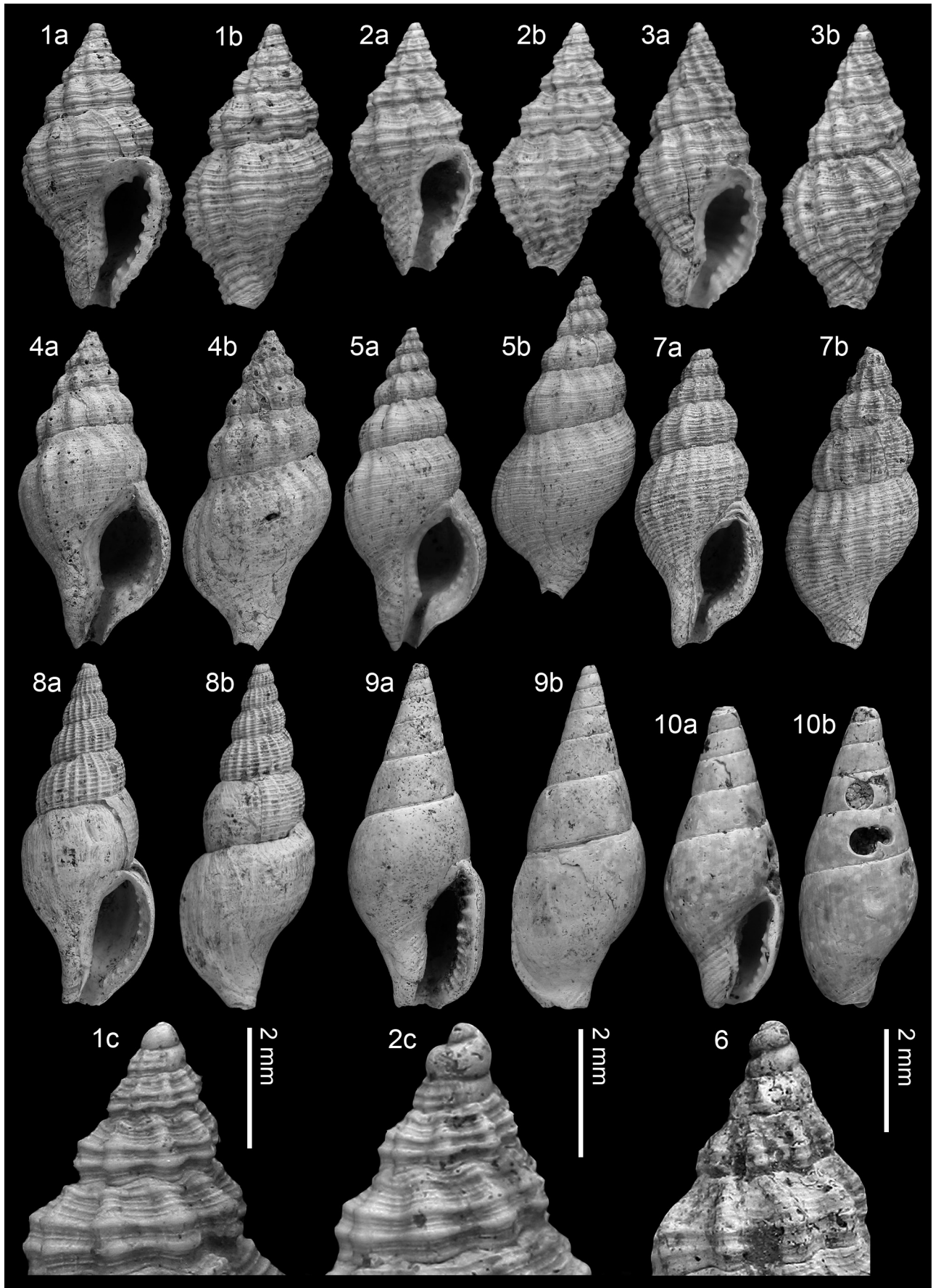


Plate 1

Plate 2

1. *Mitrella vialensis* (Sacco, 1890), NHMW 2015/0133/0374, height 11.8 mm.
2. *Mitrella vialensis* (Sacco, 1890), NHMW 2015/0133/0375, detail of protoconch (SEM).
3. *Anachis milleti* nov. sp., NHMW 2015/0133/0379, height 9.9 mm.
4. *Aptyxis omphale* (Millet, 1864), NHMW 2015/0133/0381, height 23.1 mm.
5. *Aptyxis omphale* (Millet, 1864), NHMW 2015/0133/0382, detail of protoconch.
6. *Carinofusus neogenicus* (Cossmann, 1901), NHMW 2014/0288/0001, height 87.2 mm.
7. *Polygona bellardii* (Michelotti, 1847), NHMW 2015/0133/0384, height 29.6 mm.
8. *Tritia gibbosula pliopergibbosa* (Sacco, 1904), NHMW 2015/0133/0410, height 12.4 mm.
9. *Tritia nitida* (Jeffreys, 1867), NHMW 2015/0133/0411, height 10.2 mm.
10. *Mitra* sp. 1, NHMW 2015/0133/0395, height 26.6 mm.
11. *Bartschia* (*Agassitula*) *harasewycki* nov. sp., **paratype** NHMW 2015/0133/0426, height 20.4 mm.

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

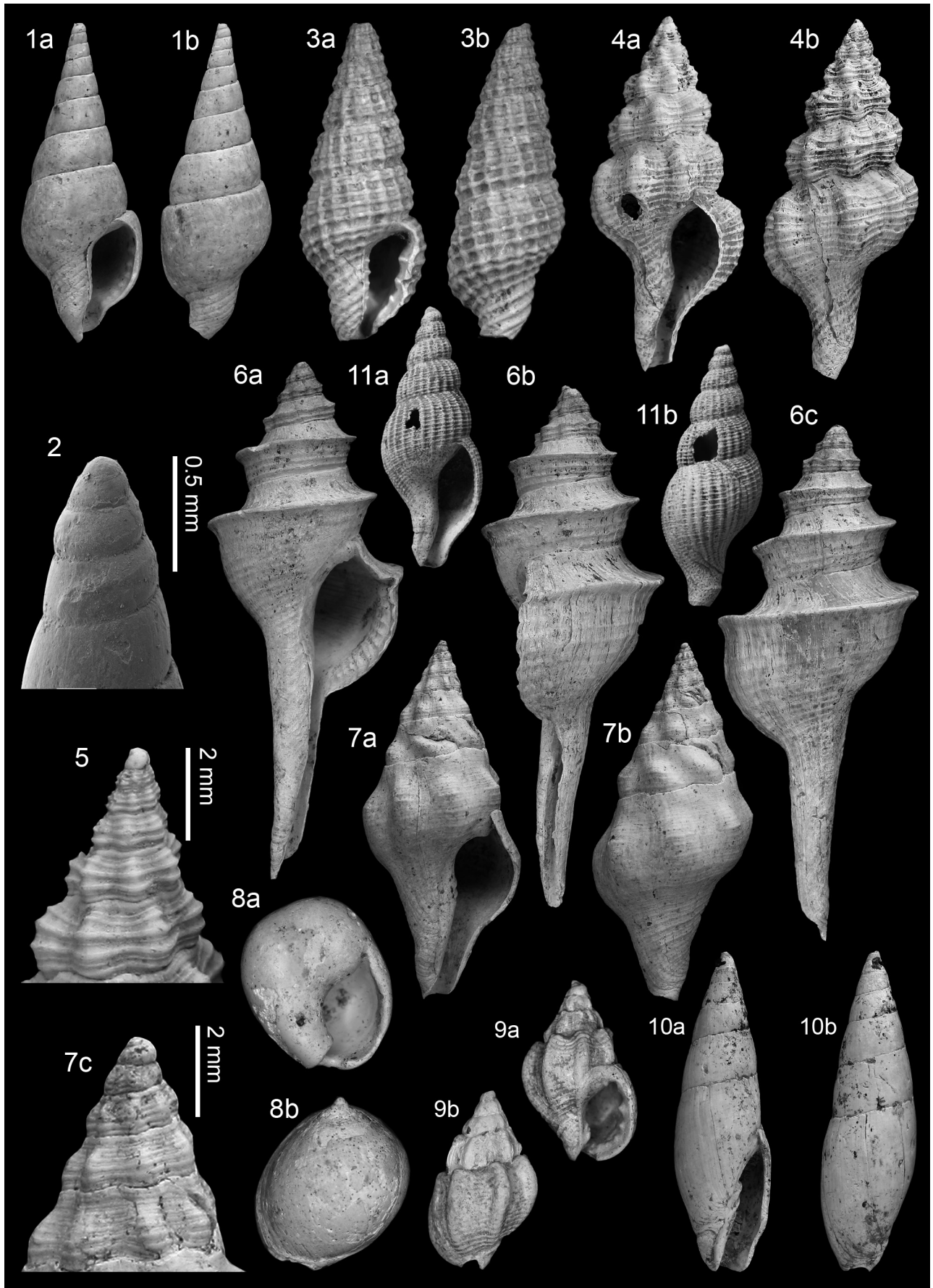


Plate 2

Plate 3

1. *Mitra gravis* Bellardi, 1887, NHMW 2015/0133/0417, height 28.4 mm.
2. *Mitra gravis* Bellardi, 1887, NHMW 2015/0133/0418, height 22.2 mm.
3. *Mitra gravis* Bellardi, 1887, NHMW 2015/0133/0419, height 23.4 mm.
4. *Mitra* cf. *atava* Bellardi, 1887, NHMW 2015/0133/0393, height 44.0 mm.
5. *Mitra* cf. *atava* Bellardi, 1887, LC coll., height 51.4 mm.
6. *Gibberula miliaria* (Linnaeus, 1758), NHMW 2015/0133/0396, height 6.3 mm.
7. *Gibberula philippii* (Monterosato, 1878), NHMW 2015/0133/0398, height 3.4 mm.
8. *Amalda glandiformis* (Lamarck, 1810) morphotype *elongata*, NHMW 2015/0133/0386, height 49.7 mm.
9. *Euroscaphella namnetensis* Van Dingenen, Ceulemans & Landau, 2014, **holotype** NHMW 2014/0287/0001, height 82.3 mm.

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

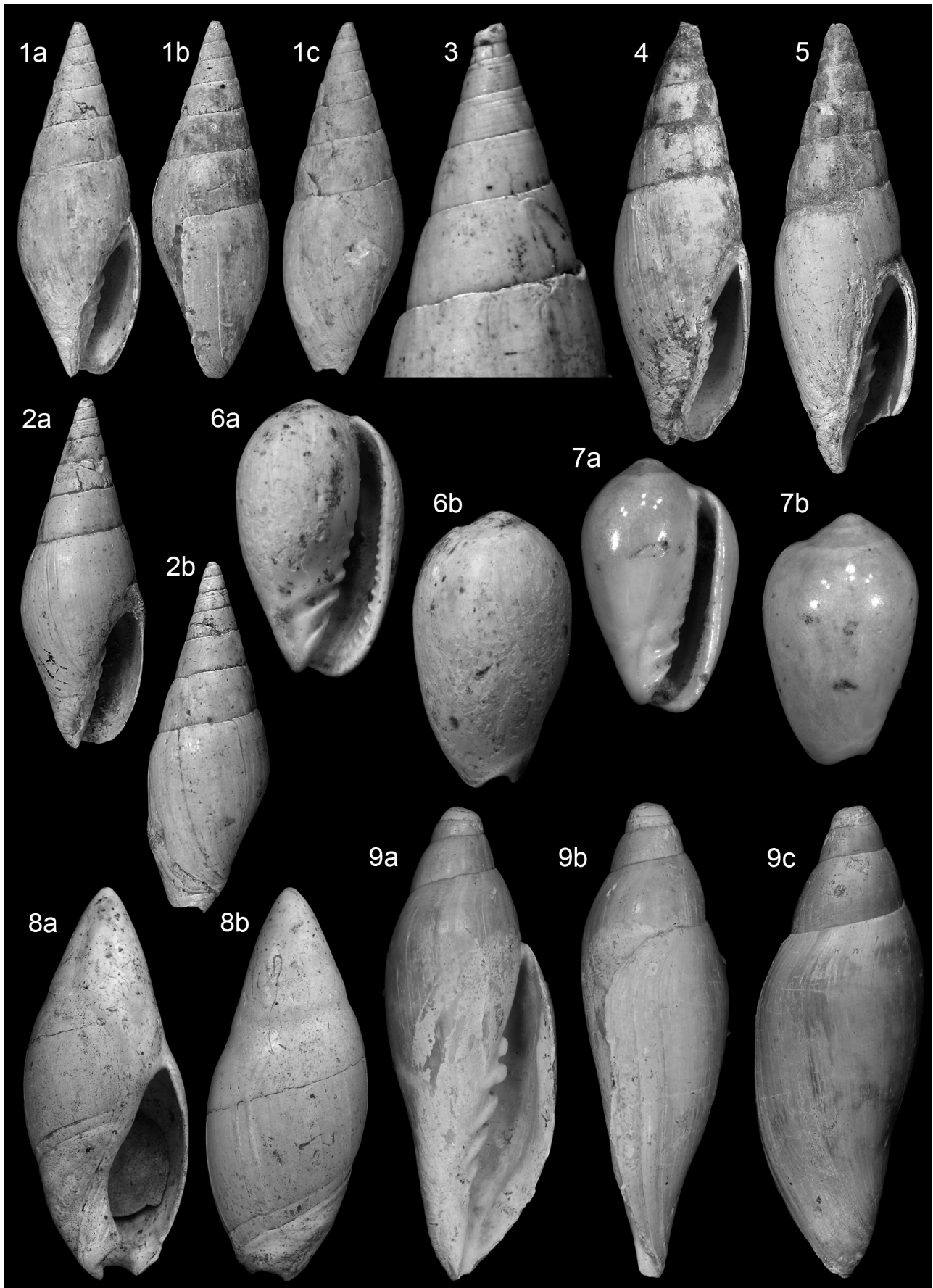


Plate 3

Plate 4

1. *Bivetiella cancellata* (Linné, 1767), LC coll., height 8.1 mm.
2. *Brocchinia pigeonblancensis* nov. sp., **holotype** MNHN.F.A57681, height 12.0 mm (photo Jocelyn Falconnet; MNHN).
3. *Brocchinia pigeonblancensis* nov. sp., **paratype 1** NHMW 2015/0133/0388, height 11.1 mm.
4. *Brocchinia pigeonblancensis* nov. sp., **paratype 5** NHMW 2015/0133/0389, detail of protoconch (SEM).
5. *Trigonostoma umbilicare* (Brocchi, 1814), NHMW 2015/0133/0413, height 34.3 mm.
6. *Trigonostoma* sp., NHMW 2015/0133/0412, height 16.2 mm.
7. *Pseudobabylonella fusiformis* (Cantraine, 1835), NHMW 2015/0133/0391, height 8.7 mm.
8. *Pseudobabylonella?* sp., NHMW 2015/0133/0392, height 11.3 mm.

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

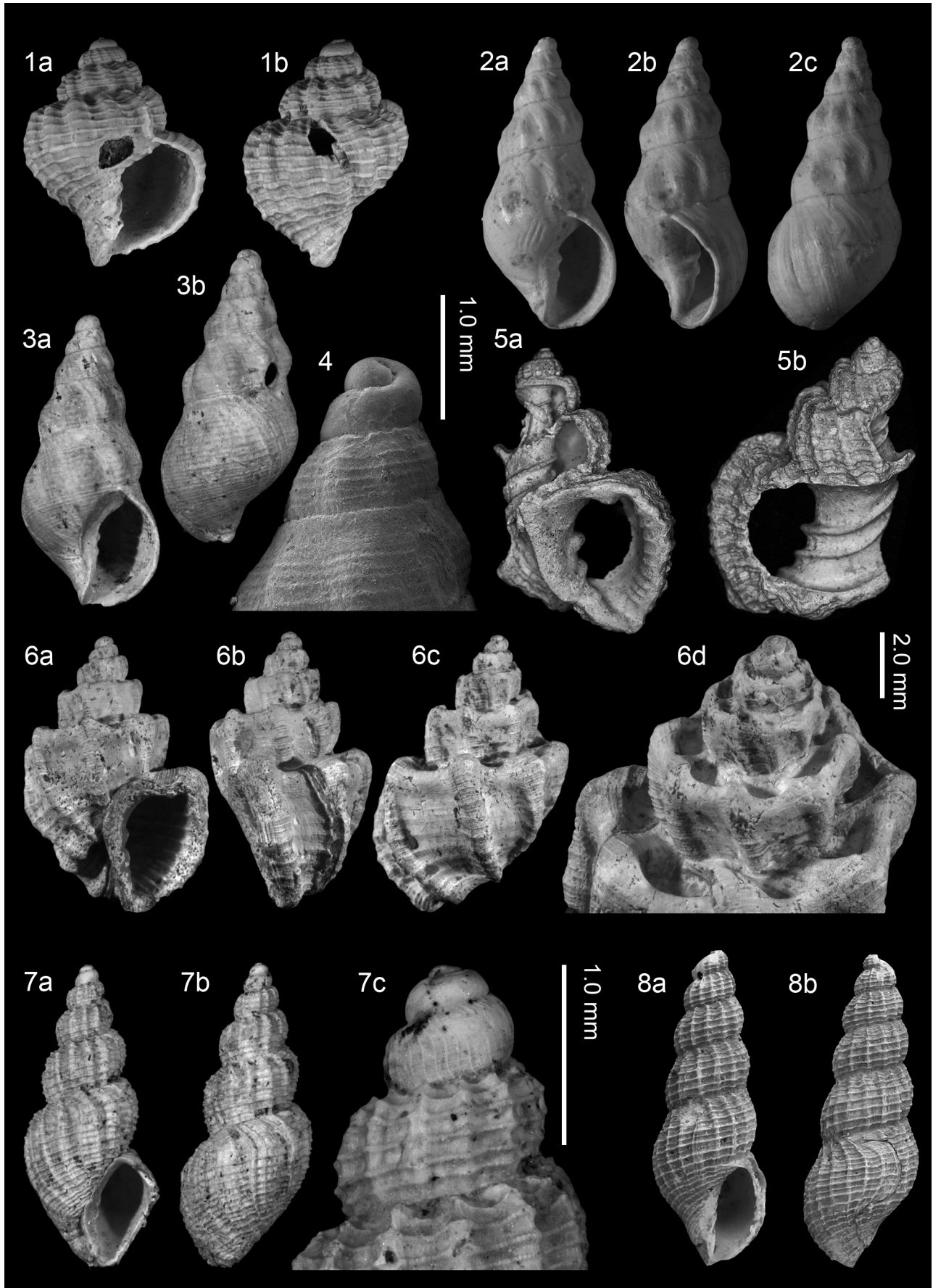


Plate 4