The upper Miocene gastropods of northwestern France, 6. Heterobranchia

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In this paper we review the Heterobranchia (in part) of the Tortonian upper Miocene (Assemblage I of Van Dingenen *et al*., 2015) of northwestern France. Twenty-three species are recorded, of which four are described as new; *Ammonicera oliveri* nov. sp., *Ebala ornatissima* nov. sp., *Coenaculum boucheti* nov. sp., and '*Acteon*' *distinctus* nov. sp.

Key words: northwestern France, upper Miocene, Gastropoda, new taxa

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al*., 2014, 2016a, b, 2018; Van Dingenen *et al*., 2015, 2016, 2017; Landau *et al*., 2017, 2018, 2019a, b, 2020): Gastropods of the Subclass Heterobranchia (in part) in the Assemblage I deposits of Van Dingenen *et al*. (2015) of Tortonian late Miocene age are revised.

In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded 15 species within the groups covered in this paper from Assemblage I deposits, one of which was described as new. However, as the thesis was never published, new names do not comply with article 13 of the ICZN code (1999) and must be considered *nomina nuda* (see comment Landau *et al*., 2020, p. 3).

Geological setting and material and methods

References for this paper (part 6) are combined with those of part 7 (directly following part 6 in this same volume of Cainozoic Research) and can be found at the end of the part 7 paper.

Landau *et al*. (2017, p. 78) gave a list of the private collections consulted during this work that had been donated to the Naturalis Biodiversity Center in Leiden (The Netherlands). This list was updated in Landau *et al*. (2019a, p. 3).

Abbreviations:

FVD	Frank Van Dingenen private collection (Brecht, Belgium).
LC	Luc Ceulemans private collection (Rixensart, Belgium).
MNHN.F	Muséum national d'Histoire naturelle, collection de Paléontologie (Paris, France).
NHMW	Naturhistorisches Museum Wien collection (Vienna, Austria).
RGM	Naturalis Biodiversity Center, collection Cainozoic Mollusca (Leiden, The Netherlands).

Systematics

Systematics has been updated following Bouchet *et al.* (2017).

Subclass Heterobranchia
Superfamily Architectonicoidea Gray, 1850
Family Architectonicidae Gray, 1850
Genus *Pseudotorinia* Sacco, 1892

Type species (by original designation) – *Solarium obtusum* Bronn, 1831, Pliocene, Italy.

1892b *Pseudotorinia* Sacco, p. 66.
1930 *Awarua* Mestayer, p. 145. Type species (by original designation): *Omalaxis amoena* Murdoch &

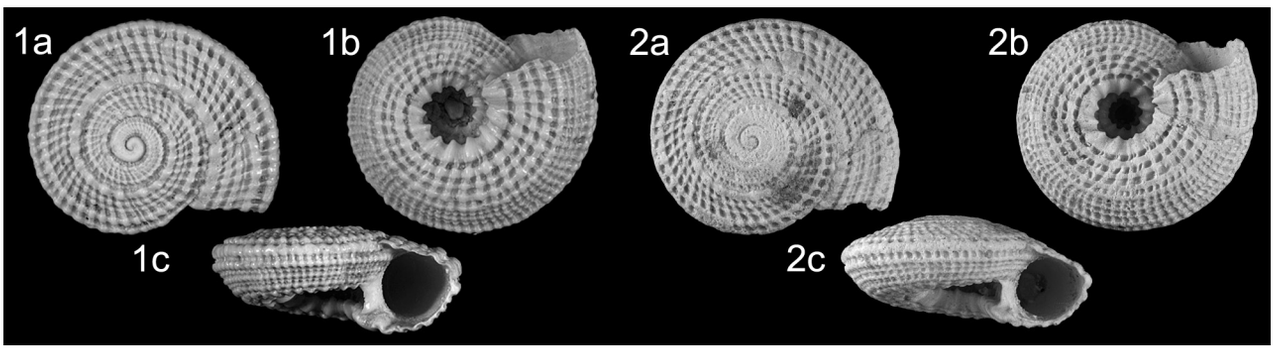

Plate 1. *Pseudotorinia subplicata* (d'Orbigny, 1852); 1. NHMW 2016/0103/1060, diameter 4.0 mm, height 1.2 mm; 2. NHMW 2016/0103/1871, diameter 3.9 mm, height 1.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Suter, 1906, present-day, New Zealand.

1935 *Calodisculus* Rehder, p. 129. Type species (by original designation): *Discohelix retifera* Dall, 1892, Pliocene, Florida, USA.

***Pseudotorinia subplicata* (d'Orbigny, 1852)**
Plate 1, figs 1, 2

*1832 *Solarium plicatum* Grateloup, p. 136.
1845 *Solarium plicatum* Grateloup, pl. 12, fig. 36.
1852 *Solarium subplicatum* d'Orbigny, p. 45 (*nov. nom. pro S. plicatum* Grateloup, 1832 *non* Lamarck, 1804).
1854 *Solarium Plicatum* Lmk. – Millet, p. 157 (*non* Lamarck, 1804).
1919 *Solarium* (*Pseudotorinia*) *subplicatum* d'Orb. – Cossmann & Peyrot, p. 673, pl. 15, figs 59-61.
1964 *Architectonica* (*Pseudotorinia*) *subplicata* d'Orbigny, 1852 – Brébion, p. 207, pl. 5, fig. 13.

Material and dimensions – Maximum diameter 6.5 mm, height 2.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1060 (1), NHMW 2016/0103/1871 (1), NHMW 2016/0103/1061 (12), RGM.1352433 (2), LC (18), FVD (9). **Sceaux-d'Anjou**: NHMW 2016/0103/1062 (2), RGM. 1348342 (1), RGM.1352450 (1), RGM.1352542 (1), RGM. 718059 (8).

Discussion – For shell terminology see Bieler (1993). *Pseudotorinia subplicata* (d'Orbigny, 1852) is typical of the first group of *Pseudotorinia* species, for which Bieler (1993, p. 276, fig. 224a) gave a schematic representation, the *P. architae* (O. G. Costa, 1841) species group. It is characterised by its small, flattened discoidal shape, the dorsum weakly elevated to flattened, the subsutural rib (SSR) is broad, there are 2-3 midribs, depending on the growth stage, the upper peripheral rib (UPR) and lower peripheral rib (LPR) are placed high, LPR thickest, inferior peripheral rib (IPR) well developed. The base is weakly carinate to rounded, bearing seven cords, broadening towards the umbilical crenae (UC). The umbilicus is moderately wide and deep. It is similar to the middle Miocene shell from the Loire Basin illustrated by Glibert (1949a) as *Solarium* (*Pseudotorinia*) *planulatum ivolasi* (Mayer-Eymar, in Ivolas & Peyrot, 1900), but *P. planulata* and its various forms differ from *P. subplicata* in having a strongly carinate base and there are fewer ribs between the basal carina and the UC.
Brébion (1964, p. 209) recorded this species from numerous Assemblage I localities (Renauleau, Sceaux-d'Anjou, St-Clément-de-la-Place, Thorigné).

Distribution – Lower Miocene (Aquitanian and Burdigalian), Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1919). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964).

Superfamily Omalogyroidea Sars, 1878
Family Omalogyridae Sars, 1878
Genus *Ammonicera* Vayssière, 1893

Type species (by monotypy) – *Omalogyra fischeriana* Monterosato, 1869, present-day, Mediterranean, Italy.

1879 *Ammonicera* Vayssière, p. 19.

***Ammonicera oliveri* nov. sp.**
Plate 2, fig. 1

Type material – Holotype MNHN.F.A70516, diameter 1.1 mm, height 0.3 mm; paratype 1 NHMW 2016/0103/0967, diameter 1.0 mm; paratype 2 NHMW 2016/0103/0968, diameter 1.1 mm, **St-Clément-de-la-Place**. Paratype 3 RGM.1362951, diameter 1.1 mm; paratype 4 RGM. 1362952, diameter 1.0 mm, **Sceaux-d'Anjou**.

Other material – Maximum diameter 1.5 mm x 1.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1874 (36), LC (4), FVD (5). **Sceaux-d'Anjou**: RGM.1348890 (1), RGM.717921 (17). **Beugnon**: NHMW 2016/0103/0969 (20), RGM.1348431 (12), RGM.1348493 (1).

Etymology – Name after Joan Daniel Oliver, Madrid,

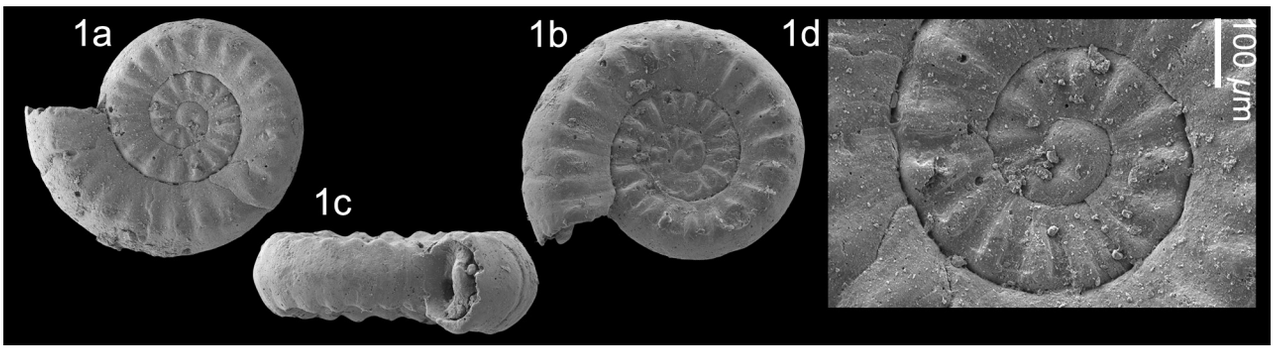

Plate 2. *Ammonicera oliveri* nov. sp.; 1. **Holotype** MNHN.F.A70516, diameter 1.1 mm x 930 μm, 1d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Spain, in recognition of his excellent work on the family. *Ammonicera* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Ammonicera* species with broad raised ribs on dorsum and venter, very broad adapical band, narrow peripheral band, almost without spiral groove separating them, groove mid-whorl on protoconch hardly developed.

Description – Shell minute, planispiral, amphiconcave. Protoconch about one whorl, bearing radial groove starting after nucleus; suggestion of rugose microsculpture on second half of protoconch whorl adapical to medial groove. Transition with teleoconch marked by raised scar. Teleoconch of 2.5 whorls bearing broad raised ribs, roughly equal in width to their interspaces, developed on both dorsum and venter, but not at periphery. Adapical band very wide, peripheral band narrow, separated by weak groove only visible on first 1.5 teleoconch whorls. Aperture subcircular (for terminology see Oliver & Rolán, 2015).

Discussion – *Ammonicera oliveri* nov. sp. is characterised by its strong axial sculpture, broad adapical band, narrow peripheral band; the bands poorly delimited by a groove or edge that is barely developed on the first 1.5 whorls. The adapical and peripheral bands are not delimited on the last whorl. The strongly developed median groove seen on the protoconch in all European species reviewed by Oliver & Rolán (2015) is only weakly developed in *A. oliveri*, and only present on one side (Pl. 2, fig. 1b). It is closest to the extant western Mediterranean *A. columbretensis* Oliver & Rolán, 2015, but that species bears a continuous spiral groove at the highest point on the dorsum and venter separating sharply the adapical and peripheral bands. The axial sculpture is very similar in both species. Oliver & Rolán (2015) showed the genus to be far more speciose than previously thought in waters surrounding the Iberian Peninsula. Electron microscopy is essential in characterising shell features in these minute gastropods. Therefore we do not attempt to compare our species with records in the palaeontological literature that identify all specimens as *A. rota* (Forbes & Hanley, 1850) (*e.g.* Peyrot, 1938; Strausz, 1966; Bałuk, 1975). All these fossil records need to be re-evaluated. *Ammonicera rota* differs from both of the preceding species in having weaker, axial sculpture, a more rounded whorl profile and aperture and a discontinuous spiral groove separating the adapical and peripheral bands.

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

Superfamily Murchisonelloidea Casey, 1904
Family Murchisonellidae Casey, 1904
Subfamily Ebalinae Warén, 1995
Genus *Ebala* Gray, 1847

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

1847b *Ebala* Gray, p. 160.

***Ebala ornatissima* nov. sp.**
Plate 3, fig. 1

Type material – Holotype NHMW 2016/0103/2081, height 2.2 mm, width 0.4 mm; paratype 1 RGM.1352724 (1), height 1.0 mm, width 0.3 mm.

Other material – Known from type series only.

Etymology – *Ebala* gender feminine.

Locus typicus – La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Ebala* species of minute size, with type A1 planorbid protoconch, very slender, teleoconch whorls, sculptured with axial riblets developed in subsutural area and spiral cords from third whorl.

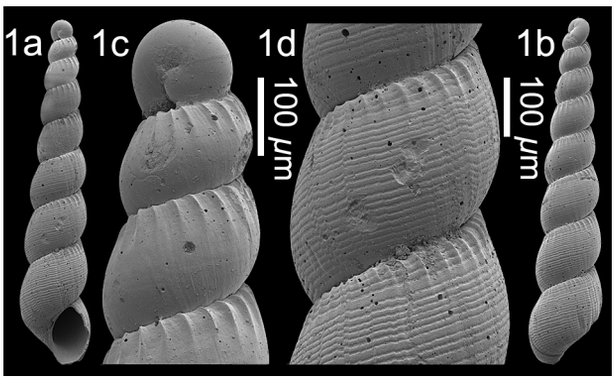

Plate 3. *Eulimella ornatissima* nov. sp.; 1. **Holotype** NHMW 2016/0103/2081, height 2.2 mm, width 0.4 mm, 1c, detail of protoconch, 1d, detail of teleoconch sculpture penultimate whorl (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell minute, very tall and slender. Protoconch type A1, planorbid, at 114° to main shell axis, composed of 1.25 whorls. Teleoconch of 7.5 convex whorls, separated by impressed, finely undulating suture, at 72° to main shell axis. Sculpture of narrow, widely spaced, prosocline riblets only developed over subsutural portion of whorl. First two teleoconch whorls without spiral sculpture. On third whorl fine, irregular, flattened spiral cords develop separated by narrow, somewhat irregular or wavy grooves, 24 cords on penultimate whorl, cords about three times width of interspaces. Last whorl 33% of total, height, regularly convex, base not delimited. Aperture small, 17% of total height, ovate, outer lip not thickened, somewhat expanded abapically. Columella broadly excavated; columellar and parietal callus thin, forming narrow, continuous callus rim.

Discussion – This new species would fit the genus *Anisocycla* Monterosato, 1880 (*auct.*; *e.g.* Peñas & Rolán, 2001a, p. 56), characterised by tall, very slender shells, with or without sculpture, without columellar fold or umbilicus and a type B planispiral protoconch with the spire entirely visible. However the type species of *Anisocycla* was found to be a *Eulimella* species and the genus was synonymised with *Eulimella* by Warén (2013). *Eulimella ornatissima* nov. sp. is similar in shape and having spiral sculpture to *Ebala nitidissima* (Montagu, 1803), but that species lacks the axial riblets seen in the subsutural area in *Eulimella ornatissima* nov. sp. None of the extant Ebalinae from the western Mediterranean or eastern Atlantic revised by Peñas *et al*. (1996) and Peñas & Rolán (2001a) respectively have axial riblets.

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

Superfamily Cimoidea Warén, 1993
Family Cimidae Warén, 1995
Genus *Coenaculum* Iredale, 1924

Type species (by original designation) – *Scala minutula* Tate & May, 1900, present-day, Tasmania, Australia.

1924 *Coenaculum* Iredale, p. 183, 244.

***Coenaculum boucheti* nov. sp.**
Plate 4, figs 1, 2

Type material – Holotype MNHN.F.A57922, height 3.3 mm, width 920 µm; paratype 1 MNHN.F.A57923, height 3.2 mm, width 900 µm; paratype 2 NHMW 2016/0103/0971, height 5.6 mm, width 1.0 mm; paratype 3 NHMW 2016/0103/0972, height 3.2 mm, width 900 µm, **St-Clément-de-la-Place**. Paratype 4 RGM.1352540, height 4.1 mm, width 900 µm; paratype 5 RGM.1362947, height 3.1 mm, width 850 µm; paratype 6 RGM.1362948, height 2.8 mm, width 850 µm, **Sceaux-d'Anjou**.

Other material – Maximum height 5.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0973 (14), LC (5), FVD (7). **Sceaux-d'Anjou**: NHMW 2016/0103/2192 (4), RGM.719000 (42), FVD (4). **Renauleau**: NHMW 2016/0103/1448 (1).

Etymology – We have great pleasure in naming this species after Philippe Bouchet (MNHN, Paris), who has given us enormous support throughout this project. *Coenaculum* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Coenaculum* species attaining more whorls

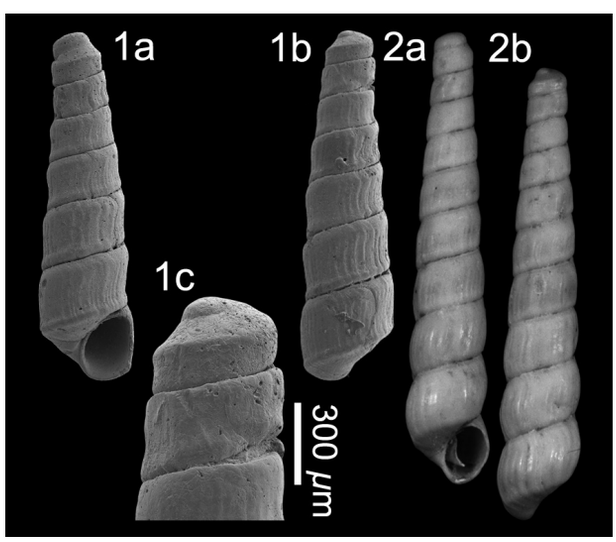

Plate 4. *Coenaculum boucheti* nov. sp.; 1. **Holotype** MNHN.F.A57922, height 3.3 mm, width 920 µm, 1c, detail of protoconch (SEM image); 2. **Paratype 2** NHMW 2016/0103/0971, height 5.6 mm, width 1.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

than usual for genus, paucispiral protoconch, medially carinate, teleoconch whorls swollen at sutures, concave between on early whorls, convex later teleoconch whorls, bearing weakly developed axial ribs, base delimited by relatively weak cord.

Description – Shell minute, narrow, elongate, cylindrical. Protoconch of 1.5 whorls, large, medially carinate. Teleoconch of up to nine whorls, separated by deeply impressed suture. Early whorls somewhat swollen just below adapical suture and bearing subobsolete cord just above abapical suture; whorl profile concave between; later teleoconch whorls convex in fully grown specimens. Sculpture reduced to low, poorly delimited axial ribs. Last whorl bearing relatively weak cord for genus delimiting base. Base flattened, weakly convex, imperforate. Aperture small, quadrate. Outer lip thin, angled at basal cord, columella short, evenly excavated.

Discussion – As far as we are aware, this is only the fifth *Coenaculum* species described, and the first fossil species for the European faunas. Until now the genus was mainly antipodean, and those species all differ from *Coenaculum boucheti* nov. sp. in having angular teleoconch whorls bearing stronger axial sculpture. The type species, *C. minutulum* (Tate & May, 1900) from Tasmania further differs in having three spiral cords on the protoconch and shouldered teleoconch whorls bearing strong axial ribs. *Coenaculum segundum* Powell, 1937, from present-day New Zealand, is more closely similar to *C. minutulum*, but differs in having a single weaker keel mid-whorl on the protoconch, and the teleoconch whorls are also angular mid-whorl. *Coenaculum tertium* Dell, 1952, also from New Zealand again differs from the French species in being more strongly axially costate. A further undescribed fossil species from New Zealand illustrated by Beu & Maxwell (1990, pl. 56, figs c, g), from the middle Miocene Serravallian (Waiauan), like the rest of the antipodean species is axially costate, but differs from its congeners in having the strongest sculpture composed of more widely spaced and more elevated ribs and a cord mid-whorl and delimiting the base. The only other non-antipodean species is *C. weerdtae* Moolenbeek & Faber, 1992 from the present-day Caribbean waters off Belize that is immediately separated from *C. boucheti* by its carinate periphery. We can find no further figures of the species following the original description, but it seems not to attain as many whorls.
Coenaculum boucheti occurs fairly widespread in the Assemblage I deposits (St-Clément-de-la-Place, Sceaux-d'Anjou, Renauleau), although it is uncommon at all localities.

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

Genus *Graphis* Jeffreys, 1867

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

1867 *Graphis* Jeffreys, p. 102.
1869 *Cioniscus* Jeffreys, p. 210. Unnecessary substitute name.

***Graphis* cf. *albida* (Kanmacher, 1798)**
Plate 5, figs 1, 2

cf. 2002 *Graphis albida* (Kanmacher, 1798) – Van Aartsen, p. 9, figs 3-4.
cf. 2014 *Graphis albida* (Kanmacher, 1798) – Giannuzzi-Savelli *et al*., p. 100, fig. 348, appendix p. 42, 89.

Material and dimensions – Maximum height 1.5 mm (fragment). **St-Clément-de-la-Place**: NHMW 2016/0103/2248-2249 (2), NHMW 2016/0103/2250 (1).

Discussion – Unfortunately, only two fragments of this species are at hand, both from St-Clément-de-la-Place. The teleoconch shape and sculpture is similar to that of the extant European Atlantic and Mediterranean *Graphis albida* (Kanmacher, 1798), but without the apical whorls and protoconch we cannot be certain. *Graphis barashi* Van Aartsen, 2002 from the eastern Mediterranean is closely similar, and differs most importantly in having a more pointed protoconch. We therefore leave it in open nomenclature.

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

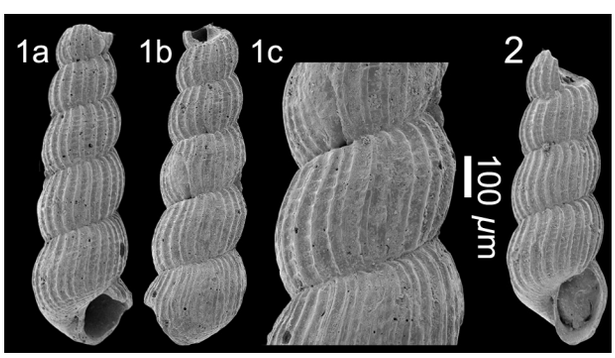

Plate 5. *Graphis* cf. *albida* (Kanmacher, 1798); 1. NHMW 2016/0103/2248, height 1.5 mm, width 440 μm, 1c, detail of teleoconch sculpture; 2. NHMW 2016/0103/2249, height 1.4 mm, width 470 μm (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Superfamily Acteonoidea d'Orbigny, 1843
Family Acteonidae d'Orbigny, 1843
Subfamily Acteoninae d'Orbigny, 1843
Genus *Acteon* de Montfort, 1810

Type species (by original designation) – *Voluta tornatilis* Linnaeus, 1758, present-day, European.

1810 *Acteon* de Montfort, p. 314.

For generic synonymy see Ceulemans *et al*. (2018, p. 112).

Note – Below we have placed the generic name *Acteon* de Montfort, 1810 within quotation marks, as species are assigned to a particular genus based on their radula rather than on shell morphology.

'*Acteon*' *distinctus* nov. sp.
Plate 6, figs 1, 2

1964 *Acteon couffoni* Brébion, p. 640, pl. 15, fig. 22.

Type material – Holotype MNHN.F.A57930, height 5.3 mm, width 3.4 mm; paratype 1 MNHN.F.A57931, height 4.6 mm, 2.8 mm; paratype 2 NHMW 2016/0103/1023, height 9.3 mm, width 6.0 mm; paratype 3 NHMW 2016/0103/1024, height 8.3 mm, width 3.6 mm; paratype 4 NHMW 2016/0103/1025, height 6.4 mm, width 3.6 mm.; Paratype 5 RGM.1352399, height 6.7 mm, width 3.5 mm, **St-Clément-de-la-Place**. Paratype 6 RGM.1352462, height 6.5 mm, width 3.2 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 9.5 mm, width 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1026 (50+), RGM.1352400 (4), RGM.1352424 (2), LC (40), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1982 (17), RGM.1352463 (6), RGM.718205 (38), RGM.1352673 (4 juveniles), LC (3), FVD (8).

Etymology – Latin '*distinctus, -a, -um*', adjective meaning separate or distinct, reflecting its very different ornament compared to its congeners. *Acteon* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Acteon* species of small size, fragile shell, with fine, even reticulated surface sculpture composed or raised cords and ribs, with small tubercles developed at intersections, weak columellar fold, imperforate.

Description – Shell small, globose, fragile. Low spired. Protoconch of about 1.2 smooth whorls. Teleoconch of 3.5 convex whorls with periphery at abapical suture. Suture deeply impressed, linear, narrowly canaliculate. Sculpture of spiral cords, four on spire whorls, crossed by numerous axial lamellae forming strongly and finely reticulated sculpture with small beads formed at intersections. Last whorl globose, 78-80% of total height, regularly convex, imperforate. Aperture large, widening anteriorly, 57% of total height, outer lip thin. Columella short, bearing subobosolete fold mid-height. Columellar callus thickened and everted covering umbilicus. Parietal callus not developed.

Discussion – '*Acteon*' *distinctus* nov. sp., as the name would suggest, is quite unlike any of its congeners and it is placed in the genus *Acteon* in the widest sense. The protoconch and shell shape are typical for the genus, but the sculpture is not. Most *Acteon* species have the surface completely or partially covered in rows of pits. Species in which the rows are close-set and the pits large may look reticulate, but on closer inspection the sculpture can be seen to be punctate. '*Acteon*' *herosae* Valdés, 2008 from the present-day southwest Pacific has similar sculpture on spire whorls and just below the suture on the last whorl, but below on the last whorl the spirals are typically pitted. We can find no other congener with which we can usefully compare this unique species.
Brébion (1964, p. 640) recorded this species from the Assemblage I locality of Sceaux-d'Anjou, to which we add St-Clément-de-la-Place.

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

'*Acteon*' *levidensis* (Wood, 1848)
Plate 7, figs 1, 2

1842 *Acteon levidensis* Wood, p. 537 (*nomen nudum*).
*1848 *Actaeon levidensis* Wood, p. 171, pl. 19, fig. 4.

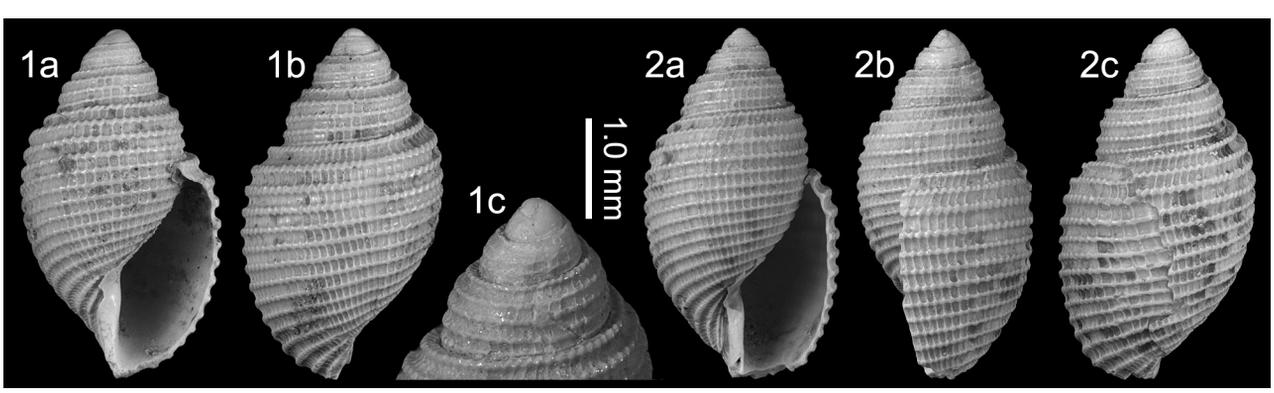

Plate 6. '*Acteon*' *distinctus* nov. sp.; 1. **Holotype** MNHN.F.A57930, height 5.3 mm, width 3.4 mm, 1c, detail of protoconch. 2. **Paratype 2** NHMW 2016/0103/1023, height 9.3 mm, width 6.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1872 *Actaeon levidensis* S. Wood – Wood, p. 74.
1897 *Actaeon* ? *levidensis* Wood – Sacco, p. 35, pl. 3, fig. 40.
1923 *Actaeon levidensis* S.V. Wood – Harmer, p. 784, pl. 62, fig. 17.
1960 *Actaeon levidensis* Wood, 1842 [*sic*] – Glibert, p. 22, pl. 4, fig. 25.
1964 *Acteon levidensis* S.V. Wood, 1848 – Van Regteren Altena *et al*., p. 2, pl. 19, fig. 181.
1964 *Acteon gourbesvillensis* Brébion, p. 639, pl. 15, fig. 21 (*nomen nudum*).
1976 *Rictaxis* (*Actaeonidea*) *achatina* (Sacco) – Pavia, p. 114, pl. 12, fig. 8 [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].
1992 *Acteonidea* [sic] *achatina* Sacco, 1897, Bonelli m.s. – Cavallo & Repetto, p. 164, fig. 471 [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].
1997 *Acteon levidensis* Wood, 1842 [*sic*] – Marquet, p. 112, pl. 10, fig. 10.
1998 *Acteon levidensis* Wood, 1848 – Marquet, p. 210, fig. 181.
1998 *Acteonidea* [*sic*] *achatina* Sacco – Ferrero *et al*., p. 49, pl. 2, fig. 5 [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].
2010 *Acteonidea* [*sic*] *achatina* Sacco, 1897 Bonelli m.s. – Sosso & Dell'Angelo, p. 53, p. 68 unnumbered fig. top right [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].
2011 *Actaeonidea* [*sic*] *acathina* [*sic*] Sacco, 1897 Bonelli m.s. – Chirli & Linse, p. 215, pl. 85, fig. 3 [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].
2013 *Acteonidea* [*sic*] *achatina* Sacco, 1897 – Chirli, p. 26, pl. 7, figs 18-23 [*non* Sacco, 1897; = *Rictaxis tornatus* (Millet, 1854)].

Material and dimensions – Maximum height 5.2 mm, width 2.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2040-2042 (1), NHMW 2016/0103/2043 (7), RGM.1352715 (1), LC (3). **Sceaux-d'Anjou**: RGM.719030 (13), RGM.1352723 (7).

Discussion – Ceulemans *et al*. (2018, p. 117) commented that a small acteonid from the Pliocene of Italy had been consistently misidentified as *Acteonidea* [*sic*] *achatina* Sacco, 1897 [= *Rictaxis tornatus* (Millet, 1854)] (Pavia, 1976, pl. 11, fig. 8; Cavallo & Repetto, 1992, fig. 471; Ferrero *et al*., 1998, pl. 2, fig. 5; Sosso & Dell'Angelo, 2010, p. 68; Chirli & Linse, 2011, pl. 85, fig. 3; Chirli, 2013, pl. 7, figs 18-23). It differed from *R. tornatus* in being considerably smaller (maximum height 4.0 mm), more slender, with relatively wider spaced spiral grooves, less pronounced axial growth lines, having a smaller aperture and different columellar characters. The same small acteonid is more widespread in the lower Piacenzian upper Pliocene of Europe, as specimens are at hand from the Atlantic of the Mondego Basin, central-western Portugal and the Estepona Basin, western Mediterranean (NHMW coll.). It also occurs in Assemblage I. We consider this small acteonid to represent '*Acteon*' *levidensis* (Wood, 1848) that was originally described from the lower Pliocene North Sea Basin of England, and is identical to the specimens figured from the North Sea Basin Pliocene of Belgium (Marquet, 1998, p. 210, fig. 181). Already Sacco (1897, p. 35, pl. 3, fig. 40) recognised its presence in the lower Pliocene of Italy, although this record seems to have been overlooked by subsequent authors. It is quite likely that this species will be found to have a wider geographic and stratigraphic distribution once it is more widely recognised. In Assemblage I we have found it at St-Clément-de-la-Place and Sceaux-d'Anjou. Brébion (1964, p. 639) described *Acteon gourbesvillensis* (*nomen nudum*) based on a single specimen from the Assemblage IV locality of Gourbesville. In our opinion this is likely to be an unusually large specimen of '*A*'. *levidensis*, a possibility considered by Brébion himself (1964, p. 640).

Distribution – Upper Miocene: Atlantic (Tortonian), northwestern France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848, 1872; Harmer, 1923), Kattendijk Formation, Belgium (Glibert, 1960; Marquet, 1997, 1998); central Mediterranean, Italy (Sacco, 1897; Pavia, 1976; Chirli, 2013). Upper Pliocene: North Sea Basin, Luchtbal sands, Belgium (Marquet, 1997, 1998); Atlantic, Mondego Basin, central-west Por-

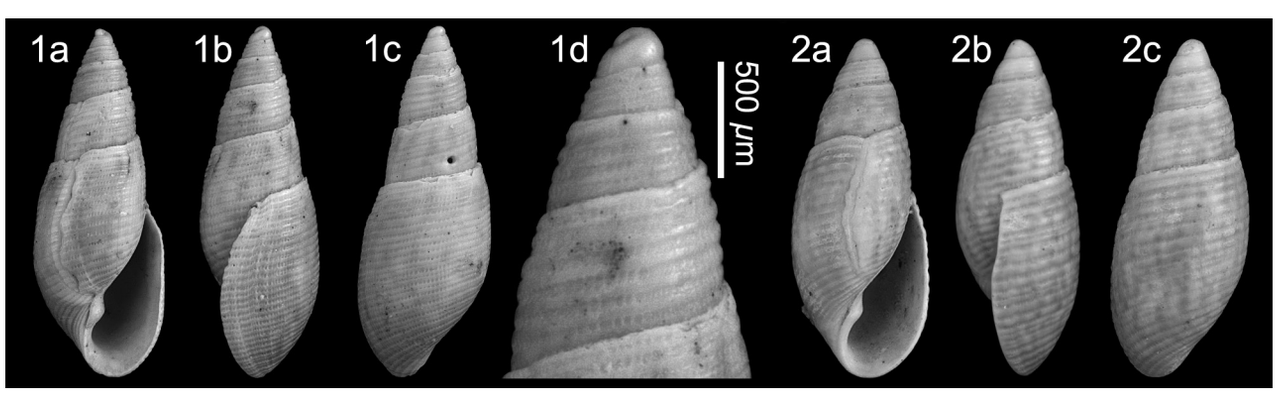

Plate 7. '*Acteon*' *levidensis* (Wood, 1848); 1. NHMW 2016/0103/2040, height 5.2 mm, width 2.0 mm, 1d, detail of protoconch; 2. NHMW 2016/0103/2041, height 4.2 mm, width 1.7 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

tugal (NHMW coll.); western Mediterranean, Estepona Basin, Spain (NHMW coll.); central Mediterranean, Italy (Cavallo & Repetto, 1992; Ferrero *et al*., 1998; Sosso & Dell'Angelo, 2010). Upper Pliocene-Pleistocene: Atlantic, northwestern France (Brébion, 1964). Lower Pleistocene: eastern Mediterranean, Greece (Chirli & Linse, 2011).

'*Acteon*' cf. *problematicus* Landau, Harzhauser, İslamoğlu & Silva, 2013
Plate 8, fig. 1

cf. *2013 '*Acteon*' *problematicus* Landau, Harzhauser, İslamoğlu & Silva, p. 324, pl. 76, fig. 11.

Material and dimensions – Maximum height 2.4 mm, width 1.5 mm. **Renauleau**: NHMW 2016/0103/1723 (1), NHMW 2016/0103/2114 (6), LC (2). **Beugnon**: RGM.740640 (2).

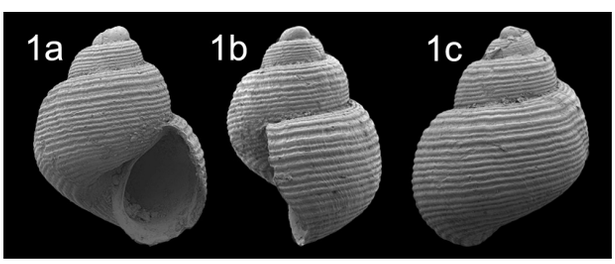

Plate 8. '*Acteon*' cf. *problematicus* Landau, Harzhauser, İslamoğlu & Silva, 2013; 1. NHMW 2016/0103/1723, height 2.2 mm, width 1.7 mm (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – This species is remarkably similar, if not conspecific with, a small acteonid described from the eastern Mediterranean middle Miocene Karaman Basin of Turkey; '*Acteon*' *problematicus* Landau, Harzhauser, İslamoğlu & Silva, 2013. Both shells are minute, although at 2.2 mm height the French shell is twice the size of the Turkish shell and their spiral sculpture is similar. The specimen from Assemblage I seems a little squatter than that from Karaman, but both photographs of the Turkish shell are slightly tilted to show the protoconch and umbilicus, which give the specimen a more elongated aspect. Both are known from a single specimen and more material would be required to confirm if they are conspecific. However, it does suggest that this species or species group was widely distributed in the European Miocene.

Distribution – Upper Miocene (Tortonian): NW France (this paper).

'*Acteon*' *semistriatus* (Férussac, 1822)
Plate 9, figs 1-3

*1822b *Tornatella semi-striata* Férussac, p. 108.
1854 *Acteon Clathratus* Millet, p. 155 (*nomen nudum*).
1865 *Acteon clathratus* Millet, p. 581.
1964 *Acteon semistriatus* Férussac, 1822 – Brébion, p. 643, pl. 15, figs 24-27.
2013 '*Acteon*' *semistriatus* (Férussac, 1822) – Landau *et al*., p. 323, pl. 52, fig. 13 (*cum syn*.).
2018 '*Acteon*' *semistriatus* (Férussac, 1822) – Ceulemans *et al*., p. 112, pl. 7, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 9.1 mm, width 4.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1030 (1), NHMW 2016/0103/2047-2048 (2), NHMW 2016/0103/1031 (50+), RGM.1352279 (1), RGM.1352376 (11), RGM.1352422 (13), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1032 (50+), RGM.1348887 (12), RGM.1349251 (6), RGM.1352338 (17), RGM.1352357 (6), RGM.1352465 (26), RGM.1357589 (16), RGM.718203 (50+), LC (50+), FVD (50+). **Renauleau**: LC (2). **Beugnon**: NHMW 2016/0103/2039 (2), RGM.1352393 (1).

Discussion – Like the Assemblage III population from Le Pigeon Blanc, the Assemblage I specimens are small compared to those found in other localities, but otherwise typical of the Pliocene forms of '*Acteon*' *semistriatus* (Férussac, 1822), with their relatively low spire and sculpture developed over most, if not the whole, surface of the last whorl. The form described from the French Atlantic Miocene as *Actaeon burdigalensis* d'Orbigny, 1852 is characterised by its more slender shape, taller spire compared with typical '*A*.' *semistriatus*, and the absence of sculpture adapically on the last whorl (see Benoist, 1889, p. 52; Glibert, 1952a, p. 384). However, specimens with combinations of these characters can be found in Miocene assemblages (*e.g.* Landau *et al*., 2013, p. 323). Indeed, the extent of sculpture on the last whorl is very variable, which led Sacco (1897) to describe numerous varieties based largely on this character. Peyrot (1932) synonymised the two forms and considered '*A*.' *semistriatus* to be a very variable, widespread and long-lived species, a position followed here.
We have excluded from the chresonymy and distribution the specimen illustrated by Chirli & Linse (2011, pl. 85, fig. 2), as it is much more inflated than usual for the species. The record from Rhodes Island was based on a single specimen, which is also much smaller than usual for the species (height 5.1 mm), even smaller than the NW France populations. As those authors correctly point out, this would be the only Pleistocene record for the species, and in our opinion requires confirmation before we can be certain that it survived into the Pleistocene.
Brébion (1964, p. 645) recorded this species from Assemblage I (Sceaux-d'Anjou, St-Clément-de-la-Place, Thorigné), to which we add Beugnon, Assemblage II (Apigné), and Assemblage III (see Ceulemans *et al*., 2018, p. 112).

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian): Aquitaine Basin, France (Benoist, 1889; Peyrot, 1932); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1897); Paratethys (Aquitanian and Burdigalian): Austria (Steininger, 1973;

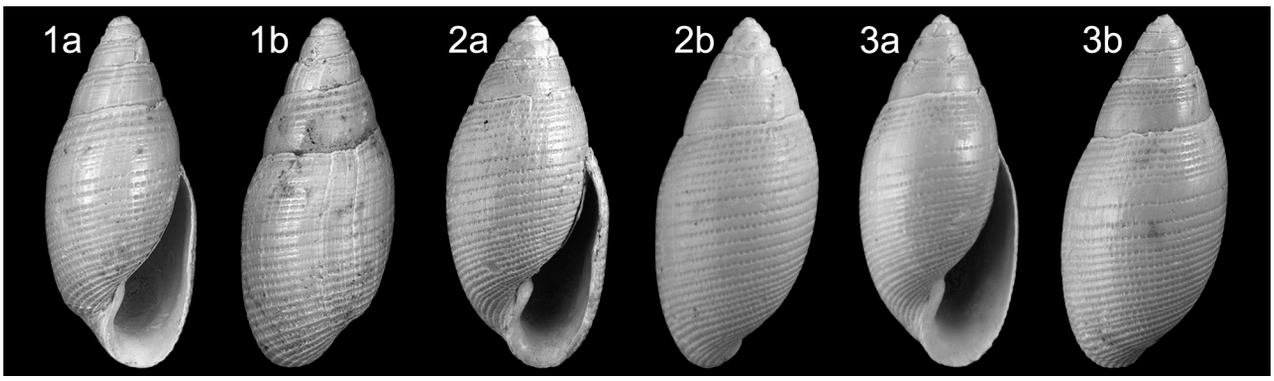

Plate 9. '*Acteon*' *semistriatus* (Férussac, 1822), 1. NHMW 2016/0103/1030, height 7.9 mm, width 3.5 mm; 2. NHMW 2016/0103/2047, height 9.1 mm, width 4.3 mm; 3. NHMW 2016/0103/1028, height 7.8 mm, width 3.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Harzhauser, 2002). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Denmark (Sorgenfrei, 1958), Germany (Anderson, 1964; Moths, 1989; Wienrich, 2007), Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984). Middle Miocene: Atlantic (Langhian and Serravallian): Aquitaine Basin, France (Grateloup, 1846; Benoist, 1889; Peyrot, 1933), (Langhian): Loire Basin, France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Kecskemétiné-Körmendy, 1962; Strausz, 1966), Poland (Friedberg, 1928); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: North Sea Basin (Tortonian): Denmark (Rasmussen, 1968; Schnetler, 2005); Atlantic (Tortonian and Messinian): NW France (Millet, 1854, 1865; Brébion, 1964), Algarve Basin, Portugal (Dollfus *et al*., 1903); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1897). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011); western Mediterranean, northeastern Spain, (Martinell, 1982), Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1897; Chirli, 2013), Tunisia (Fekih, 1975). Lower-upper Pliocene: western Mediterranean, Estepona Basin (NHMW collection), southern France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992).

'*Acteon*' *subglobosus* (Grateloup, 1828)
Plate 10, figs 1-3

*1828	*Tornatella subglobosa* Grateloup, p. 194.
1845	*Tornatella subglobosa* Grateloup, pl. 6, fig. 13.
1854	*Acteon Fasciatus* Millet, p. 154 (*nomen nudum*).
1865	*Acteon fasciatus* Millet, p. 581.
1889	*Acteon subglobosus* Grat. – Benoist, p. 34, pl. 3, fig. 4.
1933	*Acteon subglobosus* Grateloup – Peyrot, p. 160, pl. 11, figs 64-66.
1938	*Acteon subglobosus* Grateloup, 1827 [*sic*] – Peyrot, p. 311.
1952a	*Acteon subglobosus* Grateloup, 1827 [*sic*] – Glibert, p. 385, pl. 13, fig. 5.
1964	*Acteon subglobosus* Grateloup, 1827 [*sic*] – Brébion, p. 642, pl. 15, fig. 23.

Material and dimensions – Maximum height 10.5 mm,

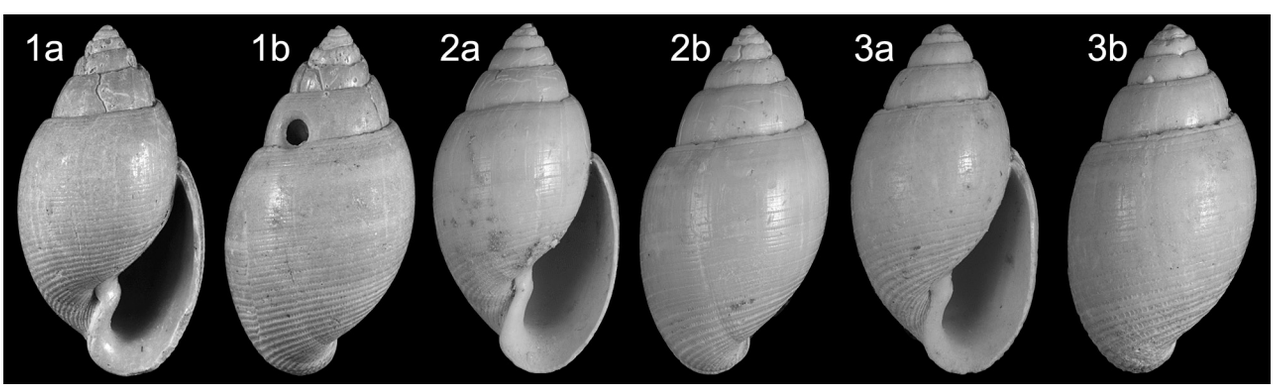

Plate 10. '*Acteon*' *subglobosus* (Grateloup, 1828); 1. NHMW 2016/0103/1027, height 9.7 mm, width 5.1 mm; 2. NHMW 2016/0103/2045, height 9.2 mm, width 4.9 mm; 3. NHMW 2016/0103/1027, height 6.9 mm, width 3.7 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

width 5.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1027 (1), NHMW 2016/0103/2045-2046 (2), NHMW 2016/0103/1028 (50+), RGM.1352415 (16), RGM.1352423 (10), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1029 (20), RGM.1352339 (10), RGM.1352464 (10), RGM.718204 (35), LC (8), FVD (12).

Discussion – '*Acteon*' *subglobosus* (Grateloup, 1828) is characterised by its globose shell shape, low spire, strongly twisted columella forming a stout columellar fold, and colour pattern of three lighter spiral bands. In Assemblage I it can only be confused with '*Acteon*' *semistriatus* (Férussac, 1822), which differs in being more slender and taller spired, with a weaker fold, or less twisted columella. In both species the spiral grooves can be absent mid-whorl on the last whorl, but the grooves tend to coarser in '*A.*' *semistriatus*. '*Acteon*' *subglobosus* is more similar to the Pliocene to present-day European '*A.*' *tornatilis* (Linnaeus, 1758), but differs in being smaller, even more globose, with finer spiral grooving, and in having three instead of two light colour bands on the last whorl. Brébion (1964, p. 643) recorded this species from the Assemblage I localities of Thorigné and Sceaux-d'Anjou, to which we add St-Clément-de-la-Place.

Distribution – Lower Miocene: Atlantic (Burdigalian), Aquitaine Basin, France (Grateloup, 1828, 1845; Benoist, 1889; Peyrot, 1933). Middle Miocene: Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1952a). Upper Miocene (Tortonian): NW France (Millet, 1854, 1865; Brébion, 1964).

Genus *Rictaxis* Dall, 1871

Type species (by original designation) – *Tornatella punctocoelata* Carpenter, 1863, present-day, California, USA.

1871 *Rictaxis* Dall, p. 136.

For generic synonymy see Ceulemans *et al*. (2018, p. 112).

***Rictaxis tornatus* (Millet, 1854)**
Plate 11, figs 1-3

*1854 *Auricula Tornata* Millet, p. 154.
1865 *Auricula tornata* Millet – Millet, p. 579.
1952a *Rictaxis achatinus* Bonelli, 1826 – Glibert, p. 386, pl. 13, fig. 6.
1964 *Rictaxis achatinus* Bonelli, 1826 – Brébion, p. 645.
2018 *Rictaxis tornatus* (Millet, 1854) – Ceulemans *et al*., p. 112, pl. 7, fig. 2 (*cum syn*).

Material and dimensions – Maximum height 8.7 mm, width 3.9 mm. **St-Clément-de-la-Place**: LC (1). **Sceaux-d'Anjou**: NHMW 2016/0103/2037-2038 (2), RGM. 1352522 (1), RGM.1352596 (1 fragment). **Beugnon**: RGM.1352410 (1), RGM.1352643 (1).

Discussion – This species was fully discussed by Ceulemans *et al*. (2018, p. 117). The specimens from Assemblage I are typical for the species, although they do not attain the larger size seen in some Pliocene populations. In the Italian Pliocene literature this species has frequently been confused with '*Acteon*' *levidensis* (Wood, 1848) (see discussion under that species).
It is uncommon in Assemblage I. Brébion (1964, p. 646) recorded a single specimen from the Assemblage I locality of Sceaux-d'Anjou, from which locality most of the material seen comes from, and we add a couple of specimens from Beugnon.

Distribution – Lower Miocene: Atlantic, Aquitaine Basin (Peyrot, 1932). Middle Miocene: (Langhian): Aquitaine Basin (Peyrot, 1932), Loire Basin (France (Glibert, 1952a). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964; this paper), Cacela Basin (Dollfus *et al*., 1903). Lower Pliocene: Atlantic, NW France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011); central Mediterranean, Italy (Chirli, 2013). Upper Pliocene: western Mediterranean, Estepona Basin (NHMW collection), central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Ferrero *et al*., 1998; Sosso & Dell'Angelo, 2010).

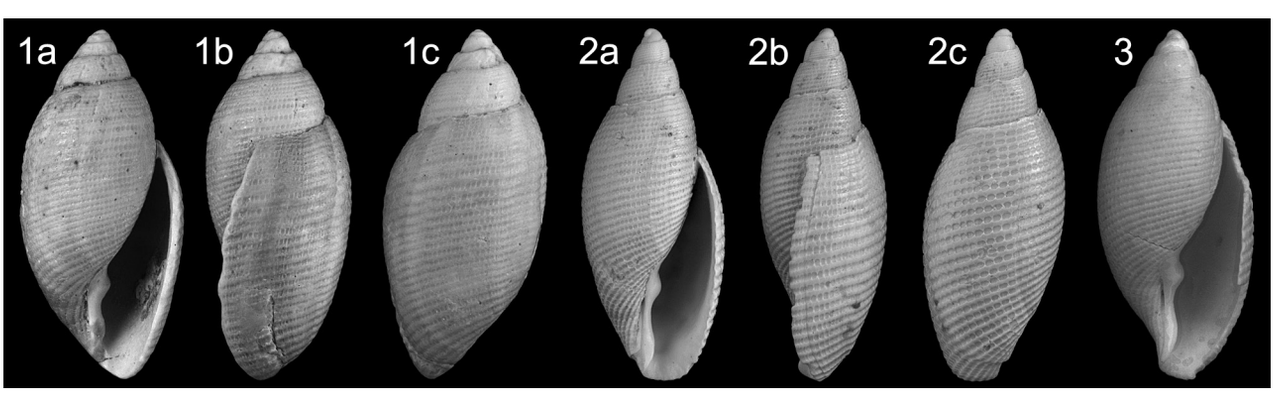

Plate 11. *Rictaxis tornatus* (Millet, 1854); 1. NHMW 2016/0103/2037, height 8.7 mm, width 3.9 mm; 2. NHMW 2016/0103/2038, height 7.8 mm, width 3.2 mm. La Presselière, Sceaux-d'Anjou. 3. RGM.1352410, height 7.4 mm, width 3.4 mm. Beugnon, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Cohort Ringipleura Kano, Brenzinger, Nützel, Wilson & Schrödl, 2016
Superfamily Ringiculoidea Philippi, 1853
Family Ringiculidae Philippi, 1853
Genus *Ringicula* Deshayes *in* Lamarck, 1838

Type species (by subsequent designation) – *Marginella auriculata* Ménard de la Groye, 1811, Anton, 1838, present-day, Europe.

1838 *Ringicula* Deshayes *in* Lamarck, p. 342.

For generic synonymy see Ceulemans *et al*. (2018, p. 113).

***Ringicula munieri* Morlet, 1880**
Plate 12, figs 1-3

1854 *Ringicula Buccinea* Desh. [*sic*] – Millet, p. 155 [*non Ringicula buccinea* (Brocchi, 1814)].
*1880 *Ringicula Munieri* Morlet, p. 169, pl. 6, fig. 5.
1964 *Ringicula* (*Ringiculina*) *buccinea* Brocchi, 1814 – Brébion, p. 649, pl. 15, figs 30-33 [*non Ringicula buccinea* (Brocchi, 1814)].

Material and dimensions – Maximum height 8.9 mm, width 5.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1087-1089 (2), NHMW 2016/0103/1090 (50+), RGM.1352343 (50+), RGM.1352358 (50+), RGM.1352384 (1 + 2 juveniles), RGM.1352570 (31), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1092 (50+), RGM.1352356 (22), RGM.1352498 (21), RGM.1352541 (43), RGM.1352544 (50+), RGM.718208 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1091 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.717789 (6), RGM.1348492 (2), RGM.1352345 (13), RGM.1352355 (23), RGM.1352375 (1), FVD (7).

Original description – '*Coquille ovale, allongée, épaisse, finement striée sur le 5 premiers tours ; le dernier marqué de côtes longitudinales et orné, à la base, de stries assez espacées, variant de 5 à 3 ; spire allongée; les tours, au nombre de 7 à 7 1/2, sont convexes, augmentant graduellement, séparés par une suture canaliculée, le dernier formant les 2/3 de la coquille, arrondi à la base; l'ouverture est large; les bords sont réunis par un dépôt calleux très-fort, qui remonte jusqu'au milieu de l'avant-dernier tour; le bord columellaire est fortement arqué à la base, garni de 4 plis, les 2 supérieurs très-empâtés dans la callosité qui les recouvre extérieurement, et qui s'étend sur toute la partie inférieure de la coquille, les 2 inférieurs épais, courts et tordus; le labre est presque droit, très-épais sur toute son étendue, très-saillant en dehors, dépassant à sa base le bord columellaire et forme, à sa jonction, un petit canal, ainsi qu'à sa partie supérieure*' (Morlet, 1880, p. 169).

Discussion – Brébion (1964) considered all the large callused ringiculids from upper Miocene to Pleistocene of NW France to represent a single species, *Ringicula buccinea* (Brocchi, 1814). Landau *et al*. (2013, p. 326) and Ceulemans *et al*. (2018, p. 119) expressed the opinion that in the European Miocene literature *R. buccinea* had been used as a dumping ground for *Ringicula* species with a plump last whorl (*e.g.* Berger, 1954, Strausz, 1966; Brébion, 1964). None of these records are conspecific with *R. buccinea*, which in our opinion is an exclusively Pliocene species with an extremely globose last whorl and lacks any spiral sculpture. We therefore resurrect the name *R. munieri* Morlet, 1880, a form described from the Assemblage I localities of Thorigné, St-Clément-de-la-Place and Renauleau. Therefore we have no doubt that Morlet (1880, p. 169) erected this taxon for these specimens. They differ from *R. buccinea*, which occurs in the Assemblage III localities of NW France (for comparison see Ceulemans *et al*., 2018, pl. 7, fig. 3), in being higher spired, the last whorl, although globose, is less so than in *R. buccinea*, the apertural callus is not as thickly developed and there are some spiral grooves on the base, absent in *R. buccinea*. Some specimens have a colour pattern preserved on the last whorl consisting of vertical stripes (Pl. 12, fig. 2). We have not seen this colour pattern in *R. buccinea*, but it does occur in lower-middle Miocene North Sea Basin specimens from the Breda Formation at Miste, Winterswijk identified as *R. buccinea* by A.W. Janssen (1984). As stated in Landau *et al*. (2013, p. 326) we do not believe these North Sea Basin Miocene forms to be that species. Whether they are conspecific

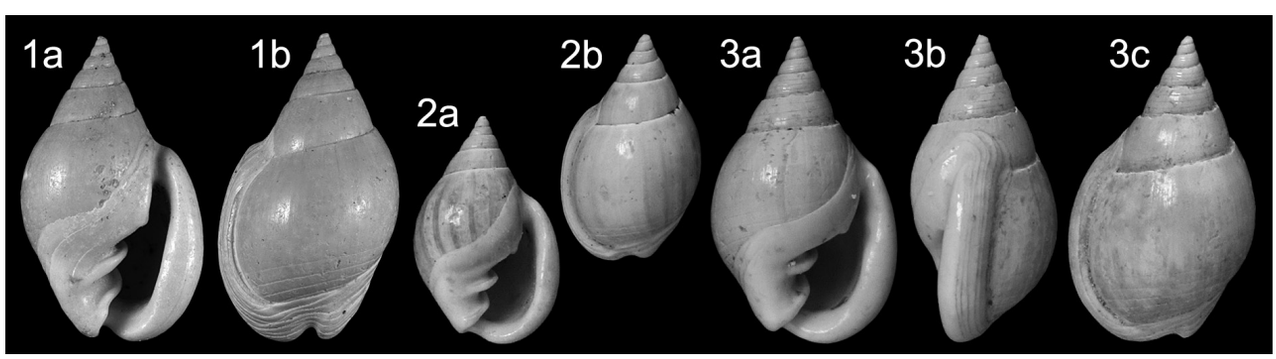

Plate 12. *Ringicula munieri* Morlet, 1880; 1. NHMW 2016/0103/1087, height 7.4 mm, width 4.5 mm; 2. NHMW 2016/0103/1088, height 5.8 mm, width 3.5 mm; 3. NHMW 2016/0103/1089, height 7.0 mm, width 4.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

with those of Assemblage I requires further study. These Miocene globose ringiculids are in need of revision and we provisionally apply the name *R. munieri* exclusively to the Assemblage I specimens, where it occurs fairly widely and is abundant (Renauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, Les Pierres Blanches, Challones and Beaulieu; Brébion, 1964, p. 651).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854; Morlet, 1880; Brébion, 1964).

***Ringicula minor* (Grateloup, 1838)**
Plate 13, figs 1, 2

*1838	*Auricula ringens* var. b. *minor* Grateloup, p. 286, pl. 6, fig. 8.
2013	*Ringicula minor* (Grateloup, 1838) – Landau *et al*., p. 326, pl. 52, fig. 16, pl. 76, fig. 14, pl. 77, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 3.0 mm, width 2.0 mm. **Sceaux-d'Anjou**: RGM.735002 (1), RGM.7352642 (1).

Discussion – *Ringicula minor* (Grateloup, 1838) is characterised by its small size and surface completely covered in spiral grooves. It is extremely uncommon in Assemblage I and represented by only two specimens from Sceaux-d'Anjou, one of which is incomplete.
Ringicula minor, although referred to as *Ringicula paulucciae* Morlet, 1878 in Paratethys literature, is a widespread species during the Miocene in the northeastern Atlantic, the Proto-Mediterranean Sea and the Central Paratethys. For further discussion see Landau *et al*. (2013, p. 327).

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (Peyrot, 1932; Lozouet *et al*., 2001; Lesport & Cahuzac, 2005; Cahuzac *et al*., 2012); Proto-Mediterranean Sea (Burdigalian-Langhian): Colli Torinesi, Italy (Sacco, 1892b); Paratethys (late Burdigalian): Slovakia (Harzhauser *et al*., 2011). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Peyrot, 1932); Paratethys (Langhian-Serravallian), Austria (Hörnes, 1852; Berger, 1954), Hungary (Strausz, 1962, 1966), Slovakia (Švagrovský, 1960); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic, NW France (this paper); Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (d'Amico *et al*., 2012).

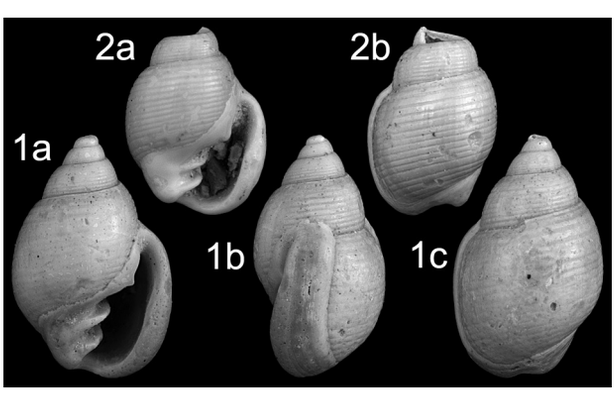

Plate 13. *Ringicula minor* (Grateloup, 1838); 1. RGM.735002, height 3.0 mm, width 2.0 mm; 2. RGM.7352642, height 2.0 mm, width 1.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Order Cephalaspidea Fischer, 1883
Superfamily Bulloidea Gray, 1827
Family Retusidae Thiele, 1925
Genus *Retusa* Brown, 1827

Type species (by subsequent designation, Iredale, 1915) – *Bulla obtusa* Montagu, 1803, present-day, British Isles.

1827	*Retusa* Brown, pl. 38.

For generic synonymy see Ceulemans *et al*. (2018, p. 118).

***Retusa truncatula* (Bruguière, 1792)**
Plate 14, fig. 1

*1792	*Bulla truncatula* Bruguière, p. 377.
1964	*Retusa truncatula* Bruguière, 1792 – Brébion, p. 662.
2011	*Retusa truncatula* (Bruguière, 1792) – Chirli & Linse, p. 221, pl. 87, fig. 3.
2013	*Retusa truncatula* (Bruguière, 1792) – Landau *et al*., p. 337, pl. 77, fig. 11 (*cum syn*.).
2018	*Retusa truncatula* (Bruguière, 1792) – Ceulemans *et al*., p. 118, pl. 7, fig. 8 (*cum syn*.).

Material and dimensions – Maximum height 3.2 mm, width 1.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1391 (1), NHMW 2016/0103/1769 (11), LC (3), FVD (2). **Sceaux-d'Anjou**: RGM.718209 (35).

Discussion – As discussed by Landau *et al*. (2013, p. 338) the shells recorded widely in the fossil literature as *Retusa truncatula* (Bruguière, 1792), represent either a species complex or an unusually long-lived and widely distributed species. The shells from Assemblage I are typical for the species (*e.g.* Chirli, 2013, pl. 11, figs 11-18), relatively truncated apically and bearing axial folds. The adapical tip of the outer lip rises above the apex, which is characteristic for the species. Two further closely similar European Recent species occur; *Retusa minutissima* (Monterosato, 1878) is very small, most specimens are about 2.0 mm in height, and have prominent axial ridges on the spire whorls; and *R. obtusa* (Montagu, 1803) has a shorter last whorl and the aperture attaches at three-quarters shell height, lower than in *R. mamillata* (Philippi, 1836) and *R. minutissima*, and the outer lip does not rise above the apex.
Brébion (1964, p. 662) recorded this species from the As-

Plate 14. *Retusa truncatula* (Bruguière, 1792); 1. NHMW 2016/0103/1391, height 3.2 mm, width 1.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

semblage I locality of St-Michel, to which we add St-Clément-de-la-Place and Sceaux-d'Anjou, the Assemblage II locality of Apigné, and Ceulemans *et al*. (2018, p. 118) recorded it from the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Miocene: Paratethys (Burdigalian): Austria, (Harzhauser, 2002). Middle Miocene: Atlantic (Langhian): Aquitaine Basin, France (Peyrot, 1932), (Langhian): Loire Basin, France (Peyrot, 1938; Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856; Berger, 1953), Poland (Friedberg, 1928; Bałuk, 1970), Hungary (Strausz, 1954, 1966), Bosnia (Atanackovič, 1985), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian) NW France (Brébion, 1964), (Tortonian), Algarve Basin, Portugal (NHMW collection); Proto-Mediterranean Sea (Tortonian and Messinian) Po Basin, Italy (Sacco, 1897; Venzo & Pelosio, 1963; d'Amico *et al*., 2012). Lower Pliocene: North Sea Basin, England (Wood, 1848; Harmer, 1923); Atlantic, northeastern France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, northeastern Spain (Martinell, 1982; Martinell & Domènech, 1984); central Mediterranean, Tunisia (Fekih, 1975). Lower-upper Pliocene: Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (NHMW coll.); central Mediterranean, Italy (Sacco, 1897; Patrini, 1930; Aimassi & Ferrero Mortara, 1983; Cavallo & Repetto, 1992; Chirli, 2013). Lower Pleistocene: Atlantic, St. Erth, England (Harmer, 1923); central Mediterranean, Italy (Cerulli-Irelli, 1910). Lower-upper Pleistocene: central Mediterranean, Italy (Brambilla *et al*., 1988). Lower Pleistocene: eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Upper Pleistocene: Atlantic, England, Ireland (Harmer, 1923). Present-day: Atlantic, British Isles, Norway, Baltic Sea to Canary Islands and Mediterranean (T.E. Thompson, 1988).

***Retusa subangystoma* (d'Orbigny, 1852)**
Plate 15, figs 1-3

1828	*Bulla angistoma* Grateloup, p. 86 [*non* Bruguière, 1792].
1847	*Bulla angistoma* Grat. – Grateloup, pl. 2, figs 6, 7.
*1852	*Bulla subangystoma* d'Orbigny, p. 95 [*nom nov. pro Bulla truncatula* Bruguière *in* Grateloup, 1847; *non* Bruguière, 1792].
1933	*Bullinella* (*Cylichnina*) *subangystoma* d'Orbigny – Peyrot, p. 189, pl. 13, figs 34, 35.
1952a	*Retusa* (*Cylichnina*) *subangystoma* d'Orbigny, 1852 – Glibert, p. 394, pl. 15, fig. 4.
1964	*Retusa* (*Cylichnina*) cf. *umbilicata* Montagu, 1803 – Brébion (*partim*), p. 663, pl. 15, fig. 35 (only).

Material and dimensions – Maximum height 3.2 mm, width 1.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1119 (1), NHMW 2016/0103/1120 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/2061-2062 (2), NHMW 2016/0103/2063 (1), RGM.718210 (50+). **Renauleau**: NHMW 2016/0103/1490 (6), LC (5), FVD (4).

Discussion – Landau *et al*. (2013, p. 336) commented that a revision of this group in the European Neogene was required. However, we are fairly confident that the speci-

Plate 15. *Retusa subangystoma* (d'Orbigny, 1852); 1. NHMW 2016/0103/1119, height 3.0 mm, width 1.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/2061, height 3.1 mm, width 1.4 mm; 3. NHMW 2016/0103/2062, height 3.1 mm, width 1.4 mm (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

mens from Assemblage I are conspecific with those described and illustrated by Glibert (1952a, p. 394, pl. 15, fig. 4) from the middle Miocene Loire Basin of France. The species is characterised by its small regularly cylindrical, almost straight-sided shell with the columella hardly excavated and with the columellar fold hardly developed. It is closely similar to the Miocene to present-day European *Retusa umbilicata* (Montagu, 1803), which differs in being shorter, broader, more inflated and with a more excavated columella. The specimen illustrated by Landau *et al*. (2013, p. 53, fig. 12) from the middle Miocene eastern Proto-Mediterranean Karaman Basin of Turkey as *Retusa* cf. *subangystoma* differs in being larger and the last whorl narrows towards the apex. This form that narrows adapically has been recorded as *Retusa subangystoma* (d'Orbigny, 1852) by workers on the Miocene Paratethys (*e.g.* Berger, 1953, pl. 19, fig. 91) and North Sea Basin (*e.g.* Wienrich, 2007, pl. 134, figs 3-4, pl. 172, fig. 5). We doubt they are conspecific and provisionally limit our synonymy to French Atlantic Miocene records. Brébion (1964, p. 663) recorded this species from the Assemblage I locality of Sceaux-d'Anjou as *Retusa* cf. *umbilicata*, to which we add St-Clément-de-la-Place and Renauleau. He also recorded, but did not figure, *Retusa* cf. *umbilicata* from the Assemblage IV locality of Gourbesville. This record will be reviewed in due course.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (Grateloup, 1828, 1847; Peyrot, 1933). Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1952a). Upper Miocene (Tortonian): NW France (Brébion, 1964).

Family Rhizoridae Dell, 1952
Genus *Volvulella* Newton, 1891

Type species (by typification of replaced name) – *Bulla acuminata* Bruguière, 1792, present-day, Mediterranean.

1891 *Volvulella* Newton, p. 268. *Nom. nov. pro Volvula* A. Adams *in* G.B. Sowerby II, 1850, *non* Gistel, 1848 [Diptera].

For generic synonymy see Ceulemans *et al*. (2018, p. 119).

***Volvulella acuminata* (Bruguière, 1792)**
Plate 16, fig. 1

*1792 *Bulla acuminata* Bruguière, p. 376.
2011 *Volvulella acuminata* (Bruguière, 1792) – Chirli & Linse, p. 224, pl. 89, fig. 1.
2013 *Volvulella acuminata* (Bruguière, 1792) – Landau *et al*., p. 339, pl. 78, fig. 2 (*cum syn*.).
2018 *Volvulella acuminata* (Bruguière, 1792) – Ceulemans *et al*., p. 119, pl. 7, fig. 10.

Material and dimensions – Maximum height 2.5 mm, width 1.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1296 (7), NHMW 2016/0103/2219 (1), LC (2), FVD (1). **Sceaux-d'Anjou**: RGM.1352291 (1), RGM.735003 (5). **Renauleau**: LC (2).

Plate 16. *Volvulella acuminata* (Bruguière, 1792); 1. NHMW 2016/0103/2219, height 2.5 mm, width 1.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – As discussed by Landau *et al*. (2013, p. 340), *Volvulella acuminata* (Bruguière, 1792) is either a species complex or an unusually long-lived and widely distributed species. It is uncommon in Assemblage I, where the shells are typical for the species; the apical rostration is variable in length and the last whorl varies slightly in slenderness. Similar variability is seen in both other fossil and recent populations.
This distinctive little species is widespread in the Mediterranean, northeastern Atlantic and North Sea Basin assemblages from the middle Miocene, and today occurs in the Atlantic from Norway southwards to Angola and throughout the Mediterranean. Interestingly, *V. acuminata* is not present in the early to middle Miocene Aquitaine Basin of France. It is replaced by *Volvulella acuta* (Grateloup, 1828), which is more cylindrical, less convex, with a straighter aperture and a longer rostration. In Assemblage I *V. acuminata* is found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1897). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (Nordsieck, 1972a; A.W. Janssen, 1984), Denmark (Ravn, 1907; Sorgenfrei, 1958), Germany (Anderson, 1964; Wienrich, 2007; Moths *et al*., 2010). Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953), Hungary (Strausz, 1962, 1966); Proto-Mediterranean Sea (Serravallian) Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): Algarve Basin, Portugal (NHMW collection). Lower Pliocene: North Sea Basin, England (Wood, 1848; Harmer, 1925), Belgium (Nyst, 1845; Glibert, 1960; Marquet, 1997); northeastern Atlantic, NW France (Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al*., 1997; Landau *et al*., 2011); western Mediterranean, Tunisia (Fekih, 1975). Lower-upper Pliocene:

Atlantic, Mondego Basin, central west Portugal (Silva, 2001); western Mediterranean, Estepona Basin (NHMW collection); central Mediterranean, Italy (Sacco, 1897; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Chirli, 2013). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910); eastern Mediterranean (Chirli & Linse, 2011). Present-day: eastern Atlantic, Norway to Angola, into Mediterranean (T.E. Thompson, 1988).

Family Tornatinidae Fischer, 1883b [= Acteocinidae Dall *in* Eastman, 1913]
Genus *Acteocina* Gray, 1847

Type species (by original designation) – *Acteon wetherelli* I. Lea, 1833, Miocene, eastern United States.

1847b *Acteocina* Gray, p. 160.

For generic synonymy see Ceulemans *et al*. (2018, p. 117).

***Acteocina lajonkaireana* (de Basterot, 1825)**
Plate 17, fig. 1

*1825 *Bullina Lajonkaireana* de Basterot, p. 22, pl. 1, fig. 25.
1964 *Acteocina lajonkaireana* Basterot, 1825 – Brébion, p. 653.
2013 *Acteocina lajonkaireana* (de Basterot, 1825) – Landau *et al*., p. 333, pl. 53, figs 3-4, pl. 77, fig. 9 (*cum syn*.).
2018 *Acteocina lajonkaireana* (de Basterot, 1825) – Ceulemans *et al*., p. 121, pl. 7, fig. 7.

Material and dimensions – Maximum height 2.1 mm, width 0.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1785 (1), RGM.1352403 (2). **Sceaux-d'Anjou**: NHMW 2016/0103/2044 (2), RGM.718211 (12). **Renauleau**: NHMW 2016/0103/2120 (1).

Discussion – *Acteocina lajonkaireana* (de Basterot, 1825) is characterised by its elongate 'terebelliform' shell, deeply canaliculate suture, almost straight outer lip, in having a fold on the columella and by the character of the protoconch, which is heterostrophic.
In the Assemblage I deposits it is very uncommon, although fairly widespread, and the specimens are smaller than those of other populations. The columellar fold is not developed in the specimens at hand, and is not seen in the specimen figured (Pl. 17, fig. 1a), but this is probably because they are all juvenile or subadult. It continued to be present in the lower Pliocene of the Ligerian Gulf Assemblage III fauna, which is the last known occurrence of this very widespread predominantly Miocene species (Ceulemans *et al*., 2018, p. 121).

Distribution – Lower Miocene: Atlantic (Aquitanian-Burdigalian): Aquitaine Basin, France (Peyrot, 1932; Lozouet *et al*., 2001); Paratethys (Burdigalian): Austria,

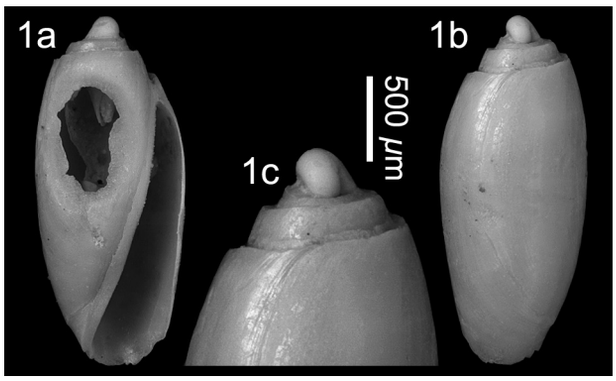

Plate 17. *Acteocina lajonkaireana* (de Basterot, 1825); 1. NHMW 2016/0103/1785, height 2.1 mm, width 0.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(Harzhauser, 2002). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Denmark (Sorgenfrei, 1958), Germany (Moths *et al*., 2010). Middle Miocene: Atlantic (Langhian-Serravallian): Aquitaine Basin, France (Peyrot, 1932), (Langhian): Loire Basin, France (Glibert, 1952a); Proto-Mediterranean Sea (Burdigalian-Langhian): Colli Torinesi, Italy (Sacco, 1897); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856; Berger, 1953; Papp, 1954), Poland (Friedberg, 1928), Hungary (Strausz, 1954, 1966), (Sarmatian): Austria (Harzhauser & Kowalke, 2002), Slovakia (Švagrovský, 1971), Romania (Simionescu & Barbu, 1940), Ukraine (Kolesnikov, 1935); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): NW France (this paper), Algarve Basin, Portugal (Dollfus *et al*., 1903); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1897; d'Amico *et al*., 2012). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018).

Superfamily Cylichnoidea H. Adams & A. Adams, 1854
Family Cylichnidae H. Adams & A. Adams, 1854
Genus *Cylichna* Lovén, 1846

Type species (by subsequent designation, Hermannsen, 1852) – *Bulla cylindracea* Pennant, 1777, present-day, British Isles.

1846 *Cylichna* Lovén, p. 142.

For generic synonymy see Ceulemans *et al*. (2018, p. 120).

***Cylichna pseudoconvoluta* (d'Orbigny, 1852)**
Plate 18, figs 1-3

1825 *Bulla cylindrica* Brug. – de Basterot, p. 20 [*non* Bruguière, 1792; = *Cylichna cylindracea* (Pennant, 1777)].
1828 *Bulla convoluta* Brocc. – Grateloup, p. 90 [*non*

Brocchi, 1814, = *Cylichna cylindracea* (Pennant, 1777)].

1845 *Bulla convoluta* Brocc. – Grateloup, pl. 3, figs 37, 38 [*non* Brocchi, 1814, = *Cylichna cylindracea* (Pennant, 1777)].

*1852 *Bulla pseudoconvoluta* d'Orbigny, p. 95 [*nom. nov. pro Bulla cylindracea* Bruguière in Grateloup, 1845; *non* Pennant, 1777].

1854 *Bulla Cylindracea* Millet, p. 167 (*nomen nudum*).

1865 *Bulla cylindracea* Millet, p. 600 [*non* Pennant, 1777].

1886 *Cylichna pseudoconvoluta* d'Orb. – Dolfuss & Dautzenberg, p. 143.

1933 *Bulinella pseudoconvoluta* d'Orbigny – Peyrot, p. 182, pl. 13, figs 7-9.

1952a *Cylihna* [*sic*] (*Cylichna*) *pseudoconvoluta* – Glibert, p. 396, pl. 15, fig. 7.

1964 *Cylichna convoluta* Brocchi, 1814 – Brébion, p. 656, pl. 15, fig. 39 [*non* Brocchi, 1814, = *Cylichna cylindracea* (Pennant, 1777)].

Material and dimensions – Maximum height 5.8 mm, width 2.2 mm. **Sceaux-d'Anjou**: RGM.1348761 (1). **Renauleau**: NHMW 2016/0103/1355-1356 (2), NHMW 2016/0103/1357 (8), NHMW 2016/0103/2031 (1), LC (5), FVD (11). **Beugnon**: RGM.1348491 (2), RGM.1352572 (16).

Discussion – We follow Glibert (1952a) in considering the French Atlantic Miocene specimens belonging to the *Cylichna cylindracea* (Pennant, 1777) species group a distinct species; *Cylichna pseudoconvoluta* (d'Orbigny, 1852). They differ from *C. cylindracea* most notably in size. In the lower Miocene Aquitaine Basin and middle Miocene Loire Basin the maximum size is about 7.0 mm (Peyrot, 1933, Glibert, 1952a), in Assemblage I maximum height is 5.8 mm, whereas *C. cylindracea* from the lower Pliocene Assemblage III locality of Pigeon Blanc (Ceulemans *et al*., 2018) and present-day specimens (Poppe & Goto, 1991) can reach 13-15 mm in height respectively. Peyrot (1933, p. 183) and Glibert (1952a, p. 397) stressed the absence of fine spiral sculpture in *C. pseudoconvoluta*, whereas *C. cylindracea* has very fine, close-set spiral sculpture. We have examined fossil *C. cylindracea* from numerous localities and note that this sculpture is extremely fine and often only visible on tangential light in the best preserved specimens. Most of the Assemblage I specimens of *C. pseudoconvoluta* are smooth, or appear to be, although some show the faintest impression of spirals, more widely spaced than those of *C. cylindracea* (Pl. 18, fig. 3), but this sculpture is only visible in the best preserved specimens. In most cases the shell of *C. pseudoconvoluta* is more regularly cylindrical than that of *C. cylindracea*, and the apex more sharply truncated and carinate, whereas in *C. cylindracea* the apex is somewhat rounded, narrowing before the apical truncation. In both species the apex of the outer lip is raised a short distance above the apex of the last whorl. *Cylichna pseudoconvoluta* seems to have been a more northern Atlantic Miocene species, as specimens at hand from the upper Miocene Tortonian of Cacela Velha, southern Portugal (NHMW coll.) represent *C. cylindracea*.

Landau *et al*. (2013, p. 332) recognised a small widespread European Miocene species of this group as *Cylichna subcylindrica* (d'Orbigny, 1852) differing from *C. pseudoconvoluta* in having the outer lip hardly rising above the apex, and the last whorl bearing very fine but distinct, wide-set spiral grooves. In view of the observations outlined above, it is possible that the two represent extremes of the same species. However, as the spirals are so weakly developed in *C. pseudoconvoluta* and the lip rises well above the apex in all specimens in Assemblage I, we provisionally consider them distinct.

Brébion (1964, p. 655) recorded this species from the Assemblage I localities of Renauleau and Beaulieu as *C. convoluta* (Brocchi, 1814), to which we add Sceaux-d'Anjou and Beugnon, although it is relatively uncommon at all these localities.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (de Basterot, 1825; Grateloup, 1828, 1845; Peyrot, 1933). Middle Miocene: Atlantic, Aquitaine Basin, France (Peyrot, 1933), Loire Basin, France (Dolfuss & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1952a). Upper Miocene (Tortonian): NW France (Millet, 1854, 1865; Brébion, 1964).

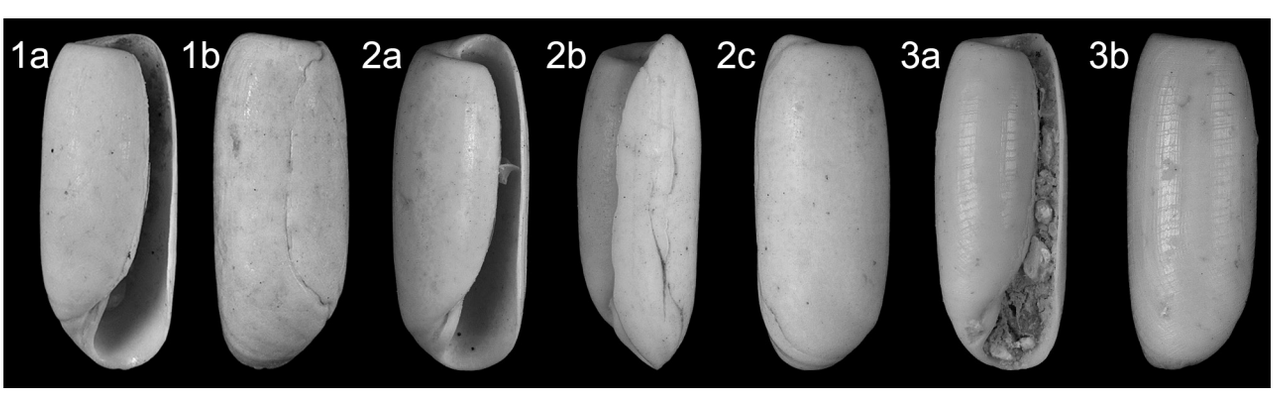

Plate 18. *Cylichna pseudoconvoluta* (d'Orbigny, 1852); 1. NHMW 2016/0103/1355, height 5.6 mm, width 2.2 mm; 2. NHMW 2016/0103/1356, height 5.0 mm, width 2.0 mm; 3. NHMW 2016/0103/2031, height 4.7 mm, width 2.1 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Cylichna ligeriensis* (Glibert, 1952)**
Plate 19, figs 1-3

1854 *Bulla Uniplicata* Millet, p. 167 (*nomen nudum*).
1865 *Bulla uniplicata* Millet, p. 599 (*non* Bellardi *in* Sismonda, 1847).
*1952a *Sabatia* (*Damoniella*) *burdigalensis ligeriensis* Glibert, p. 397, pl. 15, fig. 10.
1964 *Roxania burdigalensis* var. *ligeriensis* Glibert, 1952 – Brébion, p. 657.

Material and dimensions – Maximum height 12.9 mm, width 6.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1287 (1 juvenile), NHMW 2016/0103/1288 (50+ subadult and juveniles), RGM.1352434 (11), RGM.1352520 (50+ mainly juveniles), LC (50+), FVD (50+ subadult and juveniles). **Sceaux-d'Anjou**: RGM.718212 (1 adult + 30 subadult and juveniles), RGM.1348877 (2), RGM.1352489 (5), FVD (7 subadult and juveniles). **Renauleau**: NHMW 2016/0103/1289-1290 (2), NHMW 2016/0103/1291 (20), LC (45), FVD (18). **Beugnon**: NHMW 2016/0103/1292 (3), RGM.1352411 (3), RGM.1352414 (6), RGM.1352571 (8).

Discussion – Cylichna ligeriensis (Glibert, 1952) is easily separated from its congeners by its relatively broad and large size, and very solid thickened shell for the genus. The apex is deeply perforate and spiral sculpture is restricted to a few narrow grooves on the base. Most specimens show some remnants of colour pattern consisting of rows of lighter blotches. It is probably due to its large and relatively broad shell that Glibert (1952a) placed this species in the genus *Damoniella* Iredale, 1918, an unnecessary replacement name for *Roxania* Leach *in* Gray, 1847a (type species *Bulla cranchii* Fleming, 1828; = *Roxania utriculus* (Brocchi, 1814)], but members of this genus are even more regularly ovate and have punctate spiral sculpture. Glibert originally described this taxon as a subspecies of *Bulla burdigalensis* d'Orbigny, 1852 from the lower Miocene of the Aquitaine Basin of France, which although similar in size and contour, has much stronger spiral sculpture and a less excavated columella abapically. Brébion (1964, p. 657) recorded this species from the Assemblage I localities of Renauleau and Sceaux-d'Anjou, to which we add St-Clément-de-la-Place and Beugnon.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1952a). Upper Miocene (Tortonian): NW France (Millet, 1854, 1865; Brébion, 1964).

Superfamily Haminoeidea Pilsbry, 1895
Family Haminoeidae Pilsbry, 1895
Subfamily Haminoeinae Pilsbry, 1895
Genus *Haminoea* Turton & Kingston, 1830

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

1830 *Haminoea* Turton & Kingston, p. F8.

For generic synonymy see Ceulemans *et al*. (2018, p. 121).

***Haminoea navicula* (da Costa, 1778)**
Plate 20, figs 1, 2

*1778 *Bulla navicula* da Costa, p. 28, pl. 1, fig. 10.
1822 *Bulla cornea* Lamarck, p. 36.
1853 *Bulla* (*Haminea* [*sic*]) *folliculus* Menke, p. 141.
1854 *Bulla Globulus* Desh. – Millet, p. 166 (*non* Deshayes, 1824).
1910 *Bulla* (*Haminea* [*sic*]) *hydatis* L. – Cerulli-Irelli, p. 37, pl. 35, fig. 10 [*non Haminoea hydatis* (Linnaeus, 1758)].
1923 *Haminea* [*sic*] *hydatis* (Linné) – Harmer, p. 807, pl. 63, fig. 16 [*non Haminoea hydatis* (Linnaeus, 1758)].
1952a *Haminea* [*sic*] (*Haminea* [*sic*]) *navicula* Da Costa, 1778 – Glibert, p. 392, pl. 15, fig. 2.
1964 *Haminoea navicula* Da Costa, 1778 – Brébion, p. 660.
1987 *Haminoea navicula* (Da Costa, 1778) – Talavera *et al*., p. 56, figs 5-8.
1988 *Haminea* [*sic*] *navicula* (Costa, 1778) – T.E. Thompson, p. 42, fig. 12.
2013 *Haminoea navicula* (Da Costa, 1778) – Chirli, p. 60, pl. 13, figs 11-14.

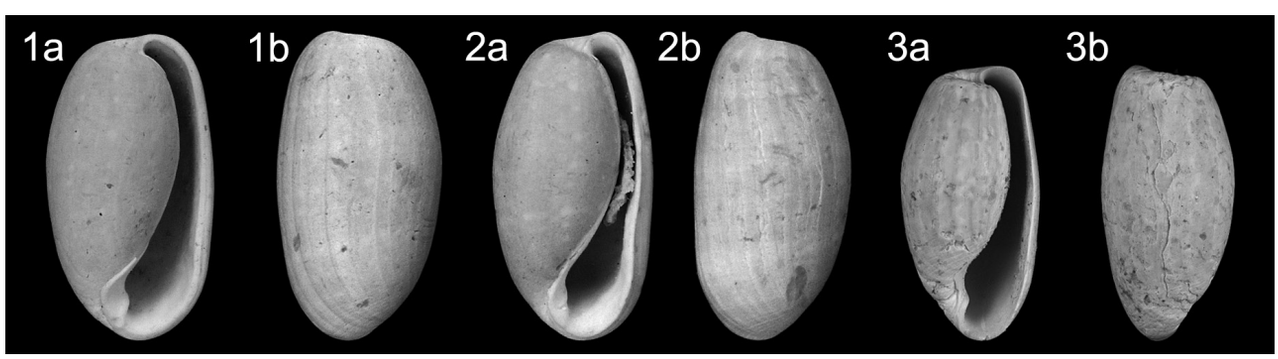

Plate 19. *Cylichna ligeriensis* (Glibert, 1952); 1. NHMW 2016/0103/1289, height 9.5 mm, width 5.1 mm; 2. NHMW 2016/0103/1290, height 8.4 mm, width 4.5 mm. Renauleau. 3. NHMW 2016/0103/1287, height 4.7 mm, width 2.3 mm (juvenile). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Plate 20. *Haminoea navicula* (da Costa, 1778); 1. NHMW 2016/0103/2123, height 10.3 mm, width 7.4 mm; 2. NHMW 2016/0103/2124, height 8.6 mm, width 6.5 mm. Renauleau Maine-et-Loire, NW France, Tortonian, upper Miocene.

Material and dimensions – Maximum height 10.3 mm, width 7.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1491 (1), LC (1). **Renauleau**: NHMW 2016/0103/2125-2126 (2), LC (2). **Beugnon**: RGM.717791 (1).

Discussion – According to Talavera *et al*. (1987, p. 61), *Haminoea orbignyana* (Férussac, 1822) is the only European *Haminoea* species that can be reliably distinguished by its shell, which is pyriform with a broad anterior part of the aperture, which does not fit the species found in Assemblage I. The species *H. navicula* (da Costa, 1778) has a globose shell with conspicuous fine spiral striae visible in shells that are well preserved. In shells with an abraded surface, *H. navicula* and *H. hydatis* (Linnaeus, 1758) cannot be reliably separated, although *H. navicula* is said to be larger, more truncated, with a wider aperture and a more excavated columella. The specimens from Assemblage I can fairly reliably be ascribed to *H. navicula*. Fine spiral striation can be seen, especially towards the outer lip (Pl. 20, fig. 1b), which has the surface less abraded, and the columella is deeply excavated. Glibert (1952a) also ascribed his middle Miocene specimens from the Loire Basin to *H. navicula*, a position with which we fully agree. The specimen from the lower Pliocene Assemblage III of Le Pigeon Blanc illustrated by Ceulemans *et al*. (2018, pl. 7, fig. 12) has a relatively narrower aperture and represents *H. hydatis*. The chresonymy and distribution are probably an underrepresentation on the distribution of this species, as we have only included fossil records we are fairly certain to be conspecific. Cerulli-Irelli (1910, p. 229) considered *H. navicula* to be the fully adult form of *H. hydatis*, but the specimen illustrated (1910, pl. 35, fig. 10) is large with a deeply excavated columella and represents *H. navicula*. Brébion (1964, p. 660) also noted the presence of *H. navicula* at the Assemblage I locality of Renauleau, where it is extremely uncommon, to which we add St-Clément-de-la-Place and Beugnon.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1952a). Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: central Mediterranean, Italy (Chirli, 2013). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Present-day: eastern Atlantic from British Isles to Gibraltar, Mediterranean and Black Sea (Talavera *et al*., 1987), Canaries, Ascension Island and St. Helena (T.E. Thompson, 1988).

Superfamily Philinoidea Gray, 1850 (1815)
Family Philinidae Gray, 1850
Genus *Philine* Ascanius, 1772

Type species (by monotypy) – *Philine quadripartita* Ascanius, 1772, present-day, Norway.

1772 *Philine* Ascanius, p. 331.
1776 *Lobaria* Müller, p. 226. Type species (by monotypy): *Lobaria quadriloba* Müller, 1776 (= *Philine quadripartita* Ascanius, 1772), present-day, Europe.
1801 *Bullaea* Lamarck, p. 63. Type species (by monotypy): *Bullaea planciana* Lamarck, 1801 (= *Philine quadripartita* Ascanius, 1772), present-day, Mediterranean.
1815 *Bullea* Rafinesque, p. 477. Incorrect subsequent spelling of *Bullaea* Lamarck, 1801.
1815 *Bullinia* Rafineque, p. 142. Substitute name for *Bullaea* Lamarck, 1801.
1870 *Utriculopsis* Sars, p. 17. Type species (by monotypy): *Utriculopsis vitrea* Sars, 1870 [= *Philine confusa* (Ohnheiser & Malaquias, 2013)], *non Philine vitrea* (Sars 1870), present-day, Norway.
1884 *Johania* Monterosato, p. 147. Type species (by monotypy): *Bulla retifera* Forbes, 1844 [= *Philine vestita* (Philippi, 1840)], present-day, Mediterranean.
1958 *Choshiphiline* Habe, p. 120. Type species (by original designation): *Philine pygmaea* Yokoyama, 1922, Pleistocene, Japan.
1967 *Rhinodiaphana* Lemche, p. 208. Type species (by original designation): *Amphisphyra ventricosa* Jeffreys, 1865b, present-day, British Isles.
1972b *Philingwynia* Nordsieck, p. 22. Type species (by original designation): *Philine monterosati* Monterosato, 1874, present-day, Mediterranean.
1972b *Retusophiline* Nordsieck, p. 20. Type species (by

original designation): *Bulla lima* Brown, 1827, present-day, British Isles.

***Philine catena* (Montagu, 1803)**
Plate 21, figs 1, 2

1803 *Bulla catena* Montagu, p. 215, pl. 7, fig. 7.
1848 *Bullaea sculpta* Wood, p. 180, pl. 21, fig. 10.
2011 *Philine catena* (Montagu, 1803) – Chirli & Linse, p. 216, pl. 86, fig. 1.
2013 *Philine catena* (Montagu, 1803) – Chirli, p. 33, pl. 9, figs 1-5 (*cum syn*.).
2013 *Philine catena* (Montagu, 1803) – Landau *et al*., p. 329, pl. 77, fig. 2 (*cum syn*.).
2018 *Philine catena* (Montagu, 1803) – Brunetti & Cresti, p. 118, fig. 525.

Material and dimensions – Maximum height 2.1 mm, width 1.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2064-2065 (2), NHMW 2016/0103/2223 (1).

Discussion – *Philine catena* (Montagu, 1803) is easily distinguished by its oval shape and very distinctive sculpture, which consists of a fan of spiral chains, composed of interconnected rings. *Philine iris* Tringali, 2001 from the present-day western Mediterranean and adjacent Atlantic is closely similar, but differs in having the chain-like sculpture composed of smaller, more rounded links.
Like many of the Assemblage I species, the specimens are considerably smaller than those found in other fossil and present-day faunas (3.2-3.7 mm height). We have so far found this species only at St-Clément-de-la-Place, where it is extremely uncommon.

Distribution – Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Berger, 1953); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene (Tortonian): Atlantic, NW France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848); western Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: central Mediterranean, Italy (Sacco, 1897; Chirli, 2013; Brunetti & Cresti, 2018). Lower Pleistocene: central Mediterranean, Italy (Ruggieri & Greco, 1965); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Present-day: Lofoten southwards along the entire coast of Norway (Høisæter *et al*., 2001), down to the British Isles, Mediterranean Sea, and Canaries (Nordsieck, 1972b).

***Philine ligustica* (Sacco, 1897)**
Plate 22, figs 1, 2

*1897 *Philine* (*Hermania*) *ventrosa* var. *ligustica* Sacco, p. 54, pl. 4, fig. 45.
2018 *Philine* cf. *ventrosa ligustica* Sacco, 1897 – Brunetti & Cresti, p. 118, fig. 527.

Material and dimensions – Maximum height 3.1 mm, width 2.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0965 (1), NHMW 2016/0103/2097-2099 (3), NHMW 2016/0103/2100 (12), RGM.1352731 (1), LC (2), FVD (2). **Sceaux-d'Anjou**: RGM.718213 (5).

Revised description – Shell small, fragile, oval, with right side convex and left side posteriorly concave and anteriorly convex. Spire involute, about one whorl. Last whorl entire shell length. Umbilicus closed. Aperture 88% total height, pyriform, widest near rounded anterior end. Outer lip not alate adapically. Columella broadly excavated, slightly thickened near anterior end. Sculpture of rows of large round to oval punctuations, wider than separations, giving fine honeycomb-like surface pattern; the punctuations interconnect narrowly mid-punctuation.

Discussion – Sacco (1897) described this as a subspecies of *Bulla ventrosa* Wood, 1848, with the brief description "*Testa minor, paulullo minus ventrosa*." (Sacco, 1897, p. 54). We therefore offer a revised description based on the Assemblage I specimens. *Philine ventrosa*, described from the lower Pliocene Coralline Crag of England, was re-illustrated by Marquet (1997, 1998, fig. 190) based on Belgian material and represents quite a different species with sculpture composed of close-set spiral cords and is

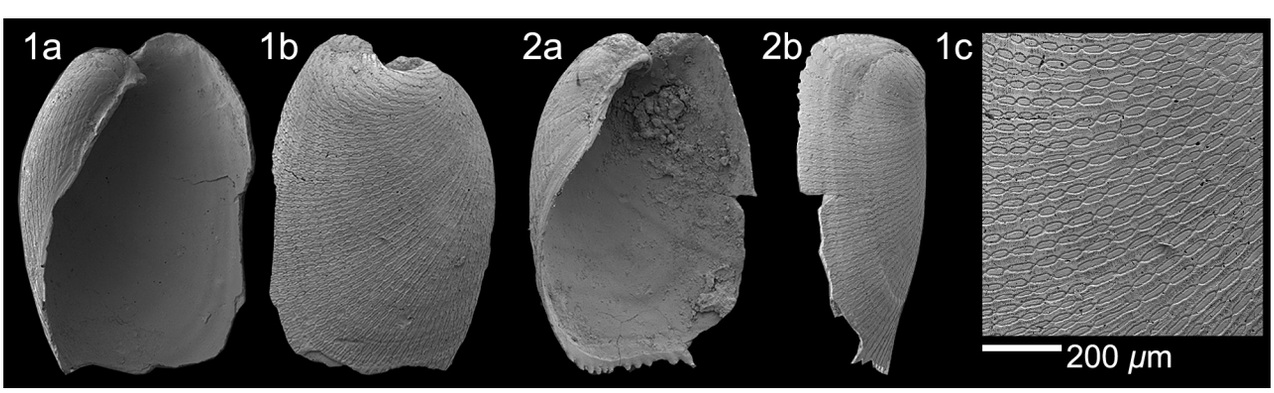

Plate 21. *Philine catena* (Montagu, 1803); 1. NHMW 2016/0103/2064, height 2.0 mm, width 1.4 mm, 1c, detail of teleoconch sculpture; 2. NHMW 2016/0103/2065, height 2.1 mm, width 1.4 mm (SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

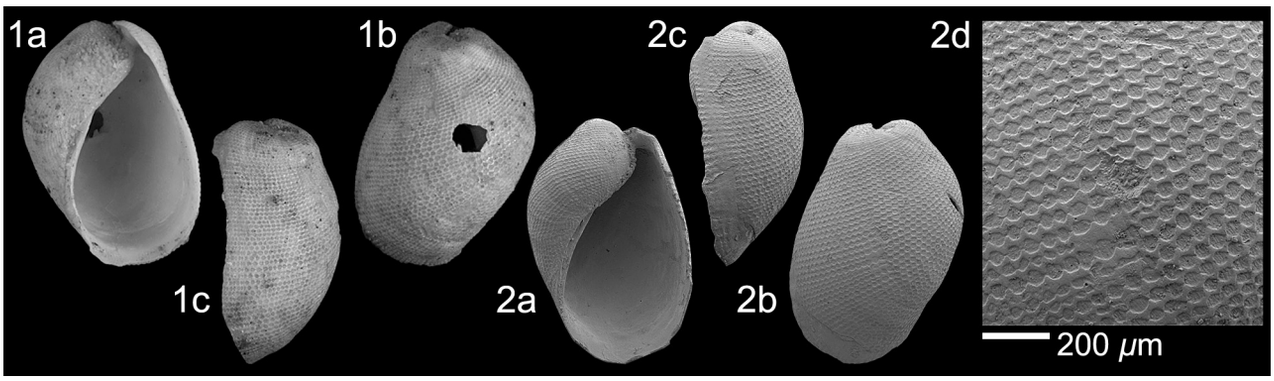

Plate 22. *Philine ligustica* (Sacco, 1897); 1. NHMW 2016/0103/0965, height 3.1 mm, width 2.2 mm; 2. NHMW 2016/0103/1301, height 2.8 mm, width 1.8 mm, 2d, detail of teleoconch sculpture (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

not punctate as described originally (Wood, 1848, p. 182). The only illustration of *Philine ligustica* (Sacco, 1897) we are aware of subsequent to its original description is that of Brunetti & Cresti, (2018, p. 118, fig. 527) based on a shell from the lower Pliocene of Orciano Pisano, Italy. This poorly known species is likely widely distributed in the Pliocene as it also occurs in the lower Piacenzian deposits of the Estepona Basin, southern Spain (NHMW coll.), where it is not uncommon, and coeval beds from the Atlantic Mondego Basin, central-west Portugal (NHMW coll.). We have compared these Iberian specimens with those from Assemblage I and confirm that they are conspecific.

Philine ligustica is not particularly similar to any extant European species. It is somewhat similar in shape to *P. finmarchica* M. Sars, 1859, but the surface sculpture in the latter is quite different, composed of fused punctuations forming spiral grooves. We can find no further European fossil species that can be compared. *Philine abyssicola* Valdés, 2008, an extant deep-water species from Fiji, is similar in shape and sculpture, but has a more expanded aperture, a straight columella and the punctuations are not interconnected.

In Assemblage I *P. ligustica* is uncommon, found in St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Sacco, 1897; Brunetti & Cresti, 2018). Upper Pliocene: Atlantic, Mondego Basin, central-west Portugal (NHMW coll.); western Mediterranean, Estepona Basin, Spain (NHMW coll.).

Philine rostrata **(Deshayes, 1830)**

Plate 23, figs 1, 2

*1830 *Bullaea rostrata* Deshayes, p. 148.
1895 *Bullaea rostrata* Desh. – Cossmann, p. 127 [discussed under *Philine* (*Megistostoma*)].
1897 *Philine* (*Megistostoma*) *rostratum* (Desh.) – Sacco, p. 54, pl. 4, fig. 41.
2011 *Megistostoma rostratum* (Deshayes, 1830) – Sosso *et al*., p. 23, figs 2A-F, 3.

Material and dimensions – Height 5.0 mm, width 3.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0966 (2 fragments).

Discussion – This interesting species was discussed by Sosso *et al*. (2011). To summarise its history, it was described by Deshayes (1830) based on material from the Piacenzian Pliocene and deposited in the collection of l'École des Mines di Parigi. Sacco (1897, p. 54) stated that the type was not in that collection, and illustrated a photograph sent to him by Cossmann of a specimen from the Pliocene of Gourbesville housed in the collection of l'École des Mines. Sosso *et al*. (2011) rediscovered the species in the Zanclean lower Pliocene deposits of Rio Torsero, Italy, confirming its presence in the Italian Pliocene.

The single incomplete specimen from the Tortonian Assemblage I locality of St-Clément-de-la-Place is closely similar to the specimen from Rio Torsero, and shows the same teleoconch microsculpture of fine, close-set axial riblets. The few records we have of this species would suggest it was relatively widely distributed geographically and stratigraphically, but is rarely preserved probably due it its fragility. We are indebted to Maurizio Sosso who kindly compared our material to his Italian specimens and provided the photograph reproduced above.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Sosso *et al*., 2011). Upper Pliocene-Pleistocene: Atlantic, NW France (Cossmann, 1895; Sacco, 1897).

Discussion

In this paper we record 23 Heterobranchia (in part) (of which two are left in open nomenclature), representing 14 genera. Four species are described as new: *Ammonicera oliveri* nov. sp., *Ebala ornatissima* nov. sp., *Coenaculum*

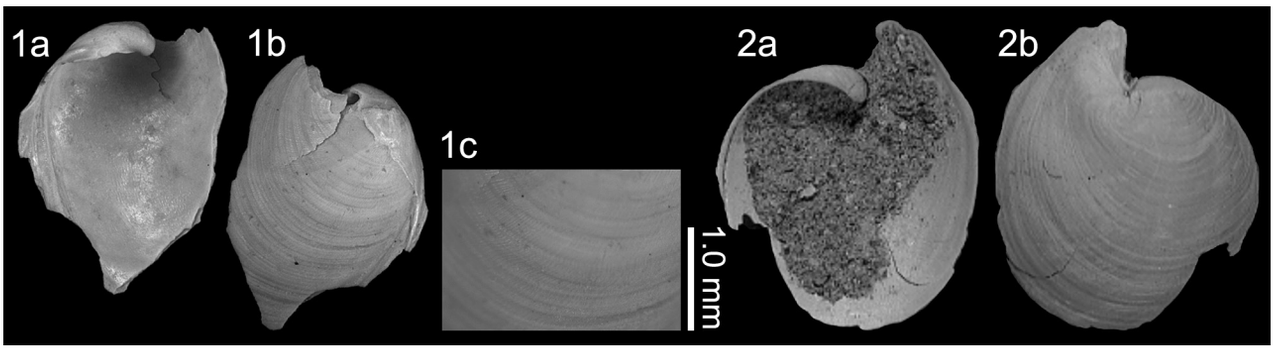

Plate 23. *Philine rostrata* (Deshayes, 1830); 1. NHMW 2016/0103/0966, height 5.0 mm, width 3.6 mm, 1c, detail of teleoconch surface sculpture. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene. 2. PMRSN 245 (ex. Maurizio Sosso collection), height 8.8 mm, width 7.2 mm, Rio Torsero, Ceriale, Savona, Italy, Zanclean, lower Pliocene (photo courtesy M. Sosso).

boucheti nov. sp., and '*Acteon*' *distinctus* nov. sp. Of the 23 Heterobranchia (in part) species recorded here, five (23%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. If we include the middle Miocene, eight (36%) are restricted to northwestern France. Stratigraphically (see Fig. 1), 11 (50%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1952a). Six (27%) are also present in the Assemblage III (sensu Van Dingenen *et al*., 2015) of northwestern France. Six (27%) are also found in the North Sea Basin Pliocene. Eleven (50%) are relatively cosmopolitan, found in the Atlantic and Mediterranean. Four (18%) are still living in European Atlantic and/or Mediterranean waters.

In this part of the series we have recognised almost all the taxa discussed by Brébion, with the exception of *Mathilda concinna* Millet, 1854, *Ringicula* (*Ringiculicosta*) *costata* (Eichwald, 1830) and *Scaphander dertonensis* Sacco, 1897 (Brébion, 1964, p. 204, 652, 658 respectively). The first two of these three species were recorded by Brébion from Renauleau, which has been extensively sampled by us without a single fragment of these species being found. None of these three species was figured by Brebion. Therefore, these records require confirmation.

A full synthesis of the Assemblage I fauna will be given at the end of the series.

Acknowledgements

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References

For references see part 7 of 'The upper Miocene Gastropods of northwestern France' starting at page 279 of this same volume of Cainozoic Research. The references are to be found on page 351.

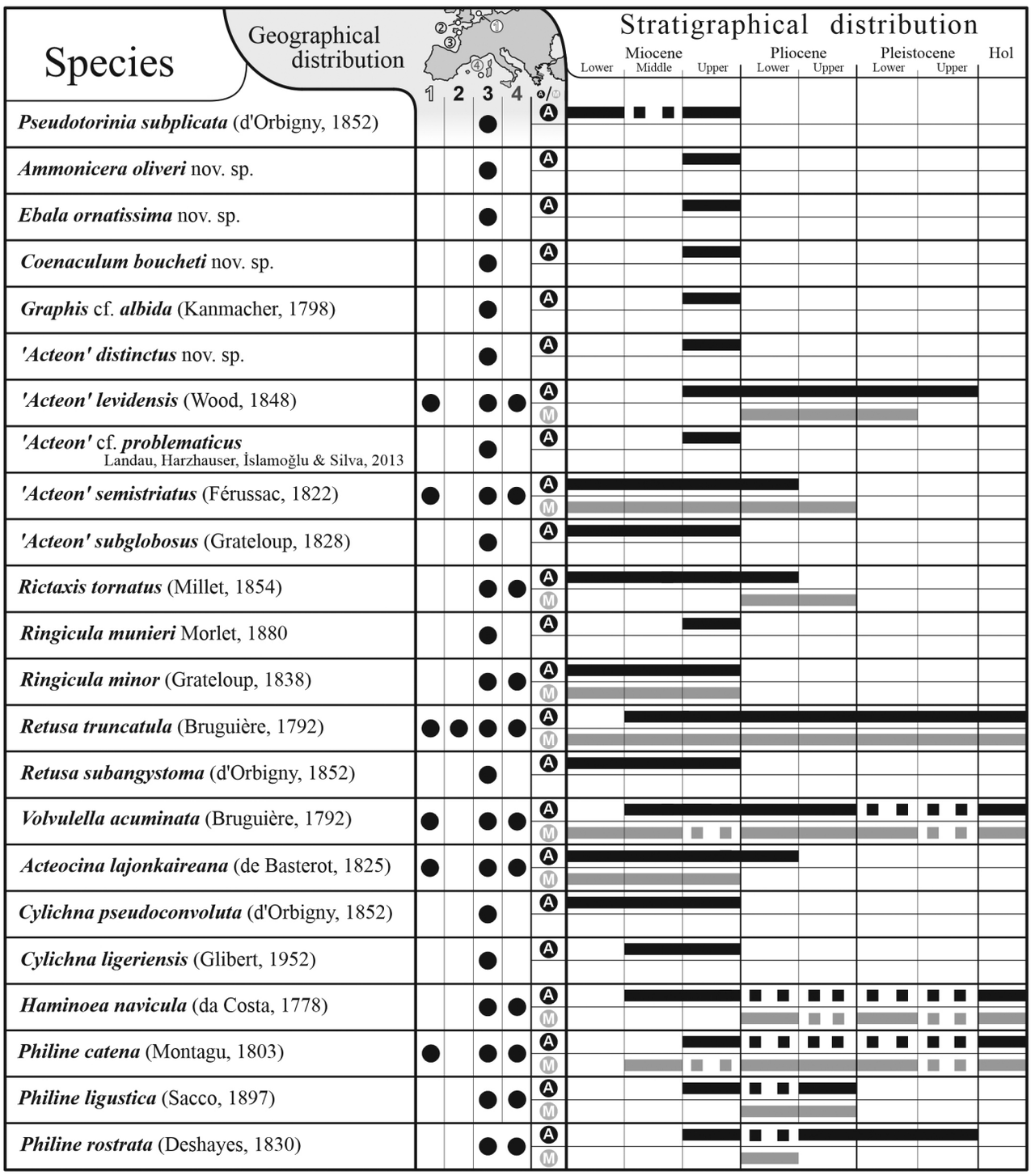

Figure 1. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black signifies Atlantic distribution (A), grey Mediterranean distribution (M).