

# The upper Miocene gastropods of northwestern France, 2. Caenogastropoda

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In this paper we review the Caenogastropoda of the Tortonian upper Miocene (Assemblage I of Van Dingenen *et al.*, 2015) of northwestern France. One hundred and seventy-four species are recorded, of which 65 are new: *Bittium crassum* nov. sp., *Bittium gallicum* nov. sp., *Bittium pingue* nov. sp., *Bittium renauleauense* nov. sp., *Semibittium brebioni* nov. sp., *Archimediella sancticlementensis* nov. sp., *Oligodia chauvereauensis* nov. sp., *Crassitonella lozoueti* nov. sp., *Acirsa sceauxsensis* nov. sp., *Papuliscala redoniensis* nov. sp., *Papuliscala presselierensis* nov. sp., *Payraudeautia obelixa* nov. sp., *Inella alia* nov. sp., *Inella rolandi* nov. sp., *Monophorus renauleauensis* nov. sp., *Obesula marshalli* nov. sp., *Triphora buscheri* nov. sp., *Triphora chauvereauensis* nov. sp., *Triphora fernandezgarcesi* nov. sp., *Triphora lherbottorum* nov. sp., *Triphora miopygmaea* nov. sp., *Triphora sancticlementensis* nov. sp., *Cerithiopsis cerithiopsoides* nov. sp., *Cerithiopsis esterae* nov. sp., *Cerithiopsis mira* nov. sp., *Dizoniopsis boucheti* nov. sp., *Seila petasa* nov. sp., *Ataxocerithium turbineum* nov. sp., *Alvania armata* nov. sp., *Alvania couffoni* nov. sp., *Alvania fezata* nov. sp., *Alvania globosa* nov. sp., *Alvania insulsa* nov. sp., *Alvania josephineae* nov. sp., *Alvania lachrimula* nov. sp., *Alvania milletispinosa* nov. sp., *Alvania miocalasi* nov. sp., *Alvania miolactea* nov. sp., *Alvania napoleoni* nov. sp., *Alvania parasusieae* nov. sp., *Alvania redoniana* nov. sp., *Alvania renauleauensis* nov. sp., *Alvania subtiliangulosa* nov. sp., *Alvania susieae* nov. sp., *Alvania tenuisculpturata* nov. sp., *Alvania turtaudierei* nov. sp., *Pseudosetia wareni* nov. sp., *Pseudosetia sergegofasi* nov. sp., *Pseudosetia peyroti* nov. sp., *Pseudosetia ivolasi* nov. sp., *Onoba redoniensis* nov. sp., *Onoba incisa* nov. sp., *Onoba fragilis* nov. sp., *Rissoa decorticata* nov. sp., *Rissoa torquata* nov. sp., *Powellisetia europaea* nov. sp., *Pusillina dollfusi* nov. sp., *Pusillina gallica* nov. sp., *Discopsis pseudocanui* nov. sp., *Tornus superlatus* nov. sp., *Teinostoma obesum* nov. sp., *Macromphalina morgani* nov. sp., *Trivia sceauxensis* nov. sp., *Niveria cylindriclementi* nov. sp. and *Cleotrivia gallica* nov. sp.

*Delphinula carinata* Millet, 1854 is a junior homonym of *D. carinata* Woodward, 1833, and is renamed *Alvania acuticarinata* nov. nom. *Rissoa suturalis* Millet, 1865 is a junior homonym of *R. suturalis* Philippi, 1844, and is renamed *Alvania milleti* nov. nom. *Rissoa notabilis* Millet, 1865 is a junior homonym of *R. notabilis* C.B. Adams, 1852, and is renamed *Rissoa obeliscoides* nov. nom. *Lacuna bourgeoisii* Tournouër, 1874 is a junior subjective synonym of *Phasianella delphinuloides* Millet, 1865. *Bithinella [sic] benoisti* Dollfus & Dautzenberg, 1886 is considered a subjective synonym of *Bithinella [sic] Fontannesii* Dollfus & Dautzenberg, 1886; as first revisers the name *Peringia fontannesii* (Dollfus & Dautzenberg, 1886) is chosen. *Tornus dollfusi* Cossmann, 1918 and *Tornus subcarinatus minor* Glibert, 1949 are considered junior subjective synonyms of *Tornus subcarinatus* (Montagu, 1803).

*Schilderia fasciolaria*, *S. incognita*, *S. lauriatae*, *S. veronicata* and *S. brebioni* Dolin & Lozouet, 2004 are all considered to represent a single species, as first revisers the name *Schilderia brebioni* Dolin & Lozouet, 2004 is chosen as valid.

We amend an omission made in part one of this series; *Trochus echinatus* Millet, 1854 is a junior homonym of *Trochus echinatus* Klöden, 1834, and is renamed *Calliostoma milletechinatum* nov. nom.

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.*, 2016; Van Dingenen *et al.*, 2014, 2015, 2016; Landau *et al.*, 2017): Gastropods of the subclass Caenogastropoda in the Assemblage I deposits of Van

Dingenen *et al.*, (2015) of Tortonian upper Miocene age are revised.

In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded 90 Caenogastropoda species from Assemblage I deposits, some of which were described as new. However, as the thesis was never published, these names do not comply

with article 13 of the ICZN code (1999) and must be considered *nomina nuda*.

### Geological setting and Material and methods

Systematics have been updated following Bouchet & Rocco (2017). For the rest of this section see Landau *et al.* (2017, pp. 76-78).

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).
NSB	North Sea Basin
RGM	Naturalis Biodiversity Center, collection Cenzoic Mollusca (Leiden, The Netherlands).

### Corrections to Part 1 of this series Landau *et al.* (2017):

p. 85: *Emarginula octaviana* Coen 1839 should read 1939, which makes *Emarginula ornata* Millet, 1865 an older name, but this is a junior homonym of *Emarginula ornata* Deshayes, 1831. A Google Scholar search of *Emarginula octaviana* returns 56 references for the period 1967-2017. Some of these may not qualify as usages under Art. 23.9 (ICZN, 1999) but it is more than likely that the conditions of Art. 23.9.1.2 are met. However, because of Glibert's (1949) usage of *E. elongata* Costa, 1830, the conditions of Art. 23.9.1.1 are not met, and at face value the valid name of the species is *Emarginula elongata*. However, *Emarginula elongata* Costa, 1830 is preoccupied by *E. elongata* Gray, 1825 and *E. elongata* Defrance, 1825. Therefore *Emarginula octaviana* Coen, 1939 remains the valid name for this species. We thank Philippe Bouchet and Serge Gofas for pointing out the original typo error and discussion on the nomenclature.

p. 94: *Clanculus (Clanculopsis) sancticlementensis* nov. sp., paratype 1 MNHN.F.A57700, should read MNHN.F.66722.

p. 102: Based on molecular data, Affenzeller *et al.* (2017) validated the genus *Steromphala* Gray, 1847 with *Trochus adansonii* (Payraudeau, 1826), the type species of *Colliculus* Monterosato, 1888, included in that clade. Therefore *Colliculus* becomes a synonym of *Steromphala*, changing the generic assignment of two species: *Steromphala biangulata* (Eichwald, 1830) and *Steromphala insignis* (Millet, 1854).

p. 122: *Trochus echinatus* Millet, 1854 is a junior homonym of *Trochus echinatus* Klöden, 1834, a Cretaceous

species from Germany. We propose *Calliostoma milletechinatum* nov. nom. for Millet's species. Our thanks to Philippe Bouchet (MNHN Paris) for bringing to our attention this homonymy missed by Landau *et al.* (2016).

### Systematic palaeontology

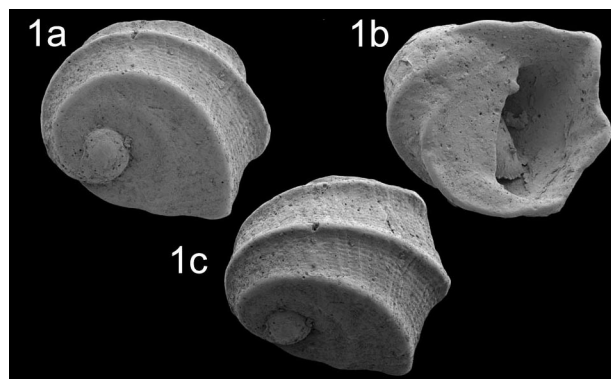
Subclass Neritimorpha  
 Superfamily Neritoidea Rafineque, 1815  
 Family Neritinae Rafinesque, 1815  
 Subfamily Neritinae Rafineque, 1815  
 Genus *Pseudodostia* Symonds, 2006

#### *Pseudodostia tricarinata* (Lamarck, 1804)?

Plate 1, fig. 1

*Material and dimensions* – Diameter 1.4 mm. **Sceaux-d'Anjou**: RGM.1348966 (1 juvenile).

*Discussion* – A single minute nerite is present in the Naturalis collection found amongst specimens picked from sediments labelled Sceaux-d'Anjou. In all the hundreds of kilograms of sediment searched by numerous collectors, this is the only nerite that has been found in the upper Miocene Assemblage I deposits of northwestern France. The specimen is likely to be juvenile, judging from the size; very few adult nerites remain this small. The prominent tooth at the septal edge placed at about one quarter of the distance from the apical end would suggest the genus *Pseudodostia* Symonds, 2006, a well-known genus from the Eocene of northwestern France and England. The dorsal sculpture composed of three strong lirae with close-set fine cords between is suggestive of *Pseudodostia tricarinata* (Lamarck, 1804), which is abundant in the upper Eocene of Loire Atlantique at Bois-Gouët. This site is popular with Dutch collectors and it is therefore possible that this specimen is a contaminant. Until further specimens are found from indisputably Assemblage I sediments, we consider this shell a contaminant.



**Plate 1.** *Pseudodostia tricarinata* (Lamarck, 1804)?; 1. RGM.1348966, diameter 1.4 mm (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene?; doubtful.



We note that Brébion (1964, p. 138) listed, but did not figure, one specimen of *Nerita* (*Theliostyla*) *funata* Du-jardin, 1837 from the Assemblage I locality of St-Michel. That is quite a characteristic species, and although we cannot verify this record, it is unlikely to be the species figured here.

*Distribution* – Probably an Eocene contaminant.

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

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

1890 *Thericium* Monterosato, p. 163.

For generic synonymy see Van Dingenen *et al.* (2016, p. 110).

### *Thericium bronni* (Hörnes, 1856)

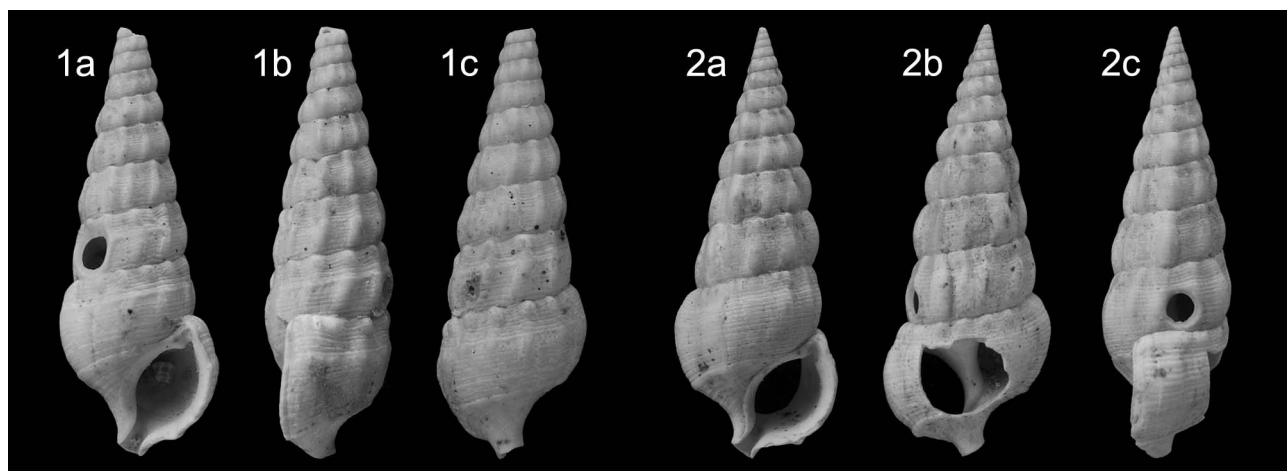
Plate 2, figs 1-2

- 1854 *Cerithium Inconditum* Millet, p. 163 (*nomen nudum*).  
\*1856 *Cerithium Bronni* Partsch – Hörnes, p. 407, pl. 42, fig. 12.  
1865 *Cerithium inconditum* Millet, p. 594.  
1889 *Cerithium heptagonum* Mayer-Eymar, p. 207, pl. 5, fig. 7.  
1949 *Cerithium (Ptychocerithium) bronni heptagonum* Mayer, 1889 – Glibert, p. 147, pl. 9, fig. 11.  
1964 *Cerithium (Ptychocerithium) bronni* Partsch in Hörnes, 1845 – Brébion, p. 239, pl. 6, figs 16-20.  
2016 *Thericium bronni* (Hörnes, 1856) – Van Dingenen *et al.*, p. 110, pl. 1, figs 1-3 (*cum syn.*).

*Material and dimensions* – Maximum height 21.7 mm. **St-Clément-de-la-Place**: RGM.1348239 (25 juveniles), RGM.1348347 (50+ juveniles), RGM.1348628 (12 fragments). **Sceaux-d'Anjou**: RGM.1348232 (4 fragments). **Renauleau**: NHMW 2016/0103/0641-0642 (2), NHMW 2016/0103/1472 (30 incomplete and juveniles), RGM.1348658 (14 juveniles), RGM.1348797 (1 adult), LC (50+ fragments), FVD (50+ fragments) **Beugnon**: NHMW 2016/0103/0463 (5), RGM.1348412 (50+ fragments and juveniles), RGM.1348413 (7 + 20 juveniles), RGM.1348414 (8), RGM.1348428 (3), RGM.1348429 (1 fragment), RGM.1348437 (1), RGM.1348485 (29 juveniles).

*Discussion* – As discussed by Van Dingenen *et al.* (2016, p. 110), Cossmann & Peyrot (1921) separated the Atlantic lower and middle Miocene specimens under the name *Cerithium (Ptychocerithium) heptagonum* from *Thericium bronni* (Hörnes, 1856) based on the shells being smaller, thinner and more elongated, and on small sculptural details. Glibert (1949) considered them a subspecies of *T. bronni*, the only constant difference between them being the smaller size of the Atlantic specimens. Brébion (1964) stressed the enormous variability in the material he had at hand and pointed out that some NW French specimens were larger than those from the Paratethys, and concluded that it was not easy to characterise *T. bronni*. However, if the Atlantic form should turn out to be distinct from that of the Paratethys, the name *Cerithium inconditum* Millet, 1865 has priority over *Cerithium heptagonum* Mayer-Eymar, 1889, at least for the Assemblage I specimens figured here.

In the Assemblage I deposits we have found relatively few well-preserved specimens at Renauleau. At the other localities only spire fragments are found. The Assemblage I specimens are smaller and have a slightly narrower spire angle than those illustrated by Van Dingenen *et al.* (2016, pl. 1, figs 1-3) from the lower Pliocene Assemblage III locality of Le Pigeon Blanc. The smaller size of specimens from the Assemblage I deposits compared to those from other stratigraphic levels is a recurring theme when dealing with these northwestern French Tortonian assem-



**Plate 2.** *Thericium bronni* (Hörnes, 1856); 1. NHMW 2016/0103/0642, height 16.9 mm, width 5.8 mm; 2. NHMW 2016/0103/0643, height 16.2 mm, width 5.8 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

blages. The sculpture is similar, the axial ribs possibly a little sharper, especially in the Beugnon specimens, but they are otherwise comparable. Again, the variation in sculpture is remarkable. In some specimens the axial ribs are strongly developed, resulting in an undulating suture (Pl. 2, fig. 1), whereas in others the ribs weaken on the last one or two whorls (Pl. 2, fig. 2). In the specimens from Renauleau there is a suggestion of a narrow paler colour band a short distance below the suture.

Brébion (1964, p. 241) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, Chalonnes, Renauleau, Beaulieu) and Assemblage III (Le Pigeon Blanc, Palluau). The latter Zanclean records are the chronologically youngest for the species.

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

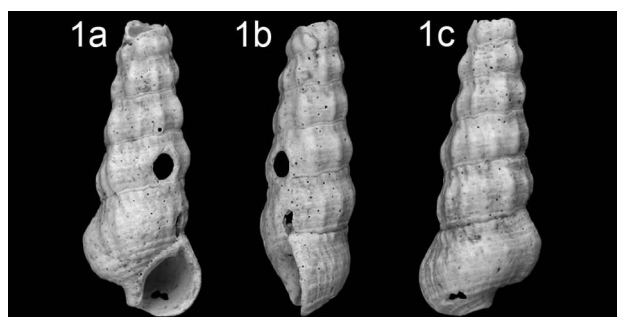
### *Thericium cf. vulgatum* (Bruguière, 1792)

Plate 3, fig. 1

- cf. \*1792 *Cerithium vulgatum* Bruguière, p. 156, pl. 10, fig. 3.  
 cf. 1996 *Cerithium vulgatum* Bruguière, 1792 – Giannuzzi-Savelli *et al.*, p. 28, figs 12-48.  
 cf. 2004a *Cerithium (Thericium) vulgatum* Bruguière, 1792 – Landau *et al.*, p. 8, pl. 1, figs 10-11.

*Material and dimensions* – Height 10.2 mm, width 4.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0703 (1).

*Discussion* – Little can be concluded based on the poor material at hand from the Assemblage I deposits, except that a species occurs that is either conspecific with, or similar to, *Thericium vulgatum* (Bruguière, 1792). The single abraded shell illustrated here (Pl. 3, fig. 1) from St-Clément-de-la-Place is more slender than usual for the



**Plate 3.** *Thericium cf. vulgatum* (Bruguière, 1792); 1. NHMW 2016/0103/0703, height 10.2 mm, width 4.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

species, with strongly convex whorls, but *T. vulgatum* is extraordinarily variable, as shown by Giannuzzi-Savelli *et al.* (1996, figs 12-48) and similar slender forms occur today.

Brébion (1964, p. 243) recorded *T. europaeum* (Mayer-Eymar, 1878) from Assemblage I (St-Michel, Beaulieu) as a variety of *Cerithium (Thericium) vulgatum*. *Thericium europaeum* is characterised by an adsutural collar of granules, which are posteriorly swollen and fade out towards the middle of the whorls. These nodes may become very densely spaced, in which case the collar appears as a band of axial furrows (Landau *et al.*, 2013, p. 41). We have not been able to verify this record, but his figure shows a much stouter shell than that figured here from St-Clément-de-la-Place. Brébion also reported a shell as *C. (T.) vulgatum* var. *gracile* Philippi, 1836 (*non* Lamarck, 1804) from the Assemblage IV locality of St-Jean-la-Poterie, which is a synonym of *Cerithium protractum* Bivona Ant. in Bivona And., 1838. This will also be reviewed in due course.

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

Subfamily Bittinae Cossmann, 1906

Genus *Bittium* Gray, 1847

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

1847a *Bittium* Gray, p. 270 [October].

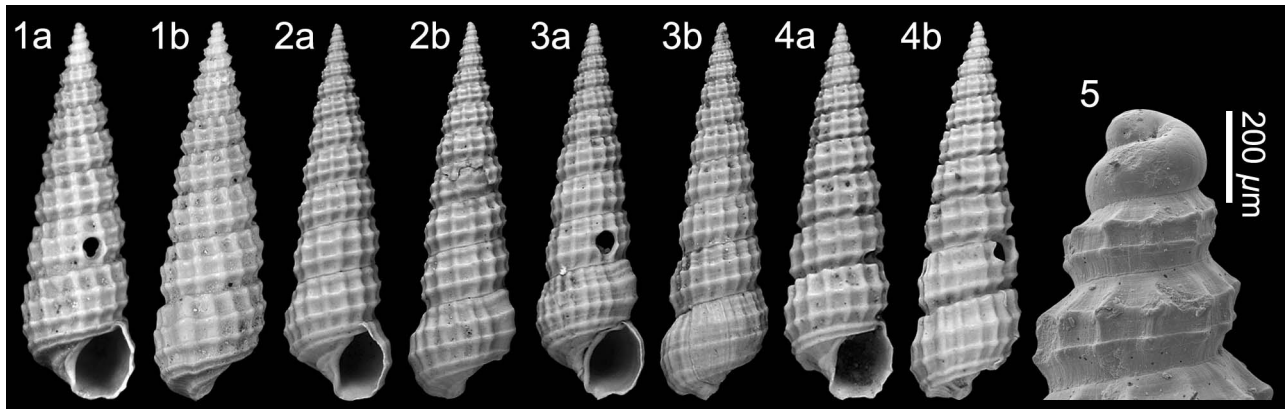
For generic synonymy see Van Dingenen *et al.* (2016, p. 111).

*Note* – Van Dingenen *et al.* (2016, p. 111) noted that the genus was well represented in the lower Pliocene Assemblage III deposits of NW France. The same observation can be made concerning the upper Miocene Assemblage I deposits, where seven *Bittium* species occur. As in the Assemblage III deposits, in all the species in which the protoconch is known it is paucispiral.

### *Bittium courtillerianum* (Millet, 1865)

Plate 4, figs 1-5

- 1854 *Cerithium Courtillerianum* Millet, p. 164 (*nomen nudum*).  
 \*1865 *Cerithium courtillerianum* Millet, p. 595.  
 1907 *Cerithium courtillerianum* Millet – Couffon, p. 192.  
 1915 *Cerithium courtillerianum* Millet – Couffon, p. 46.  
 1964 *Bittium reticulatum* var. *courtillerianum* Millet, 1854 [*sic*] (emend) – Brébion, p. 225, pl. 5, figs 24-26.  
 2016 *Bittium courtillerianum* (Millet, 1865) – Van Dingenen *et al.*, p. 112, pl. 1, fig. 9, pl. 2, fig. 4.



**Plate 4.** *Bittium courtillerianum* (Millet, 1865); 1. NHMW 2016/0103/0457, height 10.8 mm, width 3.2 mm; 2. NHMW 2016/0103/0458, height 12.0 mm, width 3.2 mm; 3. NHMW 2016/0103/0459, height 11.6 mm, width 3.5 mm; 4. NHMW 2016/0103/0460, height 11.7 mm, width 3.1 mm; 5. NHMW 2016/0103/0461, height 9.4 mm, width 2.8 mm, detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Type material* – Syntypes: Thorigné, Sceaux-d’Anjou and Renauleau, Musée d’Angers, France (*vide* Brébion, 1964, p. 225).

*Material and dimensions* – Maximum height 10.2 mm, width 2.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0457-0461 (5), NHMW 2016/0103/0462 (50+), RGM.1348052 (50+), RGM.1348071 (50+), RGM.1348343 (50+), RGM.1348522 (46), RGM.1348625 (33), RGM.1348868 (50+), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0463 (22), RGM.1348067 (50+), RGM.1348297 (50+), RGM.1348300 (50+), RGM.1348571 (50+), RGM.1348577 (50+), RGM.1348778 (50+), RGM.1348922 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1477 (50+), RGM.1349030 (30), LC (50+), FVD (50+). **Beugnon:** RGM.1348489 (32), RGM.1348506 (37), RGM.1348509 (28).

*Discussion* – *Bittium courtillerianum* (Millet, 1865) is characterised by its paucispiral protoconch composed of 1.5-1.75 whorls, with a large bulbous nucleus, its teleoconch consists of 10-11 straight-sided whorls, with spiral sculpture consisting of narrow, elevated, rounded cords, two on the first two teleoconch whorls, a third appearing above the upper cord on the third, quickly gaining in strength to become equal to the earlier cords, and axial sculpture consisting of about 13-14 slightly opisthocline rounded ribs, about equal in width to their interspaces, forming an evenly reticulated sculpture. Small rounded knobs are developed at the sculptural intersections. The concave base is sharply delimited by two peribasal cords and has a bifid periumbilical cord. For further discussion see Van Dingenen *et al.* (2016, p. 112).

Millet (1865, p. 595) recorded this species from Assemblage I localities (Thorigné, Sceaux-d’Anjou, Renauleau and St-Michel), to which Brébion (1964, p. 226) added St-Clément-de-la-Place, Les Pierres Blanches and Beaulieu and numerous localities from assemblages II-IV.

*Distribution* – Upper Miocene: Atlantic (Tortonian and

Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.* 2016). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Bittium courtillerianum* (Millet, 1865) var.**

Plate 5, figs 1-5

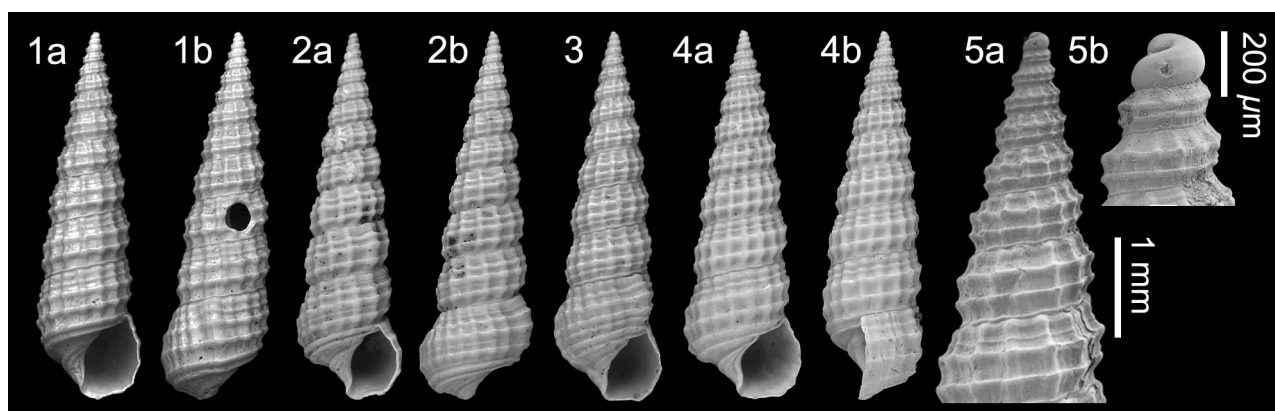
1964 *Bittium reticulatum* var. *miocaenicum* [*sic*] Peyrot, 1938 – Brébion, p. 223 (*non* Peyrot, 1938).

*Material and dimensions* – Maximum height 12.3 mm, width 3.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0464-0468 (5), NHMW 2016/0103/0469 (50+), RGM.1347966 (29 fragments), RGM.1348344 (22), RGM.1348626 (30), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0470 (18), RGM.1348068 (32), RGM.1348198 (50+), RGM.1348301 (50+), RGM.1348578 (41), RGM.1348779 (41), RGM.1348921 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1478 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1348490 (45).

*Discussion* – Brébion (1964, p. 223) recorded, but did not illustrate or discuss *Bittium reticulatum* var. *miocaenicum* [*sic*] Peyrot, 1938 from numerous Assemblage I-III localities. Unfortunately, the protoconch of this middle Miocene species from the Loire Basin of France was not described. The teleoconch of *B. reticulatum* var. *miocaenicum* was said to differ from that of *B. reticulatum* in being smaller, with less convex whorls, the early teleoconch whorls have three spiral cords, the middle and late whorls four, of which the abapical two are narrower and closer-spaced. The base bears two peribasal cords, three medial cords and a smooth mid-portion between. We have a specimen from Thenay (Indre-et-Loire, France) with the protoconch preserved, consisting of 2.5 whorls with a small nucleus.

Brébion was probably referring to the specimens illustrated here (Pl. 5, figs 1-5) when he recorded *B. reticu-*





**Plate 5.** *Bittium courtillerianum* (Millet, 1865) var.; 1. NHMW 2016/0103/0464, height 9.7 mm, width 2.6 mm; 2. NHMW 2016/0103/0465, height 11.3 mm, width 3.1 mm; 3. NHMW 2016/0103/0466, height 12.2 mm, width 3.4 mm; 4. NHMW 2016/0103/0467, height 11.9 mm, width 3.3 mm; 5. NHMW 2016/0103/0468, height 9.4 mm, width 2.6 mm, 5a, detail of early teleoconch whorls; 5b, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*latum* var. *miocenicum*, as the number of spiral cords and the order in which they appear is the same. However, they are not conspecific with *B. miocenicum*, as the Assemblage I species has a paucispiral protoconch and *B. miocenicum* has a multispiral protoconch. Moreover, the Loire Basin species is smaller (maximum height 6.1 mm vs. 12.3 mm), the whorls are straighter-sided with a deeper suture and although in both forms the fourth cord is intercalated between the first and second cords, in the Loire Basin shells all cords rapidly become equal in strength, whereas in the Assemblage I shells the fourth cord remains weaker.

A possibility that we favour is that these shells represent a variety of *Bittium courtillerianum* (Millet, 1865) (see above), but this species is characterised by having only three cords per whorl. In support of this hypothesis the protoconch in both forms is identical (Pl. 4, fig. 5; Pl. 5, fig. 5b) and although specimens from St-Clément-de-la-Place can usually be divided easily between those with three and four cords on the penultimate and last whorls, some specimens identified as *B. courtillerianum* have a fine cord intercalated between the first and second on the last whorl only (Pl. 5, fig. 3). We therefore provisionally consider them a form of *B. courtillerianum*.

*Distribution* – As for *B. courtillerianum*.

#### ***Bittium crassum* nov. sp.**

Plate 6, figs 1-4

*Type material* – Holotype MNHN.F.A57724, height 7.6 mm, width 2.6 mm; paratype 1 NHMW 2016/0103/0481, height 8.0 mm, width 2.8 mm; paratype 2 NHMW 2016/0103/0482, height 5.4 mm, width 2.3 mm; paratype 3 NHMW 2016/0103/0483, height 6.4 mm, width 2.3 mm; paratype 4 MNHN.F.A57915, height 7.5 mm, width 2.6 mm; paratype 5 RGM.1348046, height 7.3 mm, width 2.8 mm; paratype 6 RGM.1348047, height 6.7 mm, width

2.5 mm; paratype 7 RGM.1348331, height 8.9 mm, width 2.9 mm.

*Other material* – Maximum height 8.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1465 (19), RGM.1348048 (6), RGM.1348540 (3), RGM.1348866 (2), LC (2), FVD (7). **Sceaux-d'Anjou:** NHMW 2016/0103/0701 (3), RGM.1348929 (2).

*Etymology* – Latin ‘*crassus*, -a, -um’, adjective, meaning fat, broad, name reflecting the relatively broad shell shape for the genus. *Bittium* gender neuter.

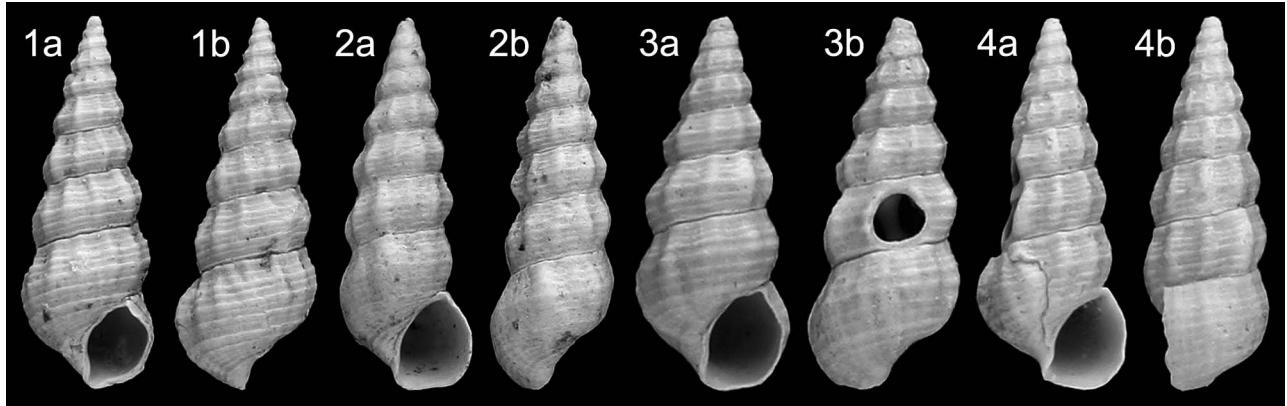
*Locus typicus* – Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Bittium* species with a broad shell, angular spire whorls, sculpture of spiral cords in which two cords appear on first teleoconch whorl, further cord appears below suture on second whorl, abapically single secondary cord intercalated in interspaces, 8-9 axial ribs, last whorl moderately constricted at base, base entirely sculptured by cords.

*Description* – Shell small, turriculate, relatively broad for genus. Protoconch not preserved. Teleoconch consisting of eight angular convex whorls, with periphery mid-whorl. Suture deeply impressed. Spiral sculpture of elevated, rounded cords, two on first teleoconch whorl placed on lower half of whorl; on second teleoconch whorl third cord appears below suture; abapically single secondary cord appears in each interspace. Axial sculpture consisting of 8-9 orthocone rounded ribs, about one-third width of their interspaces, one rib varicose on last whorl. Spiral sculpture overruns axial ribs, swollen at intersections. Last whorl regularly convex, moderately constricted at base. Base delimited by slightly stronger





**Plate 6.** *Bittium crassum* nov. sp.; 1. **Holotype** MNHN.F.A57724, height 7.6 mm, width 2.6 mm; 2. **Paratype 1** NHMW 2016/0103/0481, height 8.0 mm, width 2.8 mm; 3. **Paratype 2** NHMW 2016/0103/0482, height 5.4 mm, width 2.3 mm; 4. NHMW 2016/0103/0483, height 6.4 mm, width 2.3 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

peribasal cord, bearing a further 5-6 regular cords. Aperture ovate, outer lip thin, convex, somewhat flared abapically, ending with short broad siphonal canal. Columella slightly thickened. Columellar callus narrow.

*Discussion* – *Bittium crassum* nov. sp. differs from all of its Assemblage I congeners in having a broader shell shape, with angular teleoconch spire whorls, in having spiral sculpture on later teleoconch whorls composed of primary and secondary cords of alternating strength and in having relatively few, wide-spaced axial ribs. *Bittium crassicostatum* (Etheridge & Bell in Bell, 1898) found in the lower Pliocene NW French Assemblage III deposits (Van Dingenen *et al.*, 2016, p. 112) also has relatively few axial ribs, but these are much broader, the shell is more slender and the spire whorls are not angular. *Bittium robustum* Harmer, 1918, also from Assemblage III deposits (Van Dingenen *et al.*, 2016, p. 114) and the North Sea Basin Pliocene has a similar number of axial ribs, but these are broader, more prosocline, the spire whorls are almost straight-sided and not angular at the mid-whorl as in *B.*

*crassum*, and the spiral cords are of equal strength and do not alternate.

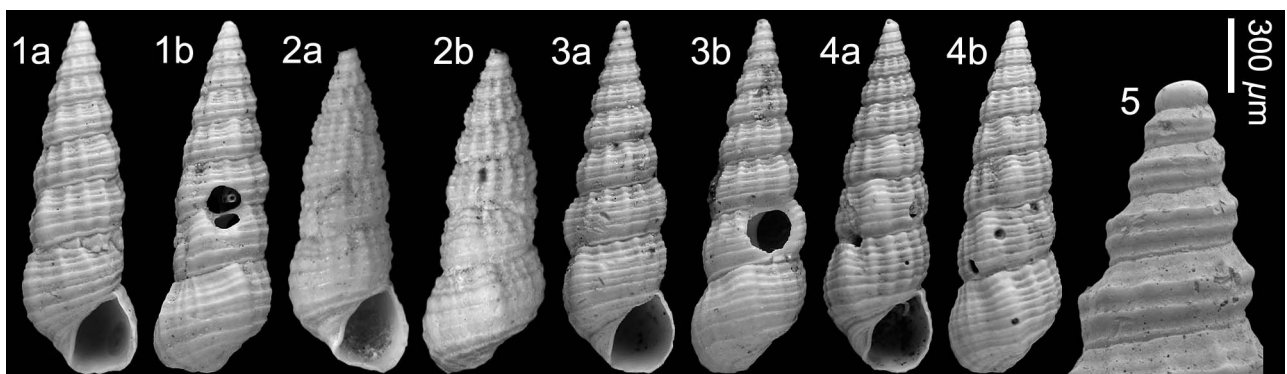
*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper).

***Bittium gallicum* nov. sp.**

Plate 7, figs 1-5

*Type material* – Holotype MNHN.F.A57722, height 5.8 mm, width 1.8 mm; paratype 1 MNHN.F.A57723, height 6.5 mm, width 2.0 mm; paratype 2 NHMW 2016/0103/0477, height 4.8 mm, width 1.7 mm; paratype 3 NHMW 2016/0103/0478, height 6.5 mm, width 2.0 mm; paratype 4 NHMW 2016/0103/0479, height 6.3 mm, width 1.8 mm; paratype 5 RGM.1348043, height 7.8 mm, width, 2.5 mm; paratype 6 RGM.1348044, height 6.7 mm, width, 2.0 mm.

*Other material* – Maximum height 7.9 mm. St-Clé-



**Plate 7.** *Bittium gallicum* nov. sp.; 1. **Holotype** MNHN.F.A57722, height 5.8 mm, width 1.8 mm; 2. **Paratype 2** NHMW 2016/0103/0477, height 4.8 mm, width 1.7 mm; 3. **Paratype 1** MNHN.F.A57723, height 6.5 mm, width 2.0 mm; 4. **Paratype 3** NHMW 2016/0103/0478, height 6.5 mm, width 2.0 mm; 5. **Paratype 4** NHMW 2016/0103/0479, height 6.3 mm, width 1.8 mm, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**ment-de-la-Place:** NHMW 2016/0103/0480 (50+), RGM.1348045 (50+), RGM.1348306 (25), RGM.1348539 (50+), RGM.1348867 (50+), RGM.1348947 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1466 (50+), LC (50+), FVD (50+).

*Etymology* – Named after the Roman province of Gaul, Latin: *Gallia*, a region of Western Europe encompassing present-day France. *Bittium* gender neuter.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Bittium* species with rather squat shell shape, paucispiral protoconch, sculpture of spiral cords in which two cords appear on first teleoconch whorl, one further cord appears below suture on second whorl, third cord between 1 and 2 on third whorl, fourth between 3 and 4 on fourth whorl, with further cords developed abapically, eight on penultimate whorl, 10-11 axial ribs, two varices per whorl on last four whorls, last whorl hardly constricted at base, base entirely sculptured by cords.

*Description* – Shell small, turriculate, relatively squat for genus, spire slender. Protoconch of 1.5 convex whorls, with large nucleus. Junction with teleoconch sharply delimited. Teleoconch of nine convex whorls, with periphery below mid-whorl. Suture impressed. Spiral sculpture of elevated, rounded cords, two placed on lower half of whorl on first teleoconch whorl; on second teleoconch whorl third cord appears below suture; on fourth whorl fourth cord appears between cords 1 and 2; on fifth whorl fifth cord between cords 3 and 4; on later whorls further cords appear in interspaces, gaining strength abapically, so that all cords of roughly equal strength, eight cords on penultimate whorl. Axial sculpture consisting of 10-11 slightly prosocline rounded ribs, about half width of their interspaces, on last four whorls two ribs per whorl strongly varicose. Spiral sculpture overruns axial ribs, forming small rounded knobs at intersections. Last whorl regu-

larly convex, weakly constricted at base. Base delimited by stronger peribasal cord, bearing further 5-6 cords of irregular strength. Aperture ovate, outer lip thin, convex, somewhat flared abapically, ending with very short broad siphonal canal. Columella slightly thickened. Columellar callus narrow.

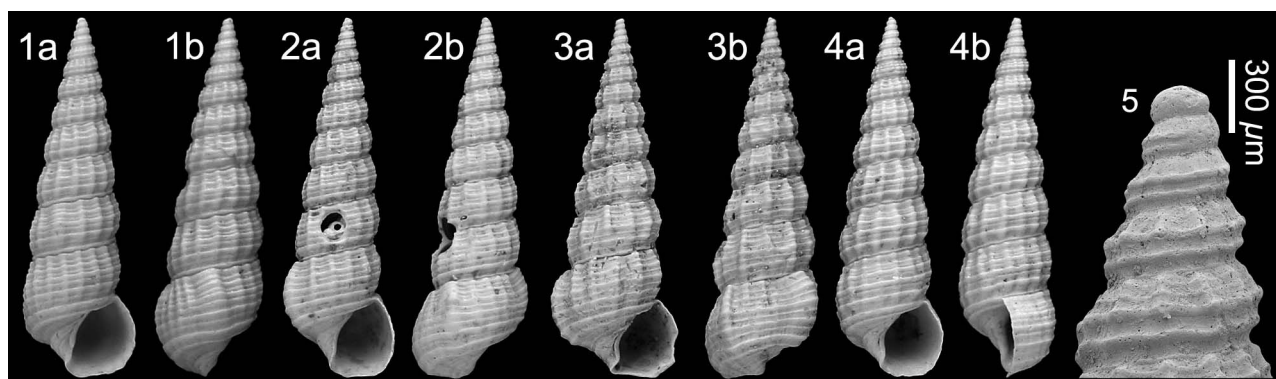
*Discussion* – *Bittium gallicum* nov. sp. is separated from all of its Assemblage I congeners in being small, in having a squatter shell shape, in the order of appearance of the spiral cords on the neanic whorls, in having more numerous teleoconch whorls with axial varices developed, and in having the last whorl weakly constricted at the base and covered in irregular spiral cords. In all the other NW French upper Miocene *Bittium* species the last whorl is strongly constricted at the base and the cords on the base are grouped; usually two peribasal cords and two to five periumbilical cords, with a smooth mid-base portion. The rather squat shell shape, relatively narrow last whorl and poorly constricted base are reminiscent of members of the tropical American genus *Bittiolium* Cossmann, 1906, but species in this genus have their protoconch sculptured with a spiral cord (Houbriek, 1993, p. 287), which is not present in *B. gallicum* (Pl. 7, fig. 5). The other small *Bittium* species in the Assemblage I deposits is *B. renauleauensis* nov. sp., which differs in the appearance of the spiral sculpture, in the number of axial ribs and in its basal sculpture (see under *B. renauleauensis* for details).

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

***Bittium lozoueti* Van Dingenen, Ceulemans & Landau, 2016**

Plate 8, figs 1-5

- 1964 *Bittium reticulatum* var. *lecointrei* nov. var. Brébion, p. 227, pl. 5, figs 27, 28 (*nomen nudum*).  
2016 *Bittium lozoueti* Van Dingenen, Ceulemans & Landau, p. 113, pl. 1, figs 11-14, pl. 2, fig. 5.



**Plate 8.** *Bittium lozoueti* Van Dingenen, Ceulemans & Landau, 2016; 1. NHMW 2016/0103/0471, height 8.3 mm, width 2.4 mm; 2. NHMW 2016/0103/0472, height 9.9 mm, width 2.9 mm; 3. NHMW 2016/0103/0473, height 10.3 mm, width 3.5 mm; 4. NHMW 2016/0103/0474, height 10.2 mm, width 2.9 mm; 5. NHMW 2016/0103/0475, height 7.6 mm, width 2.2 mm, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Material and dimensions** – Maximum height 11.5 mm, width 3.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0471-0475 (5), NHMW 2016/0103/0476 (50+), RGM.1348042 (50+), RGM.1348330 (36), RGM.1348345 (42), RGM.1348523 (7), RGM.1348865 (14), LC (50+), FVD (50+). **Sceaux-d’Anjou**: RGM.1348930 (1).

**Discussion** – *Bittium lozoueti* Van Dingenen, Ceulemans & Landau, 2016 is characterised by its paucispiral protoconch, teleoconch sculpture of two spiral cords on the first whorl, a third appearing abapically on the second whorl, a fourth cord between cords 1 and 2 on the third whorl, a fifth between cords 1 and 2 on the penultimate whorl, spiral sculpture of about 13 narrow ribs, with small tubercles developed at the intersections, and a base with two peribasal cords and a further 4-5 cords medially. This form was considered by Brébion (1964) to be a variety of *Bittium reticulatum* (Da Costa, 1778), but it differs in having a paucispiral protoconch, whereas in *B. reticulatum* it is multispiral (Van der Linden & Wagner, 1990). For further comparison see Van Dingenen *et al.* (2016, p. 113).

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016).

***Bittium pingue* nov. sp.**

Plate 9, figs 1-4

**Type material** – Holotype MNHN.A.66723, height 7.7 mm, width 2.9 mm; paratype 1, MNHN.A.66724, height 6.3 mm, width 2.1 mm; paratype 2, NHMW 2016/0103/1738, height 7.5 mm, width 2.9 mm; paratype 3, NHMW 2016/0103/1739, height 7.6 mm, width 2.6 mm; paratype 4, NHMW 2016/0103/1740 (juvenile).

**Other material** – Maximum height 8.5 mm. **Renauleau**: NHMW 2016/0103/1741 (50+), LC (50+), FVD (50+).

**Etymology** – Latin ‘pinguis, -ue, -ior’, adjective meaning

fat, plump or broad, reflecting the broad shell shape of this species. *Bittium* gender neuter.

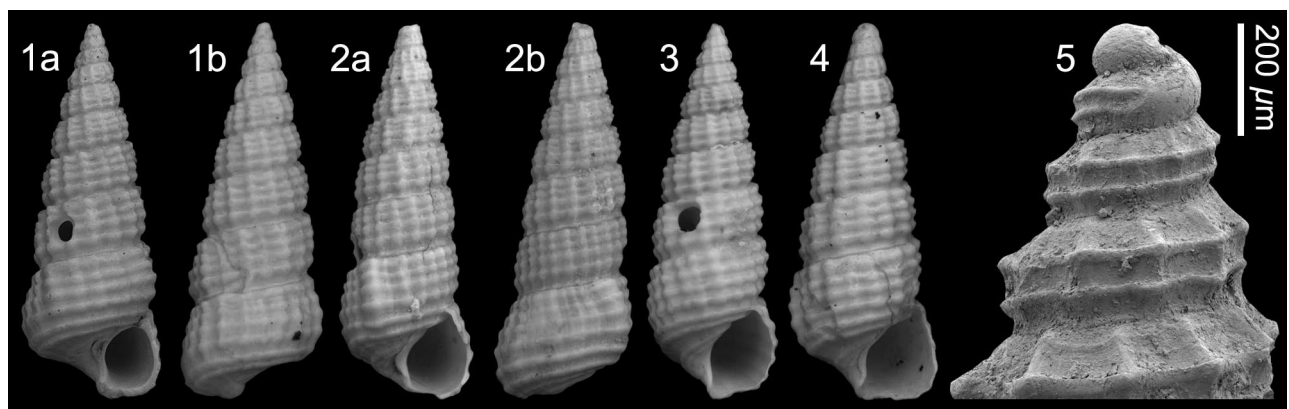
**Locus typicus** – Renauleau, Maine-et-Loire, NW France.

**Stratum typicum** – Tortonian, upper Miocene.

**Diagnosis** – *Bittium* species with rather broad squat shell shape, paucispiral protoconch, weakly convex whorls separated by canaliculate suture, sculpture of spiral cords in which two cords appear on first teleoconch whorl, two on second whorl, abapically four equal cords per whorl, 14-15 axial ribs, one varix per whorl on later whorls, last whorl sharply angled at base, two peribasal cords, three cords medially, mid-base smooth.

**Description** – Shell small, solid, turruculate, relatively squat for genus, broad spire. Protoconch consisting of 1.5 convex whorls, with a large nucleus. Junction with teleoconch sharply delimited, sinuous. Teleoconch consisting of 7-8 weakly convex whorls, with periphery below mid-whorl. Suture deeply impressed, canaliculate. Spiral sculpture of four elevated, rounded cords; cords 3 and 4 appear on first teleoconch whorl, on second teleoconch whorl cords 1 and 2 develop below suture, rapidly strengthening, subequal in strength by fifth teleoconch whorl. Axial sculpture consisting of 14-15 slightly prosocline rounded ribs, about half width of their interspaces, on last one or two whorls one rib per whorl varicose. Spiral sculpture overruns axial ribs, forming strong rounded knobs at intersections. Last whorl weakly convex, angled at base. Base concave, delimited by two smooth peribasal cords, smooth mid-base, three further cords medially. Aperture ovate, outer lip thin, convex, somewhat flared abapically, ending with very short siphonal canal. Columella slightly thickened. Columellar callus hardly developed.

**Discussion** – *Bittium pingue* nov. sp. is separated from its Assemblage I congeners by its relatively squat broad shell profile, weakly convex spire whorls separated by a



**Plate 9.** *Bittium pingue* nov. sp.; 1. **Holotype** MNHN.A.66723, height 7.7 mm, width 2.9 mm; 2. **Paratype 1**, MNHN.A.66724, height 6.3 mm, width 2.1 mm; 3. **Paratype 2**, NHMW 2016/0103/1738, height 7.5 mm, width 2.9 mm; 4. **Paratype 3**, NHMW 2016/0103/1739, height 7.6 mm, width 2.6 mm; 5. **Paratype 4**, NHMW 2016/0103/1740, juvenile, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



deep canalculated suture and its sculpture of four equal spiral cords from the third or fourth teleoconch whorl. The teleoconch of this species is similar to that of *Bittium reticulatum* (Da Costa, 1778), but *B. reticulatum* has a multispiral protoconch (Van der Linden & Wagner, 1990). The teleoconch is similar to that illustrated by Glibert (1949, pl. 9, figs 8a-c) as *B. reticulatum* forme A, which is the same as *Bittium reticulatum* var. *miocenicum* Peyrot, 1938 from the middle Miocene of the Loire Basin of France. Unfortunately, the protoconch of this middle Miocene form from the Loire Basin of France was not described. Specimen at hand from Thenay (Indre-et-Loire, France) have a protoconch of 2.5 whorls with a small nucleus. The teleoconch sculpture differs in that cord 2 develops between cords 1 and 3 on about the fifth whorl, whereas in *B. pingue* cords 1 and 2 appear earlier on the second teleoconch whorl. This species has so far been found only at Renauleau.

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

***Bittium renauleauense* nov. sp.**

Plate 10, figs 1-5

*Type material* – Holotype MNHN.A.66725, height 3.8 mm, width 1.2 mm; paratype 1, MNHN.A.66726, height 3.6 mm, width 1.2 mm; paratype 2, NHMW 2016/0103/1742,

height 3.7 mm, width 1.2 mm; paratype 3, NHMW 2016/0103/1743, height 3.8 mm, width 1.2 mm; paratype 4, NHMW 2016/0103/1744, height 3.6 mm, width 1.1 mm.

*Other material* – Maximum height 3.9 mm. **Renauleau:** NHMW 2016/0103/1745 (7), LC (50+), FVD (24).

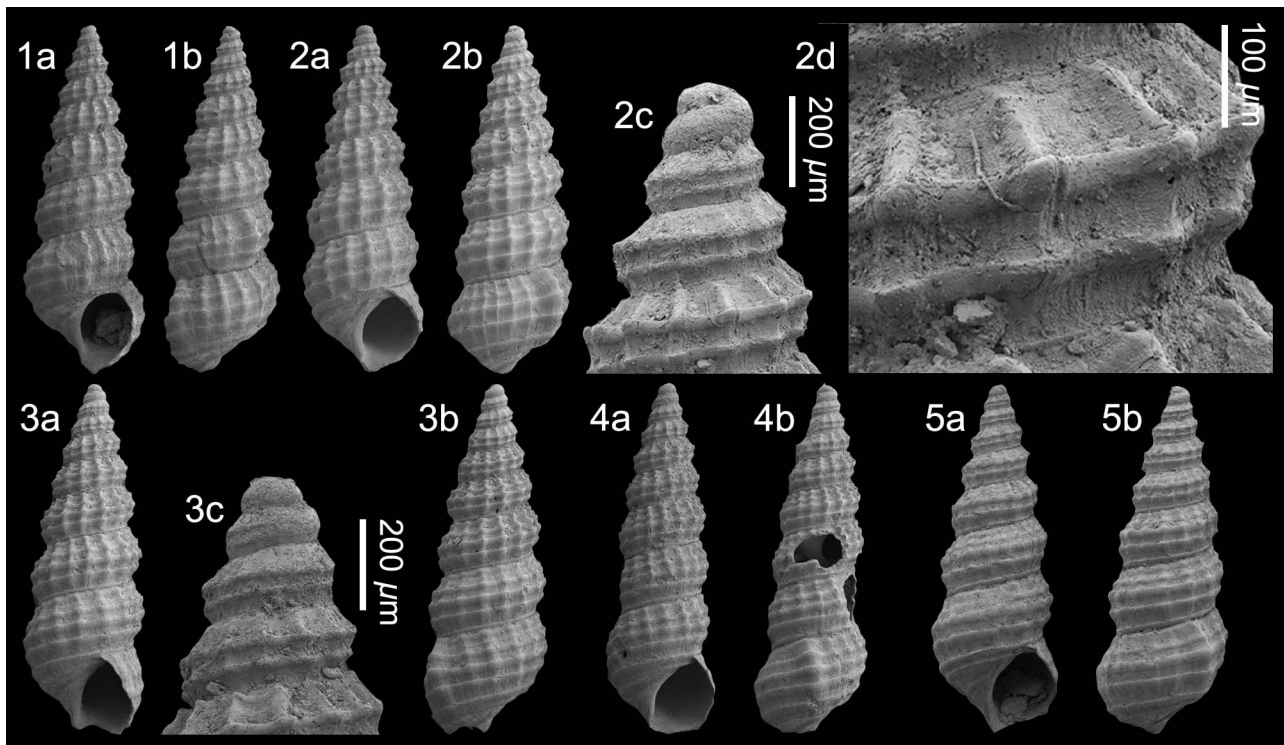
*Etymology* – Named after the type locality of Renauleau. *Bittium* gender neuter.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Bittium* species with small slender shape, paucispiral protoconch, strongly convex whorls, sculpture of spiral cords in which two cords appear on first teleoconch whorl, two third or fourth whorl, remaining weaker than cords 3 and 4, 15-17 axial ribs, one varix per whorl on last two whorls, last whorl rounded at base, two peribasal cords, two cords medially, mid-base smooth.

*Description* – Shell small, turriculate, slender spire. Protoconch consisting of 1.5 convex whorls, with a large nucleus. Junction with teleoconch sharply delimited. Teleoconch consisting of 7-8 strongly convex whorls, with periphery mid-whorl. Suture impressed. Spiral sculpture of four narrow rounded cords; cords 3 and 4 appear on first teleoconch whorl, on third or fourth teleoconch



**Plate 10.** *Bittium renauleauense* nov. sp.; 1. **Holotype** MNHN.A.66725, height 3.8 mm, width 1.2 mm; 2. **Paratype 1**, MNHN.A.66726, height 3.6 mm, width 1.2 mm, 2c, detail of protoconch, 2d, detail of teleoconch microsculpture; 3. **Paratype 2**, NHMW 2016/0103/1742, height 3.7 mm, width 1.2 mm; 4. **Paratype 3**, NHMW 2016/0103/1743, height 3.8 mm, width 1.2 mm; 5. **Paratype 4**, NHMW 2016/0103/1744, height 3.6 mm, width 1.1 mm (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



whorl cords 1 and 2 develop simultaneously below suture, strengthening abapically, but in most specimens remaining weaker than cords 3 and 4. Axial sculpture consisting of 15-17 orthocline rounded ribs, about one-third width of their interspaces, on last two whorls one rib per whorl varicose. Spiral sculpture overruns axials forming rounded knobs at intersections. Surface covered in pustular microsculpture (Pl. 10, fig. 2d). Last whorl strongly convex, Base convex, delimited by two smooth peribasal cords, smooth mid-base, two further cords medially. Aperture ovate, outer lip thin, convex, ending in very short siphonal canal. Columella slightly thickened. Columellar callus hardly developed.

*Discussion* – *Bittium renauleauense* nov. sp. is one of two small *Bittium* species found in the Assemblage I deposits. The other, *B. gallicum* nov. sp., differs in the appearance of the spiral sculpture; two cords appear on first teleoconch whorl, one further cord appears below the suture on second whorl, a third cord between 1 and 2 on third whorl, fourth between 3 and 4 on fourth whorl, with further cords developed abapically, eight on penultimate whorl. Moreover, *B. gallicum* has fewer axial ribs (10-11 vs. 15-17) and the base is entirely sculptured by cords. This species has so far been found only at Renauleau.

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

### *Bittium venustum* (Millet, 1865)

Plate 11, figs 1-5

- 1854 *Cerithium Venustum* Millet, p. 164 (*nomen nudum*).  
 \*1865 *Cerithium venustum* Millet, p. 595.  
 1907 *Cerithium pygmaeum* Phil. – Couffon, p. 11, 30, 38 [*non* Philippi, 1844 = *Cerithiopsis tubercularis* (Montagu, 1803)].  
 1964 *Bittium venustum* Millet, 1854 [*sic*] – Brébion, p. 229, pl. 5, figs 29-31.

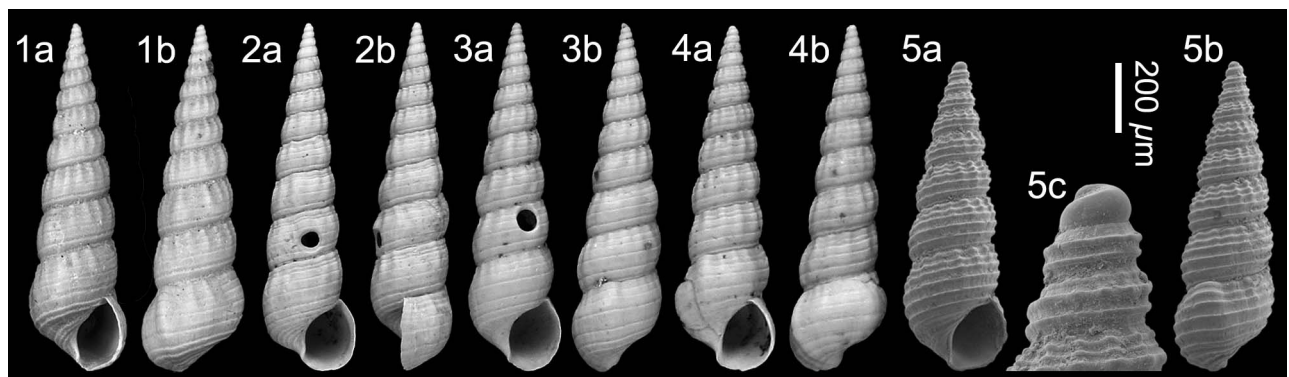
*Type material* – Syntypes: Thorigné and Sceaux-d'Anjou, Musée d'Angers, France (*vide* Brébion, 1964, p. 229).

*Material and dimensions* – Maximum height 10.2 mm, width 2.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0450-0454 (5), NHMW 2016/0103/0456 (50+), RGM.1348041 (50+), RGM.1348076 (50+), RGM.1348524 (3), RGM.1348538 (50+ subadults), RGM.1348864 (50+), RGM.1348948 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0456 (20), RGM.1348238 (17), RGM.1348579 (1), LC (5), FVD (8). **Renauleau**: LC (3).

*Discussion* – *Bittium venustum* (Millet, 1865) is characterised by its paucispiral protoconch composed of 1.5-1.75 whorls, with a large bulbous first whorl and its tall slender shell, composed of about eleven weakly convex teleoconch whorls, separated by a deeply impressed suture. The first teleoconch whorl bears two strong spiral cords, with a third appearing below the suture on the second teleoconch whorl (Pl. 11, fig. 5c). Axial sculpture appears from the second whorl and consists of axial ribs only developed immediately below the suture and obsolete by mid-whorl. The sculpture on juvenile specimens consists of raised cords separated by wider interspaces (Pl. 11, figs 5a, b). Abapically the spiral cords broaden and flatten, so that later adult whorls bear five spiral cords separated by narrow grooves, the two adapical cords narrower; of the three abapical cords, the mid-cord is widest (Pl. 11, figs 1-4). The axial ribs also broaden and weaken abapically, with one or two broad varices developed per whorl on the last one to three whorls. The paucispiral protoconch and sculpture of weak axial ribs restricted to the adapical half of the whorls and broad flattened spiral cords make *B. venustum* a distinctive species that cannot be confused with any of its congeners.

Millet (1865, p. 595) recorded this species from the Assemblage I localities of Thorigné and Sceaux-d'Anjou. Brébion (1964, p. 229) added Renauleau, St-Michel and St-Clément-de-la-Place.

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



**Plate 11.** *Bittium venustum* (Millet, 1865); 1. NHMW 2016/0103/0450, height 9.7 mm, width 2.7 mm; 2. NHMW 2016/0103/0451, height 10.2 mm, width 2.5 mm; 3. NHMW 2016/0103/0452, height 9.5 mm, width 2.5 mm; 4. NHMW 2016/0103/0453, height 8.4 mm, width 2.3 mm; 5. NHMW 2016/0103/0454, height 4.7 mm (juvenile), 5c detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Semibittium* Cossmann, 1896

Type species: (by subsequent designation Cossmann, 1897) – *Cerithium cancellatum* Lamarck, 1804, Eocene, France.

1896b *Semibittium* Cossmann, p. 29.

*Note* – Cossmann (1896b) erected the genus *Semibittium* for some French Eocene *Bittium*-like shells without varices, a thin, oblique outer lip, a thin, weakly excavated columella and an indistinct columellar border. This genus was used for Cossmann & Peyrot (1922) for some small Miocene species with predominantly spiral sculpture and weak varices, a position followed by subsequent workers (Glibert, 1949; Bałuk, 1975), who considered *Semibittium* a subgenus of *Bittium*. Whether the Miocene species are monophyletic with the Eocene type species *Cerithium cancellatum* Lamarck, 1804 is doubtful, but we do agree they form a distinct group within the Bittinae, which has left no living members in European waters, differing from *Bittium* in the features highlighted above; smaller shell, absence of axial sculpture and weak varices. The shells of this group are similar to those of the extant eastern North Pacific genus *Stylidium* Dall, 1907, which also has sculpture restricted to spiral cords, but the shells of *Stylidium* species are much larger and the cords appear as broader flattened bands.

***Semibittium brebioni* nov. sp.**

Plate 12, figs 1-3

*Type material* – Holotype MNHN.F.A57725, height 3.7 mm, width 1.2 mm; paratype 1 MNHN.F.A57726, height 3.9 mm, width 1.2 mm; paratype 2 NHMW 2016/0103/0485, height 4.5 mm, width 1.5 mm; paratype 3 NHMW 2016/0103/0486, height 4.0 mm, width 1.2 mm; paratype 4 RGM.1348049, height 3.5 mm, width 1.3 mm; paratype 5 RGM.1348050, height 3.1 mm, width 1.1 mm; paratype 6 RGM.1348696, height 4.0 mm, width 1.3 mm.

*Other material* – Maximum height 4.6 mm. **St-Clé-**

**ment-de-la-Place:** NHMW 2016/0103/0487 (50+), RGM.1348051 (45), RGM.1348305 (13), RGM.1348697 (42), LC (50+), FVD (50+). **Renauleau:** LC (2).

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

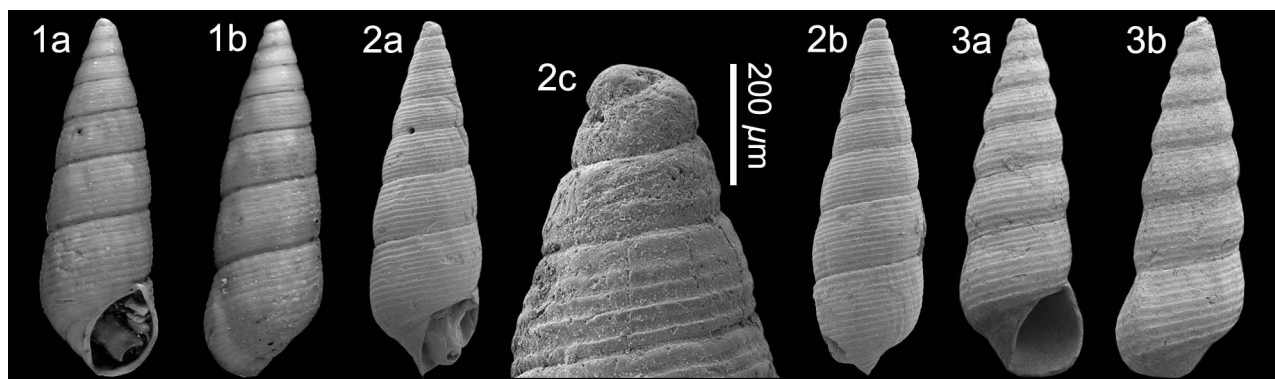
*Locus typicus* – Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Semibittium* species of small size, with paucispiral protoconch of just under two whorls, weakly convex teleoconch whorls sculptured by low, close-set narrow cords, 10-11 on penultimate whorl, low varix on last whorl, aperture small.

*Description* – Shell small, turruculate, relatively squat for genus. Protoconch consisting of just under two convex whorls, with large nucleus. Teleoconch consisting of seven weakly convex whorls, in some specimens slightly swollen in lower half, with periphery below mid-whorl. Suture impressed. Spiral sculpture of low, rounded cords of somewhat irregular strength, separated by narrow grooves, two cords on first teleoconch whorl, five on second whorl, increasing in number abapically to 10-11 on penultimate whorl. Spiral microsculpture is present between the cords consisting of threads or rows of pustules (Pl. 12, fig. 2c). Axial sculpture absent. Last whorl with straight profile adapically, rounded at base; entire surface covered by narrow spiral cords and one low, irregularly placed, broad axial varix. Base not delimited, bearing spiral cords. Aperture small, ovate, outer lip thin, convex. Columella slightly thickened. Columellar callus narrow.

*Discussion* – *Semibittium brebioni* nov. sp. differs from its congeners in having the densest spiral sculpture, with 10-11 spiral cords on the penultimate and last whorls. The base is poorly delimited and bears spiral cords similar to those covering the rest of the shell. We have found



**Plate 12.** *Semibittium brebioni* nov. sp.: 1. **Holotype** MNHN.F.A57725, height 3.7 mm, width 1.2 mm; 2. **Paratype 1** MNHN.F.A57726, height 3.9 mm, width 1.2 mm (SEM image). 3. **Paratype 2** NHMW 2016/0103/0485, height 4.5 mm, width 1.5 mm (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



this species only at St-Clément-de-la-Place, where it is common and remarkably constant in size, shape and sculpture, whereas in the other Assemblage I localities we have found only *S. duvergieri* Cossmann & Peyrot, 1922, which differs in having more convex whorls bearing only five cords on the later whorls (see below). *Semibittium multiliratum* (Brusina, 1877) from the middle Miocene Paratethys also has a relatively large number of spiral cords on the later teleoconch whorls, but still fewer than *S. brebioni* (8 vs. 10-11) and differs in having weak axial sculpture usually restricted to the early teleoconch whorls. Brébion (1964, p. 233, pl. 6, figs 6-7) described a similar species from the NW French upper Pliocene-Pleistocene Assemblage IV locality of Gourbesville under the name *Bittium (Semibittium) lehmani (nomen nudum)*. It has similarly weakly convex spire whorls, but differs in having fewer spiral cords (7 vs. 10-11) and the base is sharply delimited, which is not the case in *S. brebioni*.

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

#### *Semibittium duvergieri* Cossmann & Peyrot, 1922

Plate 13, figs 1-3

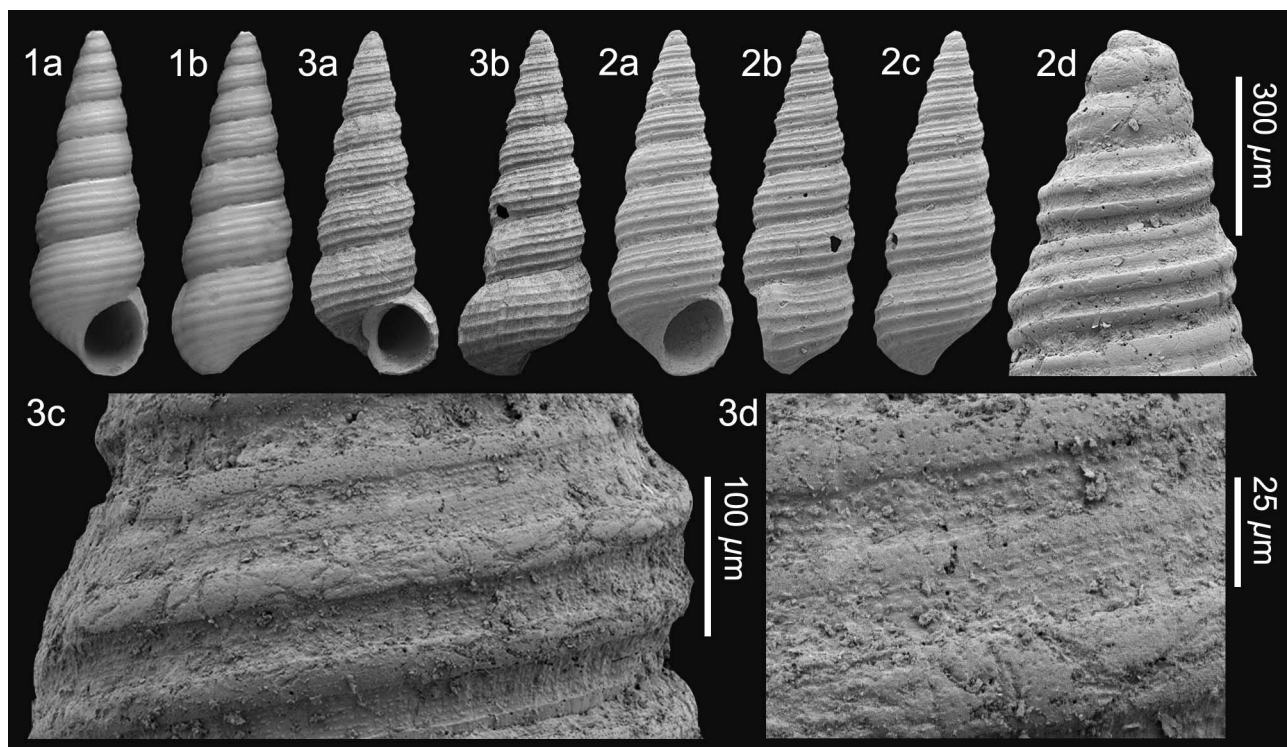
- 1922 *Semibittium Duvergieri* Cossmann & Peyrot, p. 291, pl. 7, figs 33, 34, 96.  
 1949 *Bittium (Semibittium) duvergieri* Cossmann & Peyrot, 1921 [*sic*] – Glibert, p. 143, pl. 10, fig. 1.

- 1964 *Bittium (Semibittium) duvergieri [sic]* Cossmann & Peyrot, 1922 – Brébion, p. 232.

*Material and dimensions* – Maximum height 2.7 mm, width 0.9 mm. **Renauleau:** NHMW 2016/0103/0483 (1), NHMW 2016/0103/0484 (50+), RGM.1349011 (3), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0481 (1), NHMW 2016/0103/0482 (26), RGM.1348440 (2), LC (5).

*Discussion* – *Semibittium duvergieri* Cossmann & Peyrot, 1922 is characterised by its small shell, its paucispiral protoconch and its convex teleoconch whorls sculptured with five rounded spiral cords. The number of spiral cords is constant in all specimens, although the width of the cords is variable. Glibert (1949, p. 143) commented that the occasional middle Miocene specimen from the Loire Basin showed traces of axial sculpture, but this is not present in any of the specimens from the NW French upper Miocene. Contrary to the generic description, both *S. duvergieri* and *S. brebioni* nov. sp. have a varix on the last whorl, although it is low and inconspicuous. We draw attention to microsculpture visible under SEM imagery consisting of rows of pits on the cords and rows of micropustules in the interspaces (Pl. 13, figs 3c, d). Also in *Semibittium brebioni* nov. sp., spiral microsculpture is just visible in the interspaces between the cords (Pl. 12, fig. 2c).

*Semibittium octoliratum* Cossmann & Peyrot, 1922, described from the Burdigalian lower Miocene of the Aquitaine Basin, differs in having eight spiral cords per whorl. The group is also represented in the middle Mio-



**Plate 13.** *Semibittium duvergieri* Cossmann & Peyrot, 1922; 1. NHMW 2016/0103/0481, height 2.7 mm, width 0.9 mm. Beugnon, Maine-et-Loire, NW France, Tortonian, upper Miocene. 2. NHMW 2016/0103/0483, height 3.0 mm, width 1.1 mm; 2d, detail of protoconch (SEM image); 3. NHMW 2016/0103/1746, height 3.4 mm, width 1.2 mm; 3c, d, detail of teleoconch microsculpture (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cene of the Paratethys by *S. turritella* (Eichwald, 1853), which has a taller shell, composed of a greater number of more convex whorls separated by a deeper suture and 5-7 spiral cords per whorl, and *S. multiliratum* (Brusina, 1877) which is larger (maximum height 6.0 mm; Bałuk, 1975, p. 141), with six spiral cords on the middle and late teleoconch whorls and subobsolete axial sculpture on the early teleoconch whorls, which in the occasional specimen persists, albeit weakly, onto the last whorl. Brébion (1964, p. 232) recorded this species from the Assemblage I locality of Renauleau.

*Distribution* – Middle Miocene: Aquitaine Basin, France (Cossmann & Peyrot, 1922), Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

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

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

1770 *Tenagodus* Guettard, p. 128.

For generic synonymy see Van Dingenen *et al.* (2016, p. 116).

***Tenagodus (Tenagodus) obtusus* (Schumacher, 1817)**

Plate 14, figs 1-2

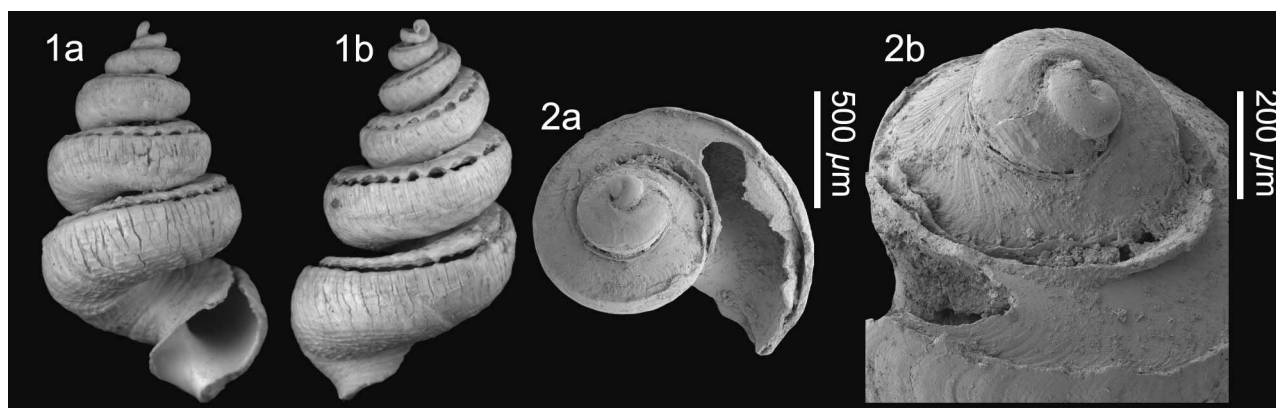
- \*1817 *Anguinaria obtusa* Schumacher, p. 262.
- 1854 *Siliquaria terebella* Lamk. – Millet, p. 158.
- 1964 *Tenagodus terebellus* Lamarck, 1818 – Brébion, p. 213.
- 2016 *Tenagodus (Tenagodus) obtusus* (Schumacher, 1817) – Van Dingenen *et al.*, p. 116, pl. 2, fig. 14 (*cum syn.*).

*Material and dimensions* – Maximum height 30.8 mm, width 13.7 mm (incomplete). **St-Clément-de-la-Place:** NHMW 2016/0103/0415 (1), NHMW 2016/0103/0416 (17), RGM.1347860 (16), RGM.1347861 (3), RGM.1347890 (18), RGM.1347904 (23), RGM.1347923 (2), LC (5), FVD (7). **Sceaux-d'Anjou:** NHMW 2016/0103/0418 (6), RGM.1347862 (50+), RGM.1347863 (50+), RGM.1347864 (13), RGM.1347874 (7), RGM.1347895 (50+), RGM.1347914 (26), RGM.1347933 (18), RGM.1347953 (27 fragments), RGM.1347987 (12), LC (5), FVD (8). **Renauleau:** NHMW 2016/0103/0417 (50+), NHMW 2016/0103/0393 (2), NHMW 2016/0103/1737 (1 juvenile), RGM.1348988 (8), LC (50+), FVD (50+). **Beugnon:** RGM.1348396 (16), RGM.1348397 (4).

*Discussion* – Van Dingenen *et al.* (2016, p. 116) commented on the taxonomic problems surrounding this species. The separation of the Miocene forms based on smaller size is not justified as specimens from the middle Miocene of the Karaman Basin of Turkey are just as large as most Pliocene specimens (Landau *et al.*, 2013). Having said that, the Assemblage I specimens are consistently smaller than those found in Assemblage III at Le Pigeon Blanc. However, so are almost all the gastropods found in Assemblage I. We therefore continue to consider the Miocene to present-day forms a single species. The protoconch (Pl. 14, fig. 2) is similar in size and shape to that of present-day specimens (see Schiaparelli, 2002). The pustules on the adapical last half protoconch whorl and the spiral ridged below described by that author can be seen here (Pl. 14, fig. 2b).

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

*Distribution* – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Landau *et al.*, 2004a). Middle Miocene: northeastern Atlantic (Aquitanian-Serravall-



**Plate 14.** *Tenagodus (Tenagodus) obtusus* (Schumacher, 1817); 1. NHMW 2016/0103/0415, height 14.0 mm, width 8.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/1737, detail of juvenile shell and protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



ian): Aquitaine Basin, (Cossmann & Peyrot, 1921), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Bulgaria (Kojumdzieva & Strachimirov, 1960), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Vienna Basin, Austria (Schultz, 1998); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian), Loire Basin, France (Brébion, 1964); Proto-Mediterranean Sea, Tortonian, Po Basin, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016); North Sea Basin, Belgium (Marquet, 1997a); western Mediterranean, Estepona Basin, Spain, (Landau *et al.*, 2004a); central Mediterranean, Italy (Anfossi *et al.*, 1983; Chirli, 2006). Lower upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); central Mediterranean, Italy (Sacco, 1896b; Malatesta, 1974; Chirli, 1988; Cavallo & Repetto, 1992). Present-day: Mediterranean to West Africa, 100-300 m depth (Poppe & Goto, 1991).

Family Turritellidae Lovén, 1847  
Subfamily Turritellinae Lovén, 1847

*Note* – In this work we follow Landau *et al.* (2013) and Van Dingenen *et al.* (2016) and have tried to use a more restricted concept of monophyletic genera. We are not aware of any molecular phylogenetic work on the group to date. Marwick (1957) reviewed the genera of the Turritellidae and drew special attention to the shape of the outer lip trace, using the terms lateral sinus for the trace on the whorl sides and the basal sinus for the trace on the base. He also highlighted the importance in the order of appearance of the cords on the neanic whorls and used a lettering system for the spiral cords in which B was the medial primary, D the peribasal primary generally involved with the suture, A was the first to appear adapical to B and C the first to appear abapical to B, between B and D (Marwick, 1957, p. 148). We have adopted this descriptive nomenclature in this section. We stress that the generic attributions here are provisional pending an in-depth review of the European Neogene turritellids and molecular phylogenetic work on the present-day species, which is beyond the scope of this work.

Genus *Archimediella* Sacco, 1896

*Type species* (by original designation) – *Turritella archimedis* Brongniart, 1823, Eocene, Italy.

1896a *Archimediella* Sacco, p. 12.

*Note* – The genera *Archimediella* Sacco, 1896 and *Torculoidella* Sacco, 1896 (here considered a synonym of *Oligodia* Handmann, 1882; see below) are closely similar, and indeed Marwick (1957) considered *Torculoidella* a subgenus of *Archimediella*.

The lateral and basal sinus is similar in both. However, in

*Torculoidella* (= *Oligodia*) the medial primary, B and the peribasal D dominate strongly, whereas in *Archimediella* the primaries B and C form the two main keels. Therefore we use them at full genus rank.

*Archimediella sancticlementensis* nov. sp.

Plate 15, figs 1-7

*Type material* – Holotype MNHN.F.A57719, height 36.0 mm, width 8.7 mm; paratype 1 MNHN.F.A57720, height 30.9 mm, width 8.2 mm; paratype 2 MNHN.F.A57721, height 10.3 mm (juvenile); paratype 3 NHMW 2016/0103/0439, height 26.4 mm, width 6.9 mm; paratype 4 NHMW 2016/0103/0440, height 20.3 mm, width 5.1 mm; paratype 5 NHMW 2016/0103/0441, height 19.8 mm, width 5.1 mm; paratype 6 NHMW 2016/0103/0442, height 24.2 mm, width 6.0 mm; paratype 7 RGM.1348550, height 22.6 mm, width 5.9 mm (incomplete); paratype 8 RGM.1348551, height 19.3 mm, width 4.9 mm (incomplete); paratype 9 RGM.1348703, height 25.9 mm, width 5.9 mm; paratype 10 RGM.1348704, height 16.5 mm, width 4.6 mm.

*Other material* – Maximum height 40.0 mm, width 12.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0443 (44), RGM.1348552 (14), RGM.1348593 (2), RGM.1348624 (2), RGM.1348634 (5), RGM.1348705 (50+), RGM.1348872 (1 + 5 juveniles), LC (50+), FVD (50+). **Sceaux-d'Anjou**: RGM.1348326 (1 fragment), RGM.1348655 (10), LC (3). **Renauleau**: NHMW 2016/0103/1474 (40), LC (50+), FVD (50+).

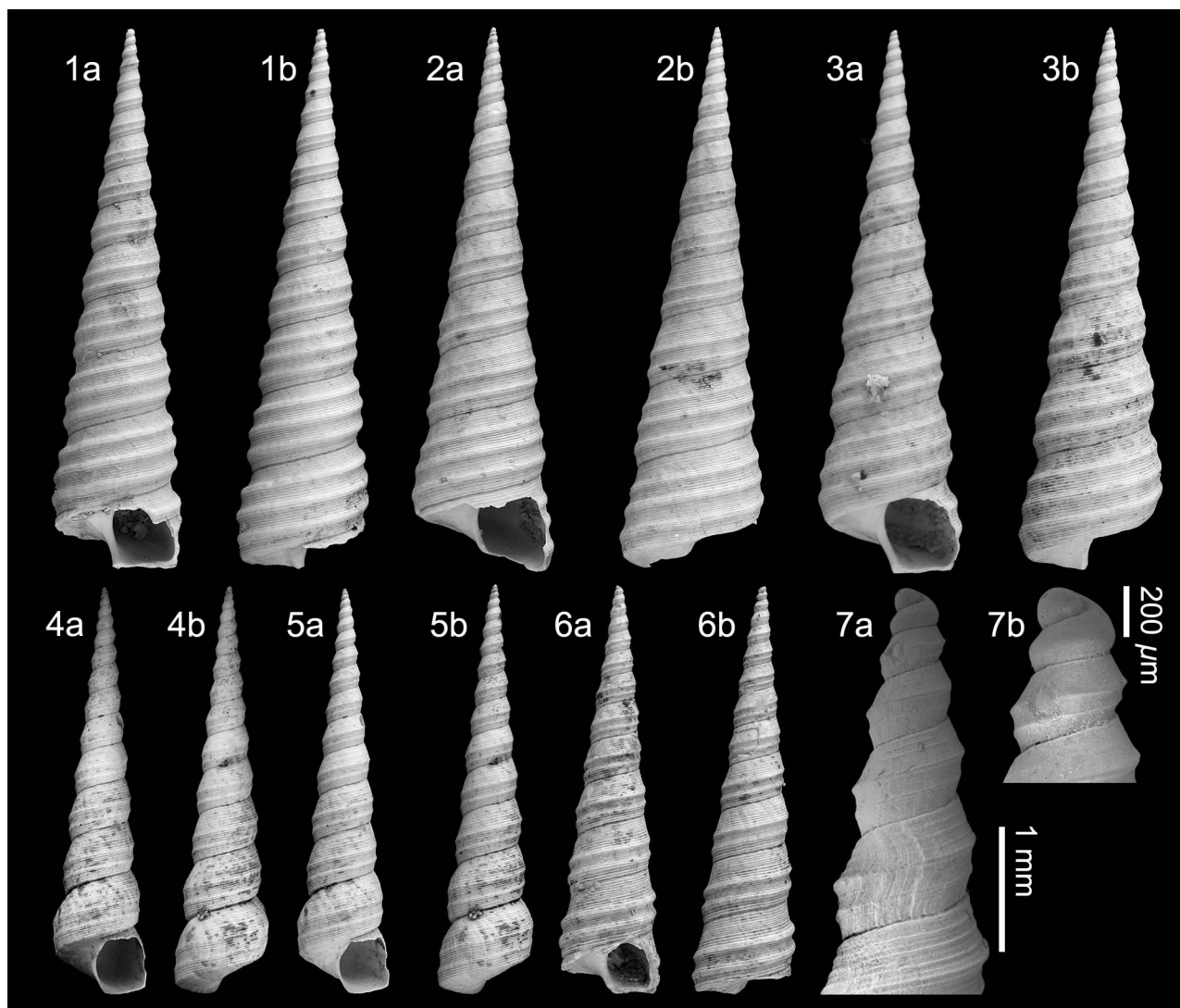
*Etymology* – Named after the type locality of St-Clément-de-la-Place. *Archimediella* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Archimediella* species of medium size, with paucispiral protoconch, slender turriculate shell shape, with angular early teleoconch whorls, in which cords B and C develop simultaneously, cord A develops late, on 11<sup>th</sup> or 12<sup>th</sup> teleoconch whorl, later adult whorls tricostate, entire surface covered in fine spiral sculpture, strongly angled, depressed, weakly concave base covered in weak spiral cords.

*Description* – Shell of medium size and thickness for genus, narrowly turriculate; apical angle 13.8° to 15.2°. Protoconch paucispiral, consisting of 1.5 smooth whorls, roundly angled mid-whorl, with a large nucleus. Teleoconch of up to 15 tall whorls. Suture impressed, linear. Early teleoconch whorls strongly carinate, with strongly developed and elevated medial primary B, placed mid-whorl, and intermediate cord C developed simultaneously. On second teleoconch whorl numerous narrow cords of subequal secondary and tertiary strength de-



**Plate 15.** *Archimediella sancticlementensis* nov. sp.; 1. **Holotype** MNHN.F.A57719, height 36.0 mm, width 8.7 mm; 2. **Paratype 1** MNHN.F.A57720, height 30.9 mm, width 8.2 mm; 3. **Paratype 3** NHMW 2016/0103/0439, height 26.4 mm, width 6.9 mm; 4. **Paratype 4** NHMW 2016/0103/0440, height 20.3 mm, width 5.1 mm (subadult); 5. **Paratype 5** NHMW 2016/0103/0441, height 19.8 mm, width 5.1 mm (subadult); 6. **Paratype 6** NHMW 2016/0103/0442, height 24.2 mm, width 6.0 mm (subadult); 7. **Paratype 2** MNHN.F.A57721; 7a, detail of early teleoconch whorls, 7b, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

velop filling interspaces. On 11<sup>th</sup> or 12<sup>th</sup> teleoconch whorl primary A develops, making last adult whorls tricostate. Last whorl strongly angled at base; base weakly concave, bearing fine, weak spiral cords. Aperture ovate, outer lip thin, angled abapically. Columella smooth, thin callus wash over base in parietal area. Basal and lateral sinuses typical for genus (see Marwick, 1957, p. 146, fig. 4).

*Discussion* – *Archimediella sancticlementensis* nov. sp. is characterised by its slender turriculate shell shape and paucispiral protoconch. The angular early whorls with cords B and C developing simultaneously place it in the genus *Archimediella*. Primary cord A develops very late in this species, on 11<sup>th</sup> or 12<sup>th</sup> teleoconch whorl, so that early neanic whorls seem unicarinate and later neanic whorls bicostate (Pl. 15, figs 4-6), whereas fully adult

specimens have tricostate late adult whorls (Pl. 15, figs 1-3). *Archimediella* species usually have tricarinate early neanic whorls. Marwick (1957, p. 160) recognised a subgroup within the genus in which the neanic whorls were unicarinate due to retardation of cords A and C and gave *A. gentili* (Chavan, 1940) from the upper Miocene of Morocco as an example. *Archimediella sancticlementensis* represents a variation of this theme in which B and C develop simultaneously and A is late to develop.

*Archimediella triplicata* (Brocchi, 1814) from the upper Miocene of the Mediterranean of Italy differs in that cord C is slightly stronger than B on early neanic whorls, but C weakens abapically and is surpassed by cord D, which emerges from the suture.

We note that specimens from Renauleau attain a larger size than those from St-Clément-de-la-Place (maximum

height 40 mm), but are all somewhat abraded and were therefore not chosen for the type material.

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

Genus *Oligodia* Handmann, 1882

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

1882 *Oligodia* Handmann, p. 212.

For generic synonymy see Van Dingenen *et al.* (2016, p. 118).

*Note* – This group is characterised by shells in which the medial primary, B and the peribasal D dominate strongly. Marwick (1957) synonymised *Eichwaldiella* Friedberg, 1933 (type species: *Turritella bicarinata* Eichwald, 1830, by monotypy) with *Torculoidella* Sacco, 1896. *Eichwaldiella* Friedberg, 1933 is preoccupied by *Eichwaldiella* Whitley, 1930 [Pisces]. Landau *et al.* (2013, p. 62) pointed out that all authors had overlooked the earlier name *Oligodia* Handmann, 1882, and designated *Turritella bicarinata* Eichwald, 1830 as the type species of *Oligodia*. Therefore *Eichwaldiella* Friedberg, 1933 (*non* Whitley, 1930) is a junior synonym of *Oligodia*. Landau *et al.* (2013, p. 62) commented that the genus *Torculoidella* might also be a junior synonym of *Oligodia*. Van Dingenen *et al.* (2016, p. 118) confirmed Marwick's (1957) generic description for *Torculoidella*; *i.e.* the predominance of medial primary B and peribasal D, and did not find them to differ from those of the genus *Oligodia*, placing *Torculoidella* also in synonymy with *Oligodia*.

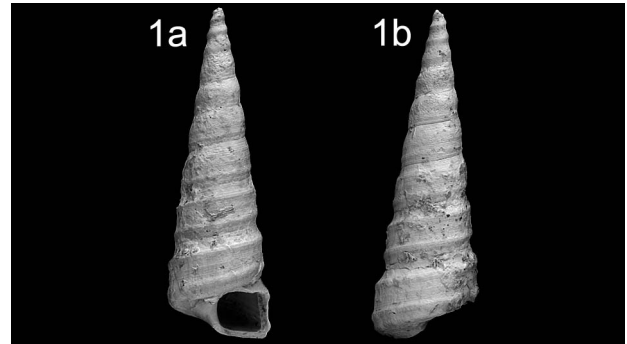
### *Oligodia bicarinata* (Eichwald, 1830)

Plate 16, fig. 1

- \*1830 *Turritella bicarinata* Eichwald, p. 220.
- 1875 *Turritella orthezensis* Tournouër *in de* Bouillé, p. 88, pl. 1, fig. 1.
- 1964 *Turritella (Archimediella) bicarinata* var. *orthezensis* Tournouër, 1875 – Brébion, p. 200.
- 2013 *Oligodia bicarinata* (Eichwald, 1830) – Landau *et al.*, p. 61, pl. 5, fig. 10, pl. 55, fig. 8, pl. 79, fig. 2 (*cum syn.*).

*Material and dimensions* – Maximum height 36.0 mm, width 11.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0449 (1). **Sceaux-d'Anjou**: RGM.1347864 (1 fragment), LC (1). **Renauleau**: NHMW 2016/0103/1476 (1). **Beugnon**: RGM.1348497 (1 fragment), RGM.1348501 (1).

*Discussion* – *Oligodia bicarinata* (Eichwald, 1830) is a species with a highly variable shell, as attested by the long



**Plate 16.** *Oligodia bicarinata* (Eichwald, 1830); 1. NHMW 2016/0103/0449, height 36.0 mm, width 11.0 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

list of synonyms and varietal names given by Landau *et al.* (2013, p. 61). Brébion (1964, p. 200) did not figure this species, but attributed the 'Redonian' forms to the variety *orthezensis* Tournouër, 1875. This form differs in having the abapical cord immediately adjacent to the suture. In the specimen at hand from St-Clément-de-la-Place the abapical cord is a short distance above the suture, and we therefore consider this difference intraspecific.

This species seems to be extremely uncommon in the Assemblage I deposits. Brébion (1964, p. 202) recorded a single specimen from Renauleau, to which we add only a few specimens from Sceaux-d'Anjou, St-Clément-de-la-Place and Beugnon.

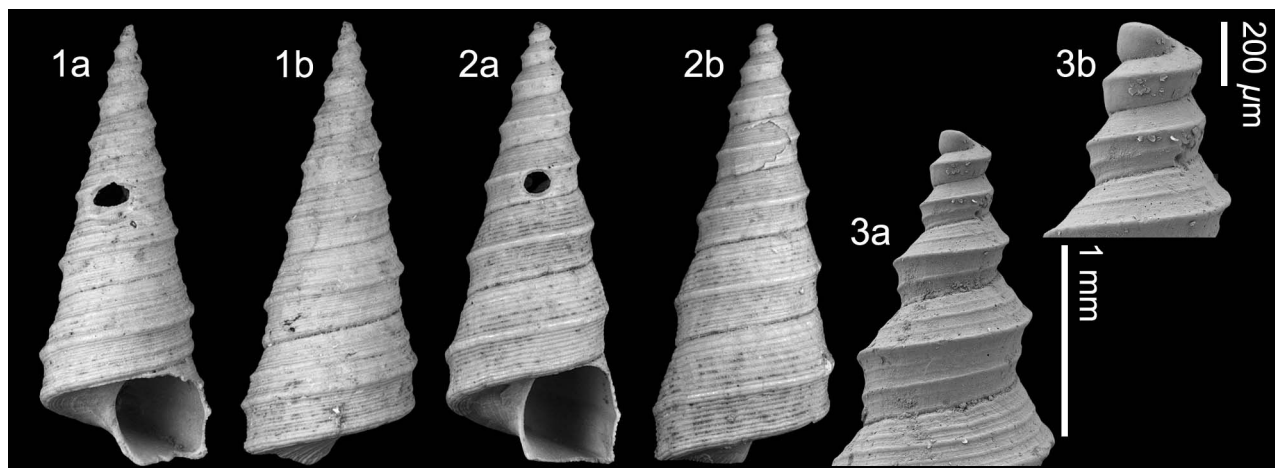
*Distribution* – Lower Miocene: Paratethys (Aquitani-an-Burdigalian): Austria, (Schaffer, 1908; Harzhauser, 2002); Proto-Mediterranean Sea (Burdigalian): Italy (Sacco, 1896a), (late Burdigalian): Kasaba Basin, Turkey (İslamoğlu, 2004). Middle Miocene: Atlantic: Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1855; Sieber, 1960; Steininger *et al.*, 1978; Schultz, 1998), Poland (Friedberg, 1909, 1914; Bałuk, 1975), Hungary (Strausz, 1954, 1962, 1966; Csepregy-Meznerics, 1956), Bulgaria (Kojumdzieva & Strachimirov, 1960), Bosnia (Eremija, 1960, 1971; Atanacković, 1985), Slovenia (Mikuž, 2009), Romania (Zilch, 1934; Moisescu, 1955; Popa & Ianoliu, 2000), Ukraine (Zelinskaya *et al.*, 1968); Proto-Mediterranean (Langhian): Kasaba Basin, Turkey (İslamoğlu, 2004); (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Proto-Mediterranean Sea (Tortonian): Proto-Mediterranean, Italy (Sacco, 1896a), (lower Tortonian): Antalya Basin, Turkey (İslamoğlu & Taner, 2003).

### *Oligodia chauvèreauensis* nov. sp.

Plate 17, figs 1-3

*Type material* – Holotype MNHN.F.A57716, height 14.7 mm, width 5.7 mm; paratype 1 MNHN.F.A57717, height





**Plate 17.** *Oligodia chauvereauensis* nov. sp.; 1. **Holotype** MNHN.F.A57716, height 14.7 mm, width 5.7 mm; 2. **Paratype 1** MNHN.F.A57717, height 14.6 mm, width 5.8 mm; 3. **Paratype 2** MNHN.F.A57718; 3a, detail of early teleoconch whorls, 3b, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

14.6 mm, width 5.8 mm; paratype 2 MNHN.F.A57718, height 7.0 mm (juvenile); paratype 3 NHMW 2016/0103/0436, height 17.3 mm, width 6.5 mm; paratype 4 NHMW 2016/0103/0437, height 15.3 mm, width 5.6 mm; paratype 5 RGM.1348233, height 15.4 mm, width 6.6 mm; paratype 6 RGM.1348234, height 14.0 mm, width 5.5 mm; paratype 8 RGM.1348553, height 14.4 mm, width 6.3 mm.

*Other material* – Maximum height 18.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0438 (44), RGM.1348235 (27), RGM.1348622 (15), LC (20), FVD (38). **Sceaux-d’Anjou:** NHMW 2016/0103/0448 (9), RGM.1347988 (50+), RGM.1347989 (50+), RGM.1348237 (50+), RGM.1348554 (18), RGM.1348654 (50+), RGM.1348689 (50+), RGM.1348764 (25), RGM.1348810 (50+), RGM.1348876 (2), RGM.1348894 (39), LC (50+), FVD (18). **Renauleau:** NHMW 2016/0103/1475 (50+), RGM.1348989 (28), LC (50+), FVD (50+). **Beugnon:** RGM.1348498 (28), RGM.1348499 (3), RGM.1348500 (4).

*Etymology* – Named after the farm on which the type material was found; Le Grand Chauvèreau. *Oligodia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Oligodia* species of small size, with paucispiral protoconch, relatively broad turriculate shell shape, with angular whorls, in which cords D and C develop simultaneously on second half of first whorl, cord A develops last, entire surface covered in fine spiral sculpture, strongly angled base with depressed, weakly concave base covered in fine spiral cords.

*Description* – Shell small for genus, thin-shelled, relatively broad, turriculate; apical angle 27.5° to 29°. Protoconch paucispiral, consisting of 1.5 smooth whorls, with a large nucleus, bearing carina placed mid-whorl. Teleoconch of up to eight whorls. Suture impressed, linear. Early teleoconch whorls strongly carinate, with medial primary B, placed mid-whorl, strongly developed and elevated. On second half of first teleoconch whorl peribasal cord D and intermediate cord C develop simultaneously. On second teleoconch whorl adapical cord A develops, with numerous narrow cords of subequal secondary and tertiary strength filling interspaces. Last whorl strongly angled at base; base weakly concave, bearing fine spiral cords. Aperture ovate, outer lip thin, angled abapically. Columella smooth, thin callus wash over base in parietal area. Basal and lateral sinuses typical for genus (see Marwick, 1957, p. 146, fig. 4).

*Discussion* – *Oligodia chauvereauensis* nov. sp. is characterised by its small size, paucispiral protoconch, rather broad turriculate shell shape, angular teleoconch whorls and surface covered in fine spiral cords. The shell shape is relatively constant, the most variable character in this species being the development of cords A and C on later teleoconch whorls; relatively prominent in some specimens (Pl. 17, fig. 1), hardly developed in others (Pl. 17, fig. 2).

The widespread European Miocene and Pliocene *Oligodia spirata* (Brocchi, 1814) is immediately separated from *O. chauvereauensis* in having a multispiral protoconch. The teleoconch shape in *O. spirata* is more slender and although both have medial primary B strongly developed making the early whorls angular, with a single carina, placed just below mid-whorl (a generic character), the adult sculpture in *O. spirata* is more variable, with two main morphotypes: *spirata*, with a strongly developed cord B, giving an angular whorl profile and the secondary cords always much weaker; morphotype *subangulata*



has a weaker central cord, the whorls are more convex and some of the secondary spiral cords more developed almost equal in strength to cord B. *Oligodia palumbina* Van Dingenen, Ceulemans & Landau, 2016 from the lower Pliocene Assemblage III localities of NW France is a much larger species, in which only the early teleoconch whorls are angulated, later whorls being rather weakly sculptured and almost straight-sided.

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

Subfamily Vermiculariinae Dall in Eastman, 1913  
Genus *Vermicularia* Lamarck, 1799

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

- 1799 *Vermicularia* Lamarck, p. 78.  
1859 *Vermiculus* Mörch, p. 348. Name attributed by Mörch to Lister (1688) (pre-Linnean; not available).

***Vermicularia milleti* (Deshayes, 1839)**

Plate 18, figs 1-4

- \*1839 *Vermetus milleti* Deshayes, pl. 70, figs 9-10.  
1854 *Vermetus Adansoni* Defr. – Millet, p. 155 (*non V. adansonii* Daudin, 1800).  
1964 *Vermicularia milleti* Deshayes, 1839 – Brébion, p. 212.  
2004a *Vermicularia milleti* (Deshayes, 1839) – Landau *et al.*, p. 26, pl. 3, fig. 18 (*cum syn.*).  
2013 *Vermicularia milleti* (Deshayes, 1839) – Landau *et al.*, p. 65, pl. 5, fig. 17 (*cum syn.*).

*Material and dimensions* – Maximum height 25.9 mm.  
**St-Clément-de-la-Place:** NHMW 2016/0103/0409-0411 (3), NHMW 2016/0103/0412 (25), RGM.1347856 (3), RGM.1347859 (19), RGM.1347866 (50+ subadult and

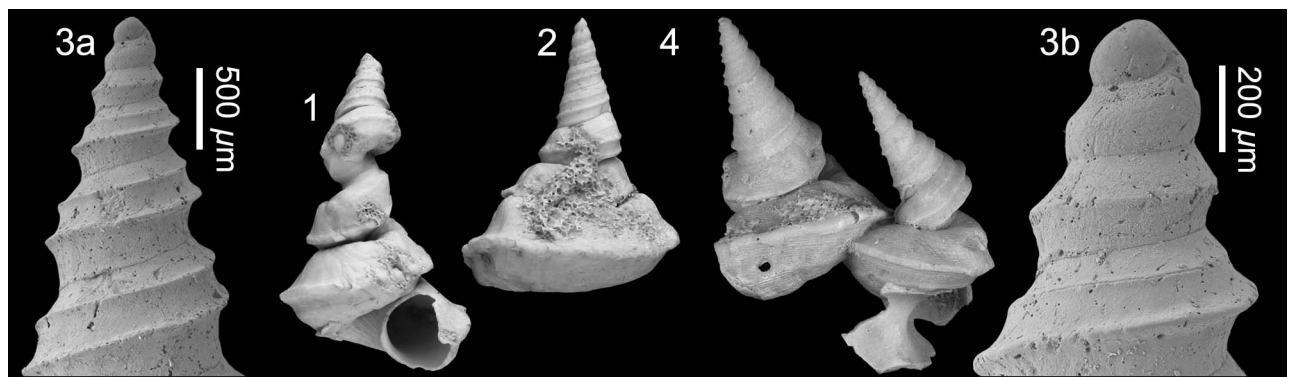
juveniles), RGM.1347905 (6), RGM.1347963 (1), RGM.1348555 (2 + 34 juveniles), RGM.1348860 (5 juveniles), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0414 (39), RGM.1347848 (5), RGM.1347849 (42), RGM.1347850 (43), RGM.1347855 (50+), RGM.1347865 (50+), RGM.1347934 (50+), RGM.1348570 (50+ juveniles), RGM.1348895 (49 juveniles), LC (40), FVD (33). **Renauleau:** NHMW 2016/0103/1419 (1), NHMW 2016/0103/0413 (50+), RGM.1348978 (26), LC (50+), FVD (50+). **Beugnon:** RGM.1348393 (13), RGM.1348394 (1), RGM.1348395 (12), RGM.1348426 (12 juveniles), RGM.1348427 (3), RGM.1348469 (18), RGM.1348505 (30).

*Discussion* – This species is very distinctive, resembling a turritellid gastropod to begin with, but with the adult whorls unwinding. The protoconch is paucispiral, composed of just over one whorl with a bulbous nucleus. The early teleoconch whorls bear two spiral cords, the abapical cord, placed mid-whorl, is the first to appear on the first teleoconch whorl, the adapical cord develops on the third teleoconch whorl. After about six regularly coiling turritellid whorls, coiling becomes abruptly irregular. The abapical spiral cord strengthens, giving the uncoiled whorls a keeled appearance. At Renauleau two coalescent specimens can occasionally be found (Pl. 18, fig. 4).

Although this is a relatively long-lived and widespread species in the Atlantic and Paratethyan Miocene, we have not found any record of the species in the Italian Miocene. Surprisingly, Landau *et al.* (2004a) illustrated this species from the upper Pliocene lower Piacenzian of the western Mediterranean, Estepona Basin of Spain, although it has not been found elsewhere in the European Pliocene.

Brébion (1964, p. 213) recorded this species from Assemblage I (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, Les Pierres Blanches, Clément-de-la-Place, Beaulieu) and Assemblage II (Apigné, Le Temple du Cerisier, Carcé, Lillion).

*Distribution* – Lower Miocene: Atlantic: Aquitaine Basin (Burdigalian), France (Cossmann & Peyrot, 1922). Middle Miocene: Atlantic: Aquitaine Basin (Langhian),



**Plate 18.** *Vermicularia milleti* (Deshayes, 1839); 1. NHMW 2016/0103/0409, height 18.2 mm, width 10.8 mm; 2. NHMW 2016/0103/0410, height 14.3 mm, width 11.3 mm; 3. NHMW 2016/0103/0411, detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place. 4. NHMW 2016/0103/1419, height 16.4 mm, width 11.3 mm, two coalescent specimens. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

France (Cossmann & Peyrot, 1922), Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Bałuk, 1975), Vienna Basin (Hörnes, 1856), Hungary (Strausz, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian) NW France (Brébion, 1964). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a).

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

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

1810 *Capulus* de Montfort, p. 54.

For generic synonymy see Van Dingenen *et al.* (2016, p. 122).

### *Capulus partimsinuosus* (Wood, 1848)

Plate 19, figs 1-2

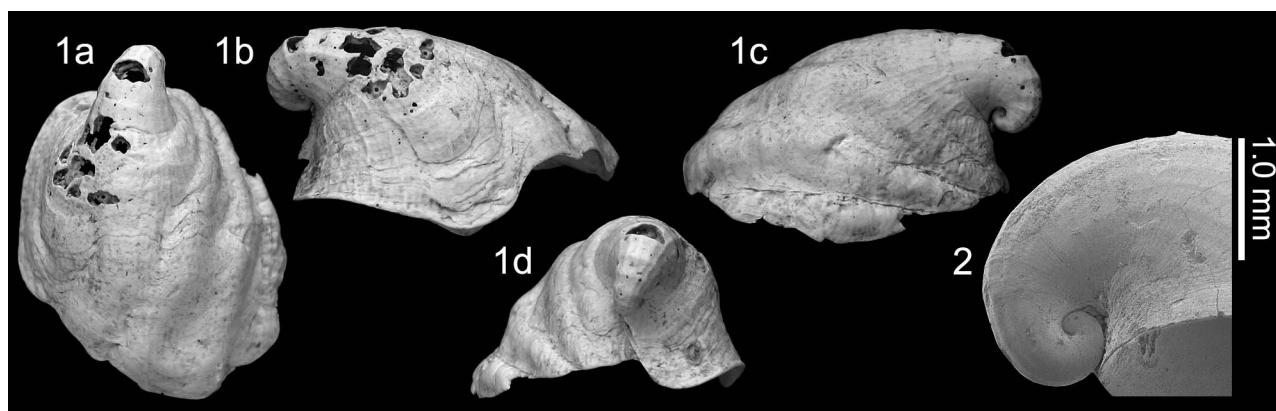
- \*1848 *Capulus militaris* var.  $\beta$  *partim sinuosus* Wood, p. 156, pl. 17, fig. 3a, b.
- 1854 *Capulus corrugatus* Millet, p. 165 (*nomen nudum*).
- 1865 *Capulus corrugatus* Millet, p. 598.
- 1870 *Capulus* (?) *incertus* Bell, p. 216.
- 1923 *Brocchia plicata* Harmer, p. 769, pl. 61, fig. 11.
- 1923 *Brocchia partim-sinuosa* (S.V. Wood) – Harmer, p. 769, pl. 61, fig. 12.
- 1923 *Brocchia incerta* (A. Bell) – Harmer, p. 770, pl. 61, figs 13, 14.
- 1964 *Capulus ungaricus* var. *neglectus* Michelotti, 1847 – Brébion (*partim*), p. 309.
- 1964 *Capulus* (*Brocchia*) *sinuosa* Brocchi, 1814 – Brébion, p. 310, pl. 7, figs 25, 26 [*non Capulus sinuosus* (Brocchi, 1814)].

- 1997b *Brocchia sinuosa* (Brocchi, 1814) – Marquet, p. 72, pl. 1, fig. 6 [*non Capulus sinuosus* (Brocchi, 1814)].
- 1998 *Brocchia sinuosa* (Brocchi, 1814) – Marquet, p. 79, fig. 54 [*non Capulus sinuosus* (Brocchi, 1814)].
- 2006 *Capulus partimsinuosa* [*sic*] (Wood, 1848) – Marquet & Landau, p. 29.

*Material and dimensions* – Maximum height 6.9 mm, diameter 13.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0557-0558 (2 juveniles), NHMW 2016/0103/0559 (1 + 20 juveniles), RGM.1347967 (1), RGM.1347969 (8 juveniles and fragments), RGM.1348032 (13 juveniles), RGM.1348828 (1 juvenile), LC (10 juveniles), FVD (11 juveniles). **Sceaux-d’Anjou**: NHMW 2016/0103/0556 (1), NHMW 2016/0103/0555 (7 fragments), RGM.1347922 (1 adult + 3 juveniles), RGM.1347924 (12 subadults and juveniles), RGM.1347958 (2 juveniles), RGM.1347991 (3), RGM.1348060 (21), LC (1). **Renauleau**: LC (2 + 2 juveniles). **Beugnon**: RGM.1348408 (1), RGM.1348409 (2).

*Discussion* – The plentiful juvenile *Capulus* material at hand from Assemblage I is not conspecific with that found in Assemblage III, having a paucispiral protoconch composed of 1.25 whorls (Pl. 19, fig. 2). The scant adult material shows a shell with a triangular outline, a pointed umbo that surpasses the posterior margin and axial plicae on the dorsum placed on the right side of the umbo when viewed from above. This record represents a range expansion for the Pliocene North Sea Basin species *Capulus partimsinuosus* (Wood, 1848) into the upper Miocene northern Atlantic.

Beu (2004) argued that the ‘plicae’ seen on the posterior slope of specimens included in the genus *Brocchia* Bronn, 1828 by all European taxonomists were a xenomorphic sculpture associated with living mode on pectinid bivalves, and synonymised the genus *Brocchia* with *Capulus*. In this scenario specimens living on smooth pectinids would lack plicae whereas those living on ribbed pectinids would develop plicae with sharp digitations at the shell margin corresponding to the ribs of the pectinid. Beu illustrated the



**Plate 19.** *Capulus partimsinuosus* (Wood, 1848); 1. NHMW 2016/0103/0556, height 6.9 mm, diameter 13.5 mm. La Presselière, Sceaux-d’Anjou. 2. NHMW 2016/0103/0557 juvenile, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

concept with the species *Capulus danieli* (Crosse, 1858) from New Zealand. Marquet & Landau (2006) questioned whether this observation held true for the North Sea Basin species, where both smooth and ribbed pectinids occur, but there are no *Capulus* shells lacking 'plicae'. The same holds true in the Assemblage I fauna, where smooth forms are lacking. Similarly in the present-day European fauna comparable specimens are lacking, despite the continued presence of both *Capulus* and pectinids. Beu (2004) suggested that *Capulus ungaricus* (Linnaeus, 1758) and *Brocchia sinuosa* (Brocchi, 1814) might be conspecific, but there are differences in the size of the protoconch, shell thickness and surface ornament (see Marquet & Landau, 2006). *Capulus ungaricus* (Linnaeus, 1758) is immediately separated by its protoconch of two whorls (Fretter & Graham, 1981, fig. 225; Van Dingenen *et al.*, 2016, pl. 4, fig. 4b). *Capulus deurganckensis* Marquet & Landau, 2006 from the Pliocene North Sea Basin also has a paucispiral protoconch of only one whorl, but the apex is less elevated and placed more centrally, and the plicae are much more oblique, almost concentric.

Brébion (1964, p. 309) recorded this species (as *Capulus ungaricus* var. *neglectus* Michelotti, 1847) from Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, Les Pierres Blanches) and as *Capulus (Brocchia) sinuosa* Brocchi, 1814 from Sceaux-d'Anjou and Thorigné. *Capulus sinuosus* (Brocchi, 1814) from the Pliocene Mediterranean differs in having a protoconch of 2.5 whorls (Landau *et al.*, 2004a, p. 69) and stronger axial folds which extend along the posterior portion of the dorsum.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: NSB, Coralline Crag (Wood, 1848; Harmer, 1923). Upper Pliocene: NSB, Red Crag (Wood, 1848; Bell, 1870; Harmer, 1923), Oorderen Sands, Belgium (Marquet, 1997b; 1998).

Superfamily Cingulopsoidea Fretter & Patil, 1958  
Family Cingulopsidae Fretter & Patil, 1958  
Genus *Eatonina* Thiele, 1912

*Type species* (by monotypy) – *Eatoniella pusilla* Thiele, 1912, present-day, South Africa.

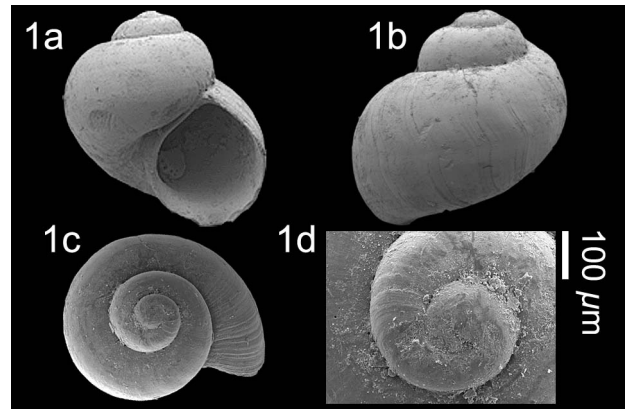
1912 *Eatonina* Thiele, p. 279.

*Note* – The subgenera of *Eatonina* recognised by Ponder & Yoo (1981) were based mainly on radular morphology and therefore no attempt is made here to ascribe the French fossil material to a subgenus.

***Eatonina* sp.**  
Plate 20, fig. 1

*Material and dimensions* – Height 1.3 mm, width 1.3 mm. **St-Clément-de-la-Place**: NHMW 2016/1571 (1).

*Description* – Shell minute, naticiform, smooth, except



**Plate 20.** *Eatonina* sp.; 1. NHMW 2016/0103/1571, height 1.3 mm, width 1.3 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

for growth lines more evident towards the aperture. Protoconch paucispiral, composed of 1.5 whorls with large nucleus (dp = 360  $\mu$ m, dn = 130  $\mu$ m, dp1 = 210  $\mu$ m). Teleoconch of 1.8 convex whorls separated by impressed suture. Last whorl globose, strongly and evenly convex, base with relatively wide umbilicus. Aperture relatively large, ovate, outer lip rounded, somewhat flared abapically, smooth within. Columella smooth; callus thickened, erect.

*Discussion* – The shell from St-Clément-de-la-Place is similar to that of some of the more turbiniform European species, such as *E. pumila* (Monterosato, 1884) and *E. matildae* Rubio & Rodríguez Babío, 1995, but the spire in the fossil species is lower than in either of these extant species. All these species have a paucispiral protoconch. We await further material to better characterise this species.

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

Family Eatoniellidae Ponder, 1965  
Genus *Crassitoniella* Ponder, 1965

*Type species* (by original designation) – *Crassitoniella carinata* Ponder, 1965, present-day, New Zealand.

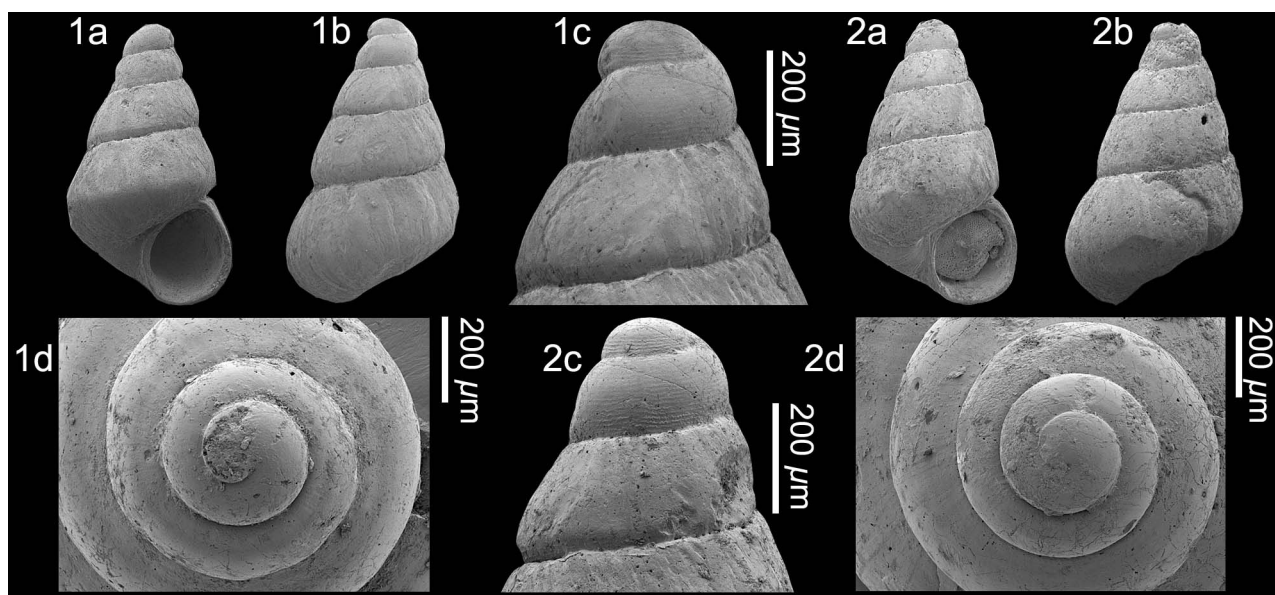
1965a *Crassitoniella* Ponder, p. 93.

***Crassitoniella lozoueti* nov. sp.**  
Plate 21, figs 1-2

*Type material* – Holotype MNHN.F.A66705, height 1.4 mm, width 780  $\mu$ m; paratype 1 NHMW 2016/0103/1572, height 1.4 mm, width 850  $\mu$ m; paratype 2 NHMW 2016/0103/1573, height 1.3 mm, width 760  $\mu$ m.

*Other material* – Maximum height 1.5 mm. **St-Clément-**





**Plate 21.** *Crassitoniella lozoueti* nov. sp.; 1. **Holotype** MNHN.F.A66705, height 1.4 mm, width 780 µm; 1c-d, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1572, height 1.4 mm, width 850 µm; 2c-d, detail of protoconch (all SEM images). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**de-la-Place:** NHMW 2016/0103/1574 (50+), LC (40), FVD (27).

*Etymology* – Named for Pierre Lozouet of the MNHN (Paris), who first recognised the presence of this genus in the European fossil assemblages. *Crassitonella* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Crassitonella* species of minute size, with conical turbiniform shell, protoconch of about one finely spirally sculptured whorl, teleoconch of three smooth, weakly convex whorls separated by deep suture, penultimate whorl somewhat swollen abapically, overhanging suture, last whorl roundly angled at periphery, base slightly flattened with small umbilical chink.

*Description* – Shell minute, conical turbinate. Protoconch paucispiral composed of about one whorl, bearing fine regular spiral sculpture (dn = 240 µm, dp1 = 150 µm). Protoconch/teleoconch junction not sharply delimited. Teleoconch consisting of three smooth, weakly convex whorls, with periphery at abapical suture. On penultimate whorl adapical portion of whorl swollen, slightly overhanging suture. Suture linear, impressed. Last whorl roundly angled at periphery, base somewhat flattened, with small umbilical chink. Aperture ovate, outer lip simple, Peristome complete, slightly erect abapically.

*Discussion* – Lozouet (1998) recognised the presence of the genus *Crassitoniella* Ponder, 1965 in the upper Oli-

gocene of southwestern France with the description of *C. europaea* Lozouet, 1998. This is only the second record for the genus in Europe, but with such minute shells it is possible that it has been overlooked previously and will turn out to be more widely distributed. The older Oligocene species is closely similar in size and shape, but differs in having a smooth protoconch, the penultimate whorl does not seem to be swollen abapically and the last whorl is less angled at the periphery.

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

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

*Note* – Robertson (1983) recommended that rib counts should be based on larger samples of shells and, in order to take into account ontogenic changes, the ribs on each teleoconch whorl (or on the last whorl at each shell length) be analysed separately. Unfortunately epitonids are uncommon and almost always fragmentary in the Assemblage I localities, making such counts on large samples difficult. When possible we have counted the axial ribs or lamellae on the first teleoconch whorl (or first preserved whorl), on the mid teleoconch whorl and on the last whorl, giving ranges where available. The number of ribs is recorded thus: ‘Axial sculpture consists of (16-18: 14-15: 12-13) narrow...ribs/lamellae’.

Genus *Epitonium* Röding, 1798

*Type species* (by subsequent designation, Suter, 1913) –

*Turbo scalaris* Linnaeus, 1758, present-day, Mediterranean.

1798 *Epitonium* Röding, p. 91.

For generic synonymy see Van Dingenen *et al.* (2016, p. 164).

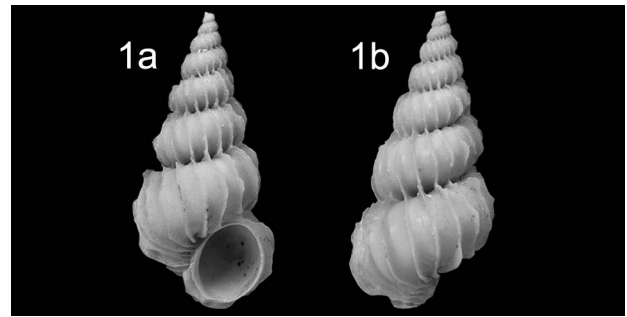
***Epitonium clathratulum clathratulum* (Kanmacher, 1798)**

Plate 22, fig. 1

- \*1798 *Turbo clathratulus* Kanmacher, p. 637, pl. 14, fig. 19.
- 2006 *Epitonium clathratulum clathratulum* (Kanmacher, 1798) – Landau *et al.*, p. 23, pl. 6, figs 7-9 (*cum syn.*).
- 2009 *Epitonium clathratulum* (Kanmacher, 1798) – Chirli, p. 23, pl. 10, figs 3-9.
- 2011 *Epitonium clathratulum clathratulum* (Kanmacher, 1798) – Landau *et al.*, p. 20, pl. 9, fig. 2 (*cum syn.*).

**Material and dimensions** – Maximum height 8.2 mm, width 3.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1393 (1), LC (2 fragments).

**Discussion** – *Epitonium clathratulum clathratulum* (Kanmacher, 1798) is characterised by its fragile, glossy shell, with delicate, relatively numerous, continuous axial lamellae, and lack of spiral sculpture. Our specimen from St-Clément-de-la-Place is somewhat smaller than usual (max 8.0 mm vs. 12-15 for modern shells, see Fretter & Graham, 1982; Giannuzzi-Savelli *et al.*, 1999). It has rather angular whorls and a small spine developed at the shoulder. This morphotype agrees with the form *Epitonium spinosum* Jeffreys, 1884, which is now considered a synonym of *E. c. clathratulum* (Weil *et al.*, 1999, p. 184). The North Sea Basin Pliocene specimens are considered a distinct subspecies; *E. clathratulum minutum* (J. de C. Sowerby, 1823), which differs from *E. c. clathratulum* in



**Plate 22.** *Epitonium clathratulum clathratulum* (Kanmacher, 1798); 1. NHMW 2016/0103/1393, height 8.2 mm, width 3.7 mm. St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

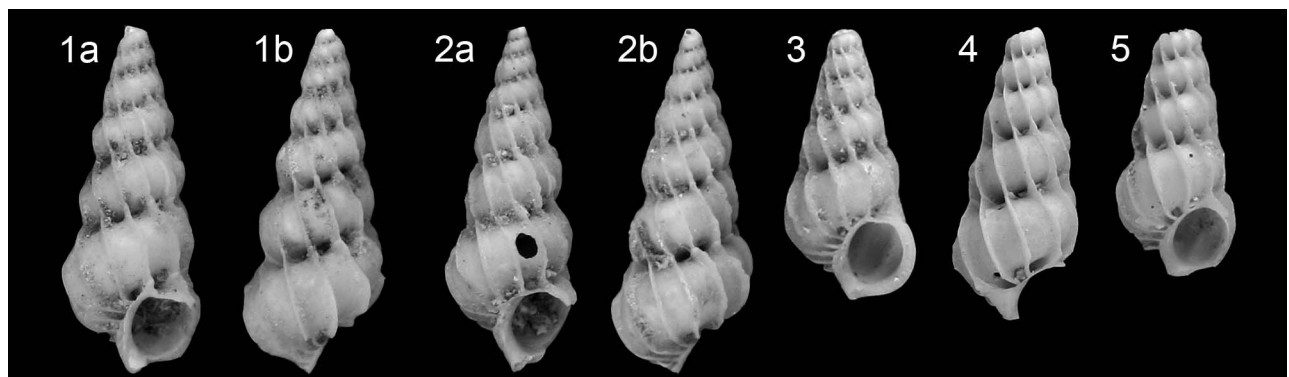
having slightly higher, less convex whorls, less arched but more erect lamellae and above all differs in the character of the funicle, far more strongly developed in *E. c. minutum* (Landau *et al.*, 2006, p. 23). The shell illustrated from St-Clément-de-la-Place does not have a well developed funicle. For further discussion see Landau *et al.* (2006).

**Distribution** – Upper Miocene: Atlantic, NW France (this paper). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2011); central Mediterranean, Italy (Chirli, 2009). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Landau *et al.*, 2006); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2006); central Mediterranean, Italy (Aimassi & Ferrero Mortara, 1983; Cavallo & Repetto, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914). Present-day: From the western Mediterranean north to Norway and the Kattegat (Fretter & Graham, 1982).

***Epitonium falunicum* (de Boury, 1900)**

Plate 23, figs 1-5

- \*1900 *Scalaria (Clathrus) falunica* de Boury in Ivolas & Peyrot, 1900, p. 61, pl. 2, fig. 9.



**Plate 23.** *Epitonium falunicum* (de Boury, 1900); 1. NHMW 2016/0103/0699, height 8.3 mm, width 3.4 mm; 2. NHMW 2016/0103/0700, height 8.0 mm, width 3.1 mm. La Presselière, Sceaux-d'Anjou; 3. NHMW 2016/0103/0444, height 6.7 mm, width 2.9 mm; 4. NHMW 2016/0103/0445, height 5.0 mm, width 2.2 mm; 5. NHMW 2016/0103/0446, height 5.1 mm, width 2.4 mm. St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- 1949 *Scala (Clathrus) falunica* de Boury, 1900 – Glibert, p. 171, pl. 11, fig. 5.

**Material and dimensions** – Maximum height  $\approx$ 11 mm (reconstructed), width 4.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0444-0446 (3), NHMW 2016/0103/0447 (5 fragments), LC (5), FVD (6). **Sceaux-d’Anjou**: NHMW 2016/0103/0699-0700 (2), NHMW 2016/0103/1788 (6), RGM.1348058 (1 fragment), RGM.1348293 (4), RGM.1348448 (2 + 4 fragments), RGM.1348813 (2), RGM.1348923 (1 + 3 fragments). **Renau-leau**: NHMW 2016/0103/1451 (8), LC (1), FVD (3). **Beugnon**: RGM.1348436 (2), RGM.1348443 (1 + 1 fragment).

**Discussion** – *Epitonium falunicum* (de Boury, 1900) is characterised by its smooth, strongly convex whorls, devoid of spiral sculpture, separated by a deeply impressed suture and axial sculpture consisting of 10-12 elevated, erect, prosocline fragile lamellae on last whorl, which are fused and continuous on each succeeding whorl, winding around the shell in a clockwise direction. There are no varices, basal cord or disc, although there is a slight change of profile at the base. The number of lamellae agrees with the range given by Glibert (1949, p. 171), although the specimens at hand from the Assemblage I localities are more slender than the specimen illustrated from the Loire Basin, similar to the type illustrated by Ivolas & Peyrot (1900, pl. 2, fig. 9).

**Distribution** – Middle Miocene: Atlantic, Loire Basin, France (de Boury in Ivolas & Peyrot, 1900; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).

#### *Epitonium cf. pliosubappenninum* (Sacco, 1891)

Plate 24, fig. 1

- cf. \*1891 *Parviscala pliosubappennina* Sacco, p. 29, pl. 1, fig. 41.  
2006 *Epitonium cf. pliosubappenninum* (Sacco, 1891) – Landau *et al.*, p. 31, pl. 10, figs 4-5.

**Material and dimensions** – Maximum height 4.9 mm, width 2.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0432 (1), NHMW 2016/0103/0433 (2), LC (2 fragments). **Sceaux-d’Anjou**: RGM.1348814 (1 fragment).

**Discussion** – This seems to be the same species as that illustrated by Landau *et al.* (2006, pl. 10, figs 4-5) as *Epitonium cf. pliosubappenninum* (Sacco, 1891). It is characterised by its smooth polished shell, without spiral sculpture, rather broad shape, and low, weakly reflected lamellae, the adapical portion of the lamellae are somewhat irregular, forming one or two spines at or below the shoulder. The specimens from the Atlantic Assemblage I deposits of NW France are small compared to the Pliocene ones from Estepona, but share the same shell characters. They differ from *E. pliosubappenninum* in being squatter-shelled. The scant material from France

does not allow an idea of the intraspecific variability.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Sacco, 1891). Upper Pliocene: western Mediterranean, Estepona Basin (Landau *et al.*, 2006); central Mediterranean, Italy (Sacco, 1891).

#### *Epitonium proximus* (de Boury, 1890)

Plate 24, fig. 2

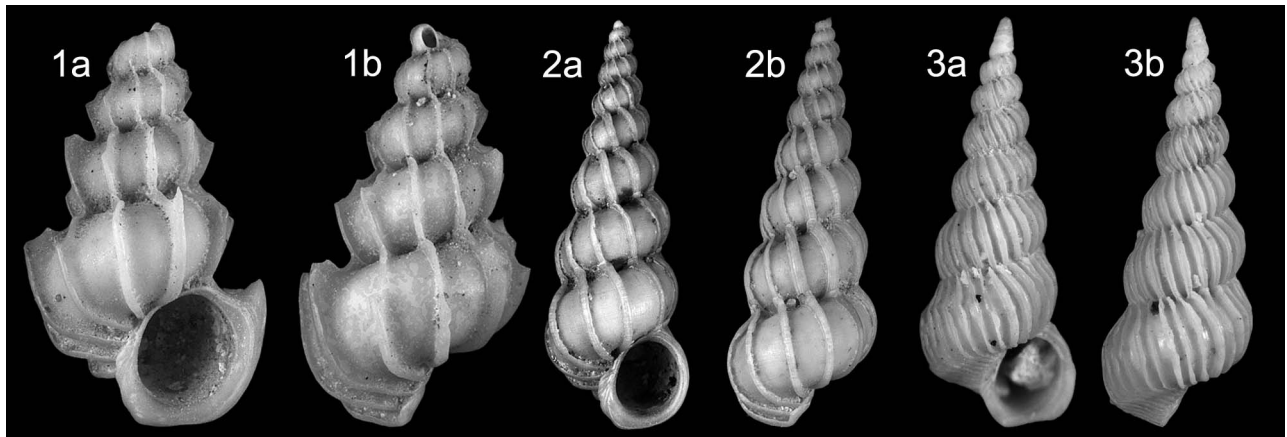
- \*1890 *Clathrus proximus* de Boury, p. 94, pl. 4, fig. 9.  
1964 *Scala (Clathrus) subulata* Sowerby, 1823 – Brébion (?partim), p. 264, pl. 6, fig. 35 [*non Epitonium subulatum* (J.de C. Sowerby, 1823)].  
2006 *Epitonium proximus* (de Boury, 1890) – Landau *et al.*, p. 31, pl. 10, fig. 6, pl. 11, figs 1, 2 (*cum syn.*).

**Material and dimensions** – Maximum height 18.0 mm (reconstructed), width 4.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0434 (1), NHMW 2016/0103/0435 (25), RGM.1348081 (1), RGM.1348240 (20), RGM.1348239349 (4 + 6 fragments), LC (15 + 6 fragments), FVD (19). **Sceaux-d’Anjou**: RGM.1348057 (3 fragments), RGM.1348574 (2 fragments). **Renau-leau**: LC (3 + 3 fragments). **Beugnon**: RGM.1348442 (4 fragments).

**Discussion** – De Boury (1890) considered the fossil species *Epitonium proximus* (de Boury, 1890) and its present-day analogue *E. clathrus* (Linnaeus, 1758) distinct. The differences between the two were discussed by Landau *et al.* (2006). Although closely related, sharing the same number of ribs, fine spiral sculpture, funicle and chromatic pattern, *E. proximus* shells are smaller, more fragile and elongated, the axial lamellae are more delicate and the funicle possibly less well developed. The specimens from Assemblage I fit within the range of variability for *E. proximus. Epitonium subulatum* (J. de C. Sowerby, 1823) from the North Sea Basin Pliocene is similar in shape, but has fewer axial ribs and lacks the fine spiral sculpture.

The specimens recorded by Brébion (1964, p. 264) as *Scala (Clathrus) subulata* Sowerby, 1823 are at least in part what we consider here *E. proximus*, as Brébion's description states: ‘...; stries spirales extrêmement fines’ (1964, p. 265). The whorl surface between the axial ribs in *E. subulatum* is smooth. Therefore we consider his Assemblage I records (Sceaux-d’Anjou, Thorigné, Renau-leau) to be this species. Brébion included *Scalaria costolamellosa* Millet, 1865 in his synonymy of *S. (C.) subulata*, which is indeed possible, but it cannot be a synonym of *E. proximus* as Millet describes: ‘..., garnis de côtes assez élevées, lisses, ainsi que l’espace qui les sépare’ (1865, p. 580). Van Dingenen *et al.* (2016, p. 165) also recorded a species similar to, but probably not conspecific with, *E. subulatum* from the lower Pliocene Assemblage III locality of Le Pigeon Blanc. Therefore,





**Plate 24.** *Epitonium* species. 1. *Epitonium* cf. *pliosubappenninum* (Sacco, 1891); NHMW 2016/0103/0432, height 4.9 mm, width 2.9 mm; 2. *Epitonium proximus* (de Boury, 1890), NHMW 2016/0103/0434, height 11.0 mm, width 3.8 mm; 3. *Epitonium pulchellum* (Bivona, 1832). NHMW 2016/0103/0430, height 5.2 mm, width 1.9 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Brébion's Assemblage III records are excluded from the synonymy of *E. proximus*.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964; as *E. subulatum*). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2006); central Mediterranean, Italy (Cavallo & Repetto, 1992). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914).

***Epitonium pulchellum* (Bivona, 1832)**

Plate 24, fig. 3

- \*1832 *Scalaria pulchella* Bivona, p. 168, pl. 2, fig. 1.
- 2006 *Epitonium pulchellum* (Bivona, 1832) – Landau *et al.*, p. 33, pl. 11, fig. 3 (*cum syn.*).
- 2009 *Epitonium pulchellum* (Bivona Ant., 1832) – Chirli, p. 34, pl. 13, figs 7-17.

**Material and dimensions** – Maximum height 6.6 mm, width 2.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0430 (1), NHMW 2016/0103/0431 (1 complete + 16 fragments), RGM.1348241 (1 complete + 4 fragments), RGM.1348239350 (1), RGM.1348843 (1), LC (7 + 10 fragments), FVD (21 fragments). **Sceaux-d'Anjou:** NHMW 2016/0103/1796 (1 fragment), RGM.1348479 (3), RGM.1348815 (2 fragments), RGM.1348924 (1 fragment).

**Discussion** – *Epitonium pulchellum* (Bivona, 1832) is similar to the Pliocene to present-day European *E. clathratulum clathratulum* (Kanmacher, 1798), but differs in having more numerous axial lamellae (20-30 vs. 10-20), which are slightly more prosocline and more or less continuous with those of consecutive whorls, the whorls are more evenly convex and not shouldered and the last whorl is broader, more inflated. Landau *et al.* (2006) ascribed upper Pliocene shells from the Estepona Basin of southern Spain to this species with some hesitation,

pointing out that they differed from present-day specimens in lacking the very faint spiral sculpture between the axial ribs. The same observation can be made about most of the Atlantic upper Miocene Assemblage I specimens from NW France, although two fragments do show some microscopic spiral sculpture. We therefore feel confident in ascribing these fossil forms to *E. pulchellum*. If our shells truly represent *E. pulchellum*, it would be unusual, as spiral sculpture is either present or not, varying only in strength, within a given species of *Epitonium*. Nevertheless, we maintain this classification, as our fossil material corresponds with this taxon in every other shell feature. Landau *et al.* (2013, p. 139) recorded *E. cf. pulchellum* from the middle Miocene Proto-Mediterranean of the Karaman Basin, Turkey. They are very similar, but smaller still, with even more crowded axial lamellae than the French fossil specimens.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli, 2009). Upper Pliocene: western Mediterranean, Estepona Basin (Landau *et al.*, 2006); central Mediterranean, Italy (Cavallo & Repetto, 1992). Present-day: From northern Spain and the Canaries, into the Mediterranean. A shallow water species, generally occurring between 20 and 40 m depth (Poppe & Goto, 1991).

Genus *Acirsa* Mörch, 1857

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

1857 *Acirsa* Mörch, p. 77.

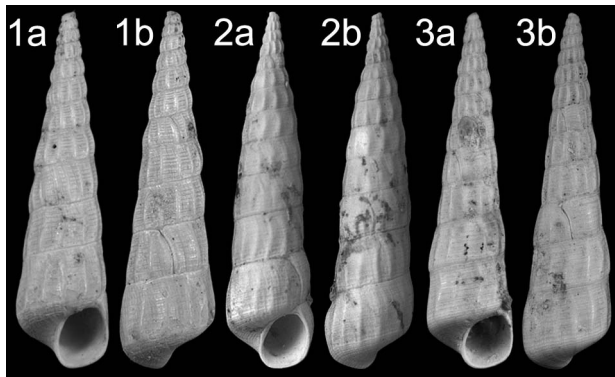
For generic synonymy see Van Dingenen *et al.* (2016, p. 167).

***Acirsa lanceolata* (Brocchi, 1814)**

Plate 25, figs 1-3

- \*1814 *Turbo lanceolatus* Brocchi, p. 375, pl. 7, fig. 7.  
 1854 *Melania Strigosa* Millet, p. 154 (*nomen nudum*).  
 1864 *Melania strigosa* Millet, p. 677 (*non* I. Lea, 1842).  
 1964 *Acirsa (Hemiacirsa) strigosa* Millet, 1854 [sic] – Brébion, p. 253, pl. 6, figs 26, 27.  
 2013 *Acirsa lanceolata* (Brocchi, 1814) – Landau *et al.*, p. 141, pl. 20, fig. 14 (*cum syn.*).

**Material and dimensions** – Maximum height 20.0 mm, width 4.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0423 (1), NHMW 2016/0103/1629 (3 fragments). **Sceaux-d’Anjou:** NHMW 2016/0103/0425 (1), NHMW 2016/0103/0426 (8), NHMW 2016/0103/1691 (1), RGM.1348515 (4), RGM.1348580 (1), RGM.1348586 (2), RGM.1348657 (2), LC (2 + 3 fragments). **Renauleau:** NHMW 2016/0103/1450 (2 fragments), LC (1 + 1 fragment).



**Plate 25.** *Acirsa lanceolata* (Brocchi, 1814); 1. NHMW 2016/0103/0423, height 11.5 mm, width 3.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place; 2. NHMW 2016/0103/0425, height 16.5 mm, width 4.1 mm; 3. NHMW 2016/0103/1691, height 11.5 mm, width 2.8 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Discussion** – This species was described by Millet (1864) as *Melania strigosa*, which is invalid as it is a primary homonym of *M. strigosa* I. Lea, 1842. Brébion (1964, p. 253) followed Millet and considered the upper Miocene specimens as distinct from the widespread Miocene to Pleistocene European *Acirsa lanceolata* (Brocchi, 1814) in having lower spire whorls and a greater number of narrower axial ribs. Considering the variability present in *A. lanceolata* (see Chirli, 2009, pl. 16, figs 13-18; specimens with the same number of equally narrow ribs as the French specimens illustrated here Pl. 25, figs 1-3), we consider the French fossil shells to fit within the range of variability for the species. We note again that the shells from the Assemblage I population are small compared to other populations, attaining a maximum height of only 16.5 mm compared to the 32.5 mm seen in Italian specimens (Chirli, 2009).

In the lower Pliocene Assemblage III locality of Le Pigeon Blanc, Van Dingenen *et al.* (2016, p. 167) recorded *A. semicorrugata* Chirli, 2009, which differs in having the axial sculpture disappearing early, so that middle and late teleoconch whorls lack ribs, whereas in *A. lanceolata* the ribs persist onto the last whorl.

Millet (1854, p. 154) recorded this species from Assemblage I localities (Sceaux-d’Anjou, Thorigné, Renauleau), to which we add St-Clément-de-la-Place. Brébion (1964, p. 255) added the Assemblage II locality of Apigné.

**Distribution** – Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian), Netherlands, Belgium (Glibert, 1952b; Janssen, 1984), Germany (Kautsky, 1925; Janssen, 1967; Wienrich, 2001; Moths, 1989; Moths *et al.*, 2010). Middle Miocene: Paratethys (Langhian-Serravallian): Vienna Basin, Austria, (Hörnes, 1856), Hungary (Csepregy-Meznerics, 1956); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1864; Brébion, 1964). Lower Pliocene: northeastern Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2011); central Mediterranean, Italy (de Boury, 1890; Chirli, 2009). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2006); central Mediterranean, Italy (de Boury, 1890; Sacco, 1891; Robba, 1968; Cavallo & Repetto, 1992; Sosso & Dell’Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (de Boury, 1890; Cerulli-Irelli, 1914).

***Acirsa sceauxsensis* nov. sp.**

Plate 26, figs 1-4

**Type material** – Holotype NHMW 2016/0103/0424, height 12.9 mm, width 3.9 mm; paratype 1 NHMW 2016/0103/0702, height 7.9 mm, width 2.8 mm; paratype 2 RGM.1348581, height 7.4 mm, width 2.7 mm; paratype 3 RGM.1348767, height 7.2 mm, width 2.7 mm; paratype 4 NHMW 2016/0103/1690, height 12.7 mm, width 3.9 mm; paratype 5 NHMW 2016/0103/1693, height 9.3 mm, width 3.0 mm; paratype 6 NHMW 2016/0103/1694, height 7.9 mm, width 2.8 mm.

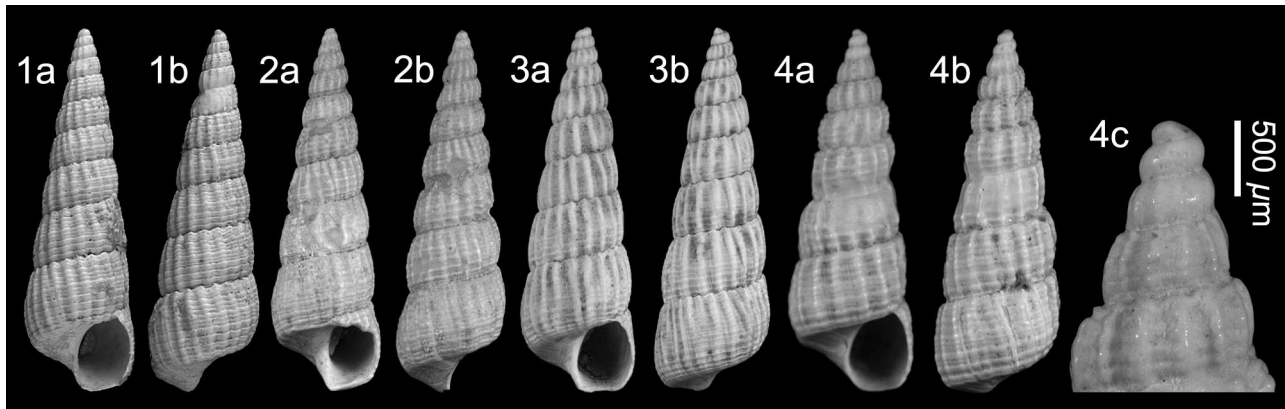
**Other material** – Maximum height 12.9 mm. **St-Clément-de-la-Place:** LC (2 + 1 fragment). **Sceaux-d’Anjou:** NHMW 2016/0103/1734 (1), RGM.1348925 (1 fragment). **Renauleau:** LC (1 + 1 fragment).

**Etymology** – Named after the type locality of Sceaux-d’Anjou. *Acirsa* gender feminine.

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

**Stratum typicum** – Tortonian, upper Miocene.

**Diagnosis** – *Acirsa* species of small size, with strong sculpture that persist on late teleoconch whorls, consisting of close-set axial ribs crossed by narrow cords of ir-



**Plate 26.** *Acirsa sceauxsensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/0424, height 12.9 mm, width 3.9 mm; 2. **Paratype 4** NHMW 2016/0103/1690, height 12.7 mm, width 3.9 mm; 3. **Paratype 5** NHMW 2016/0103/1693, height 9.3 mm, width 3.0 mm; 4. **Paratype 6** NHMW 2016/0103/1694, height 7.9 mm, width 2.8 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

regular width, sculpture on last whorl stops abruptly at base, base smooth, concave.

*Description* – Shell small, narrowly turriculate. Protoconch of about 2.5 whorls, surface apparently smooth, but may be abraded. Teleoconch of ten weakly convex whorls, with periphery just below mid-whorl. Suture deeply impressed, finely undulating. Sculpture of close-set rounded ribs that extend between sutures (12: 17: 22), roughly equal in width to their interspaces, crossed by narrow flattened cords of irregular width, 11 on penultimate whorl, separated by narrow grooves. Last whorl weakly convex, strongly angled at base; ribs stop abruptly at peribasal cord. Base slightly concave, bearing weak spiral cords. Aperture subquadrangular, outer lip not thickened by varix. Columellar and parietal callus thin, narrow.

*Discussion* – *Acirsa sceauxsensis* nov. sp. is relatively small-shelled and strongly sculptured for the genus. It differs from the European Miocene and Pliocene *Acirsa corrugata* (Brocchi, 1814) and *A. lanceolata* (Brocchi, 1814) in having more numerous axial ribs and stronger spiral sculpture. The Pliocene Mediterranean species

*Acirsa pecchiolii* (G. Seguenza, 1876) is broader, with more convex whorls, sharper axial ribs and subobsolete spiral sculpture. *Acirsa clathrata* (de Basterot, 1825) from the lower and middle Miocene of the French Atlantic and the Pliocene *A. semicorrugata* Chirli, 2009 are both species that differ from *A. sceauxsensis* in that the axial sculpture weakens or disappears completely on the last teleoconch whorls.

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

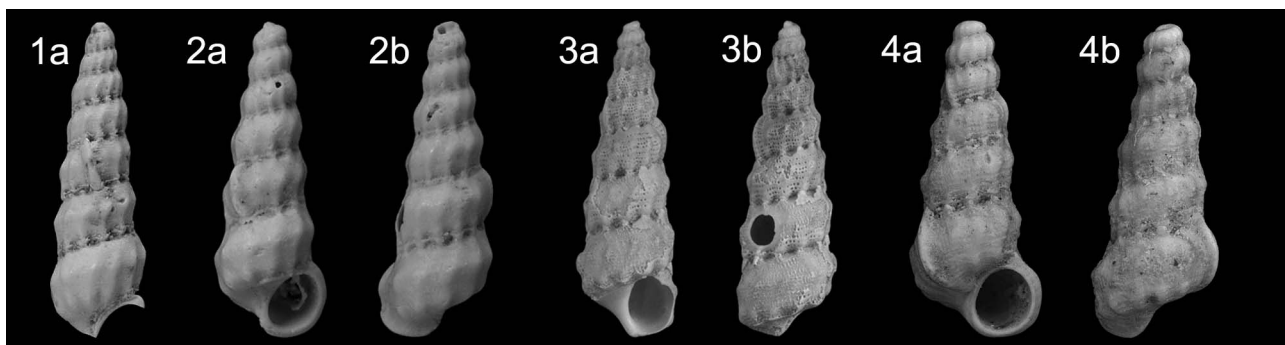
Genus *Nodiscala* de Boury, 1890

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

1890 *Nodiscala* de Boury, p. 168.

*Nodiscala* aff. *scacchii* (Hörnes, 1856)

Plate 27, figs 1-4



**Plate 27.** *Nodiscala* aff. *scacchii* (Hörnes, 1856); 1. NHMW 2016/0103/0710, height 5.6 mm, width 1.6 mm; 2. NHMW 2016/0103/1340, height 3.9 mm, width 1.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 3. RGM.1348433, height 6.6 mm, width 2.2 mm; 4. LC coll. Height 4.2 mm, width 1.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.



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

*Material and dimensions* – Height 5.6 mm, width 1.6 mm.  
**St-Clément-de-la-Place:** NHMW 2016/0103/0710 (1), NHMW 2016/0103/1340 (1). **Sceaux-d’Anjou:** NHMW 2016/0103/1792 (1), RGM.1348433 (1). **Renauleau:** NHMW 2016/0103/1449 (1).

*Discussion* – The material at hand is too poor to say more than that a *Nodiscala* species similar to *Nodiscala scacchii* (Hörnes, 1856) occurs in the Assemblage I fauna, with two rows of tubercles on the last whorl. The ribs seem to be less sinuous than in *N. pontileviensis* (de Boury *in* Ivo-las & Peyrot, 1900) from the middle Miocene of the Loire Basin of France. The pitted intritacalx typical of the genus is illustrated in one of the specimens figured (Pl. 27, fig. 3). We await better material to further characterise this species. As in most assemblages, *Nodiscala* is extremely uncommon in the Assemblage I deposits.

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

Genus *Dentiscala* de Boury, 1886

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

1886 *Dentiscala* de Boury, p. xxi.

*Note* – While we accept that the genera with a pitted intritacalx are not well defined, *Dentiscala* includes a relatively well-defined group of species with axial sculpture of rather low ribs, which can become obsolete other than as crenulations at the suture. A basal ridge can be present or absent. We therefore use *Dentiscala* at the generic level.

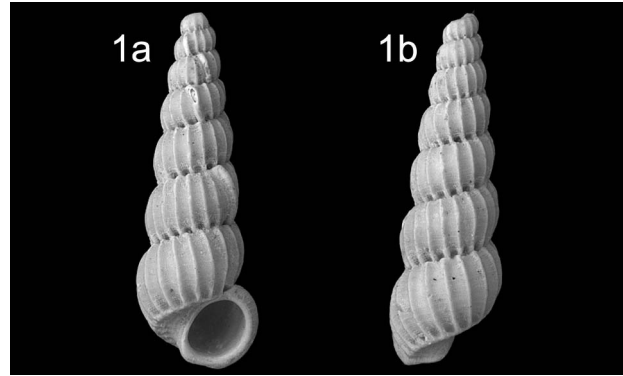
***Dentiscala fratercula* (Glibert, 1949)**

Plate 28, fig. 1

- \*1949 *Opalia (Dentiscala) fratercula* Glibert, p. 159, pl. 10, fig. 8.

*Material and dimensions* – Height 6.7 mm, width 2.2 mm.  
**St-Clément-de-la-Place:** NHMW 2016/0103/0427 (1), RGM.1348034 (1 fragment), LC (2), FVD (1). **Sceaux-d’Anjou:** NHMW 2016/0103/1793 (1 fragment).

*Discussion* – *Dentiscala fratercula* (Glibert, 1949) is characterised by its relatively tall and slender shell for the genus, narrow axial ribs (12: 14: 20), finely crenulating the sutural margin adapically, spiral sculpture consisting of rows of microscopic pits and moderately narrow basal disc bordered by a peribasal cord of moderate strength. The axial ribs extend onto the periphery of the basal disc,



**Plate 28.** *Dentiscala fratercula* (Glibert, 1949); 1. NHMW 2016/0103/0427, height 6.7 mm, width 2.2 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

weakening rapidly towards the centre. The Pliocene to present-day European *Dentiscala crenata* (Linnaeus, 1758) is separated by its larger, broader, squatter shell, and fewer, broader axial ribs coarsely crenulating the whorls adapically.

*Distribution* – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene (Tortonian): NW France (this paper).

Genus *Cirsotrema* Mörch, 1852

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

1852 *Cirsotrema* Mörch, p. 49.

For generic synonymy see Van Dingenen *et al.* (2016, p. 168).

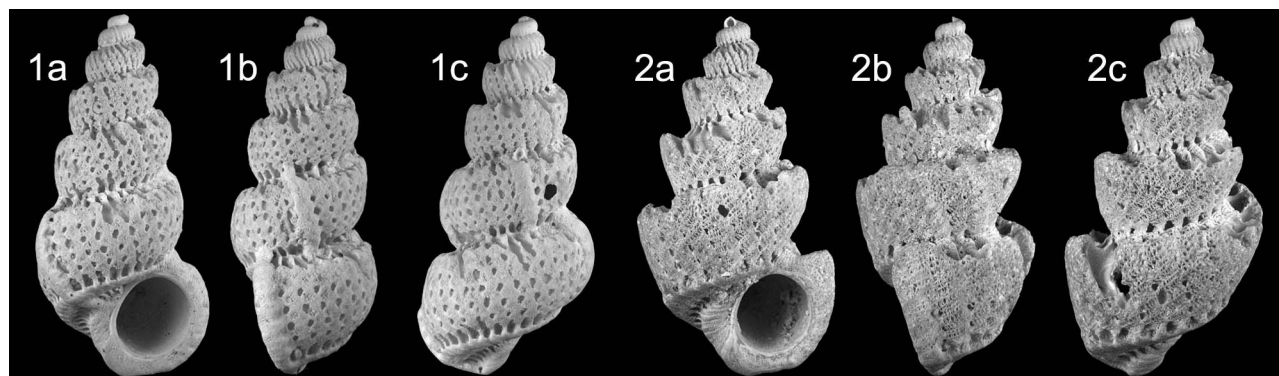
***Cirsotrema bourgeoisi* de Boury *in* Cossmann, 1912**

Plate 29, figs 1-2

- \*1912 *Cirsotrema Bourgeoisi* de Boury *in* Cossmann, p. 179, pl. 4, figs 9, 10.  
 1921 *Cirsotrema Bourgeoisi* de Boury – Cossmann & Peyrot, p. 145, pl. 4, figs 71-72.  
 1949 *Scala (Cirsotrema) bourgeoisi* de Boury, 1912 – Glibert, p. 164, pl. 10, fig. 19.

*Material and dimensions* – Maximum height 13.3 mm, width 7.3 mm. **Sceaux-d’Anjou:** NHMW 2016/0103/1427 (1), RGM.1348033 (1), RGM.1348083 (1), RGM.1348812 (1 incomplete), RGM.1348933 (2 fragments). **Renauleau:** NHMW 2016/0103/1416-1417 (2). **Beugnon:** RGM.1348441 (3), RGM.1348449 (2 fragments).

*Discussion* – *Cirsotrema bourgeoisi* de Boury *in* Cossmann, 1912, was said to differ from the Pliocene to



**Plate 29.** *Cirsotrema bourgeoisii* de Boury in Cossmann, 1912; 1. NHMW 2016/0103/1416, height 12.4 mm, width 5.6 mm. 2. NHMW 2016/0103/1417, height 13.3 mm, width 7.3 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

present-day *C. pumiceum* (Brocchi, 1814) in being smaller and squatter (not more elongated as stated by Landau *et al.*, 2006, p. 41; Landau *et al.*, 2006, p. 140; *lapsus*), in having a narrower sutural canal in having frillier sculpture, the axial ribs slightly less fused, in having fewer or weaker varices, a less strongly developed basal cord, and a less oblique aperture in profile.

Unfortunately, it is uncommon in all assemblages, so we have little information on its intraspecific variability. However, the two specimens illustrated here show an important variability in the development of the sutural canal. If we reassess the differences discussed by previous authors, it seems that neither the width of the sutural canal nor the obliqueness of the aperture can be used to separate *C. bourgeoisii* from *C. pumiceum*; the aperture is more nearly vertical in the specimens illustrated than in numerous present-day specimens of *C. pumiceum*.

Nevertheless, they are smaller and squatter than usual for *C. pumiceum*; most of the extant specimens have a couple more teleoconch whorls, the varices are certainly less strongly developed and entirely absent in one specimen (Pl. 29, fig. 2). The basal cord is somewhat narrower than seen in most *C. pumiceum*. The sculpture seems to be more fused and less frilly in the *C. bourgeoisii*. *Cirsotrema pumiceum* was until relatively recently considered a wide ranging amphiatlantic species, but as discussed by Landau *et al.* (2006, p. 41), the western Atlantic form is a separate species; *C. dalli* Rehder, 1945. Therefore, although the differences between *C. bourgeoisii* and *C. pumiceum* seem small, they probably are sufficient to warrant separation at species level.

**Distribution** – Middle Miocene: Atlantic, Aquitaine Basin, France (de Boury in Cossmann, 1912; Cossmann & Peyrot, 1921); Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).

#### ***Cirsotrema funiculus* (Wood, 1872)**

Plate 30, figs 1-4

1854 *Scalaria crenulata* Millet, p. 155 (*nomen nudum*).

1865 *Scalaria crenulata* Millet, p. 580 (*non* Kiener, 1838).

\*1872 *Scalaria funiculus* Wood, p. 98.

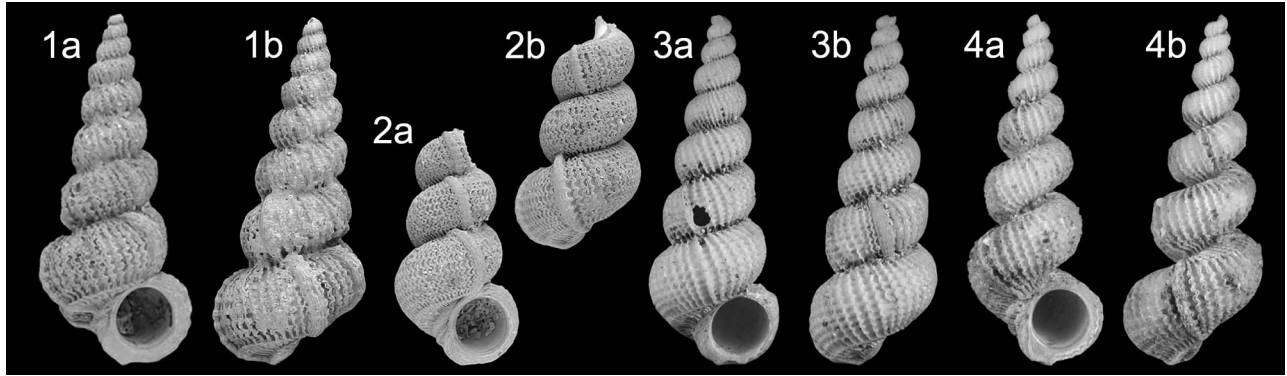
1964 *Cirsotrema funiculus* Wood, 1872 – Brébion, p. 257, pl. 6, fig. 29.

2016 *Cirsotrema funiculus* (Wood, 1872) – Van Dingenen *et al.*, p. 168, pl. 15, fig. 13 (*cum syn.*).

**Material and dimensions** – Maximum reconstructed height  $\approx$  30 mm, width 9.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0419-0420 (2), NHMW 2016/0103/0421 (2 complete, 4 fragments), RGM.1348030 (27), RGM.1348035 (2), RGM.1348080 (1), RGM.1348348 (13 + 15 fragments and juveniles), RGM.1348846 (1 fragment), LC (12 + 10 fragments), FVD (14 fragments). **Sceaux-d'Anjou:** NHMW 2016/0103/0422 (5 fragments), NHMW 2016/0103/1700-1701 (2), RGM.1347980 (1 fragment), RGM.1348056 (4 + 11 fragments), RGM.1348066 (3 + 7 fragments), RGM.1348082 (1 + 2 fragments), RGM.1348377 (1), RGM.1348432 (3 + 8 fragments), RGM.1348573 (5 + 4 fragments), RGM.1348811 (11 fragments), RGM.1348905 (5 + 15 fragments), LC (9 + 2 fragments), FVD (1 + 12 fragments).

**Discussion** – As discussed by Van Dingenen *et al.* (2016, p. 169), two similar *Cirsotrema* species have been recognised in the North Sea Basin Pliocene: *C. fimbriosum* (Wood, 1842) and *C. funiculus* (Wood, 1872), said to differ in that *C. funiculus* has more numerous weaker axial ribs (11-14 in *C. fimbriosum* vs. 20+ in *C. funiculus*). In typical specimens the difference is apparent. However, some specimens are difficult to ascribe to one or other species and have an intermediate number of ribs. Van Dingenen *et al.* (2016) recognised both species in the lower Pliocene Assemblage III localities of northwestern France. However, in the upper Miocene Assemblage I localities only the finely-ribbed *C. fimbriosum* occurs. This led the authors to keep the two forms separate, a position that we follow here. We note that in some of the specimens from St-Clément-de-la-Place the whorls tend to become disjunct (Pl. 30, fig. 4).

Brébion (1964, p. 258) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, Les Pierres Blanches), to which we add St-Clément-de-la-Place, Assemblage II (Apigné, Carcé), Assemblage III



**Plate 30.** *Cirsotrema funiculus* (Wood, 1872); 1. NHMW 2016/0103/0419, height 19.8 mm, width 8.1 mm; 2. NHMW 2016/0103/0420, height 19.4 mm, width 9.5 mm. Le Grand Chauvreau, St-Clément-de-la-Place. 3. NHMW 2016/0103/1700, height 17.5 mm, width 6.5 mm; 2. NHMW 2016/0103/1701, height 9.4 mm, width 3.6 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(Le Pigeon Blanc, Le Girondor, La Gauvinière) and Assemblage IV (Gourbesville).

**Distribution** – Upper Miocene (Tortonian and Messinian): NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016); NSB, Coralline Crag, England (Harmer, 1920); Kattendijk Formation, Belgium (Glibert, 1958; Marquet, 1997b, 1998). Upper Pliocene: NSB, Red Crag, England (Wood, 1848, 1872; Harmer, 1920). Pliocene (indeterminate): The Netherlands (VVan Regteren Altena *et al.*, 1955). Upper Pliocene-Plesitocene: NW France (Brébion, 1964).

Genus *Papuliscala* de Boury, 1911

**Type species** (by original designation) – *Acirsa praelonga* Jeffreys, 1877, present-day, NE Atlantic, deep water.

1911 *Papuliscala* de Boury, p. 220.

***Papuliscala redoniensis* nov. sp.**

Plate 31, fig. 1

**Type material** – Holotype NHMW 2016/0103/0428, height 5.1 mm, width 1.3 mm; paratype 1 NHMW 2016/0103/0429, height 5.5 mm, width 1.3 mm, **St-Clément-de-la-Place**. Paratype 2 NHMW 2016/0103/1617, height 4.5 mm, width 1.2 mm, **Renauleau**.

**Other material** – **St-Clément-de-la-Place**: LC (3). **Sceaux-d'Anjou**: RGM.1348236 (1 juvenile).

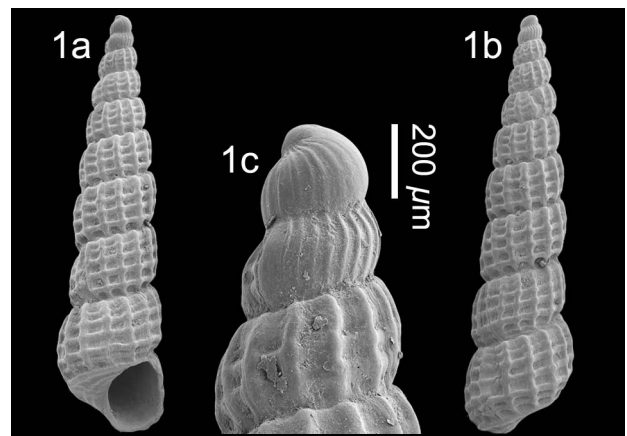
**Etymology** – Named after the 'Redonian' stage, the name used until recently for these NW French post-middle Miocene assemblages. *Papuliscala* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Papuliscala* species of small size, with protoconch of just over two whorls, bearing axial riblets, teleoconch with moderately coarsely reticulated sculpture formed by 12-14 rounded ribs and 4-5 cords on spire whorls; ribs slightly predominant, with small tubercles formed at sculptural intersections, base delimited by prominent peribasal cord, aperture roundly angled abapically.

**Description** – Shell small, of medium thickness, elongate-turriculate, with moderately coarse reticulated sculpture. Protoconch of just over two whorls, with small nucleus; nucleus smooth, later bearing sinuous axial riblets. Junction with teleoconch abrupt. Teleoconch of 7.5 weakly convex whorls, with periphery below mid-whorl. Suture deeply impressed. Axial sculpture of elevated rounded ribs (12: 12: 14), about half the width of their interspaces. Spiral sculpture of rounded cords,



**Plate 31.** *Papuliscala redoniensis* nov. sp.; 1. Holotype NHMW 2016/0103/0428, height 5.1 mm, width 1.3 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



slightly weaker than ribs and narrower than their interspaces, four on spire whorls, five on penultimate, six on last whorl, forming small rounded tubercles at intersections. Last whorl convex, angled at base. Base delimited by prominent peribasal cord, bearing two further cords abapically. Aperture subovate, outer lip simple, roundly angulated abapically.

**Discussion** – The presence of axial riblets on the protoconch places this species in the Nystiellinae Clench & Turner, 1952 and the adult whorl character of the axial ribs, non-lamellar, and rather strong spiral cords, distinct basal disc and aperture angular at the base place it in the genus *Papuliscala* de Boury, 1911 (Bouchet & Warén, 1986). We note that Bouchet & Rocroi (2017) did not consider these differences sufficient and synonymised Nystiellinae with Epitoniinae.

*Papuliscala redoniensis* nov. sp. differs from the extant Atlantic *P. elongata* (Watson, 1881) and *P. praelonga* (Jeffreys, 1877) in having much broader axial and spiral sculpture. *Papuliscala cerithielloides* Bouchet & Warén, 1986 has much finer reticulate sculpture. The late Pleistocene Mediterranean *P. tavianii* Bouchet & Warén, 1986 and *P. presselierensis* nov. sp. (see below) are the only species with similarly thick sculpture to that of *P. redoniensis*, but *P. tavianii* has only two spiral cords per whorl and *P. sceauxensis* three. All the species compared above have a paucispiral protoconch. The earliest European member of the genus is from the Atlantic upper Oligocene of France, *P. ambulator* Lozouet, 1999. The

sculpture of this species is very similar to that of *P. redoniensis*, but the cords and ribs are narrower and the protoconch is multispiral with an extra whorl. In the middle Miocene of the North Sea Basin *P. koeneni* (Janssen, 1967) also has a multispiral planktotrophic-type protoconch (see Janssen, 1967, pl. 14, figs 1-2; Wienrich, 2001, pl. 91, fig. 9), and differs from *P. redoniensis* in having finer sculpture and angular whorls.

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

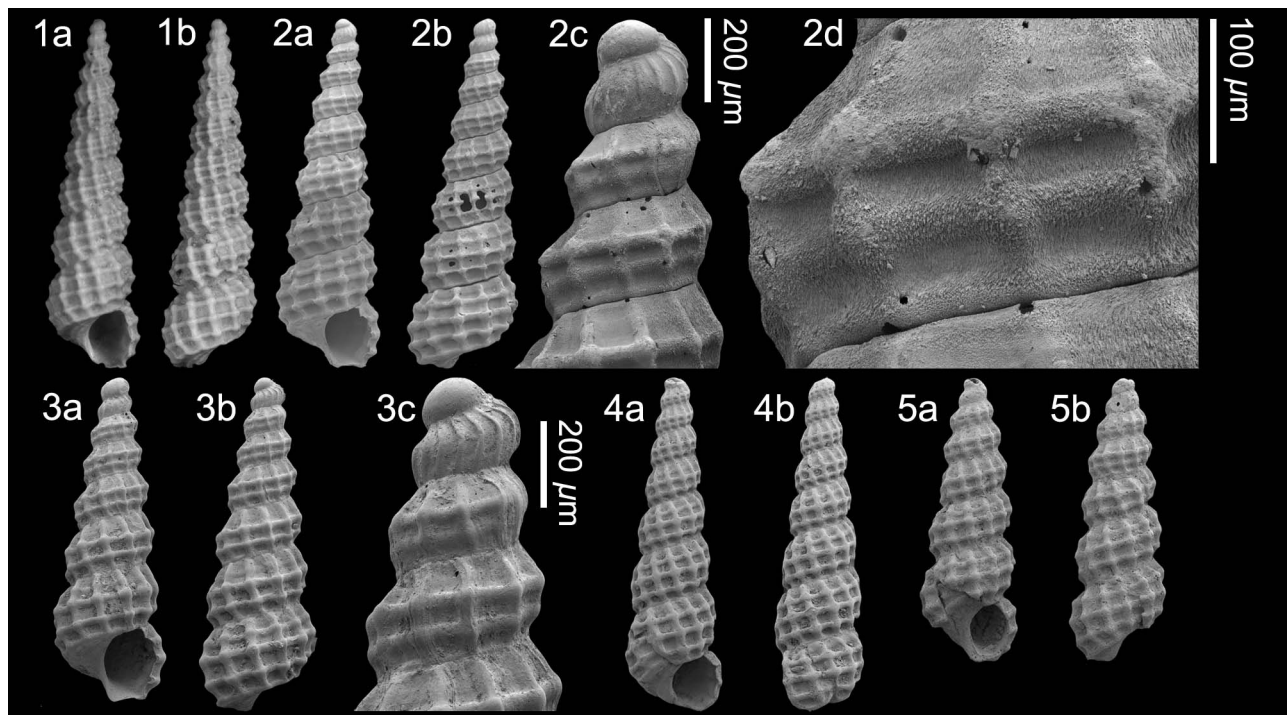
***Papuliscala presselierensis* nov. sp.**

Plate 32, figs 1-5

**Type material** – Holotype NHMW 2016/0103/1687, height 5.8 mm, width 1.6 mm; paratype 1 NHMW 2016/0103/1688, height 4.0 mm, width 0.8 mm; paratype 2 NHMW 2016/0103/1689, height 3.0 mm, width 1.1 mm, **Sceaux-d'Anjou**. Paratype 3 NHMW 2016/0103/1620, height 4.2 mm, width 1.2 mm; paratype 4 NHMW 2016/0103/1621, height 2.5 mm, width 0.9 mm, **Renauleau**.

**Other material** – **St-Clément-de-la-Place**: RGM.1348038 (2 fragments), RGM.1348264 (1 fragment).

**Etymology** – Named after the type locality of Sceaux-d'Anjou. *Papuliscala* gender feminine.



**Plate 32.** *Papuliscala presselierensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1687, height 5.8 mm, width 1.6 mm; 2. **Paratype 1** NHMW 2016/0103/1688, height 4.0 mm, width 0.8 mm, 2c, detail of protoconch, 2d, detail of teleoconch microsculpture; 3. **Paratype 2** NHMW 2016/0103/1689, height 3.0 mm, width 1.1 mm, 3c, detail of protoconch, La Presselière, Sceaux-d'Anjou. 4. **Paratype 3** NHMW 2016/0103/1620, height 4.2 mm, width 1.2 mm; 5. **Paratype 4** NHMW 2016/0103/1621, height 2.5 mm, width 0.9 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Papuliscala* species of small size, with protoconch of two whorls bearing axial riblets, coarsely reticulated teleoconch sculpture formed by 2-4 rounded cords and 10-12 ribs; ribs slightly predominant, with small tubercles formed at sculptural intersections, base delimited by prominent peribasal cord, bearing single subobsolete cord abapically.

**Description** – Shell small, of medium thickness, elongate-turriculate, with coarse reticulate sculpture. Protoconch composed of about two whorls with medium-sized nucleus; nucleus smooth, later bearing sinuous axial riblets. Teleoconch of up to eight whorls; early whorls angular, later whorls convex, with periphery mid-whorl. Suture deeply impressed. Axial sculpture of elevated prosocline rounded ribs (10: 11-12: 10), about one-third the width of their interspaces. Spiral sculpture of rounded cords, slightly weaker than ribs and narrower than their interspaces, two on first three or four teleoconch whorls, three on later whorls, four on last whorl, forming small rounded tubercles at intersections. Whorl surface finely papulose. Last whorl convex. Base concave, strongly delimited by prominent peribasal cord, bearing one subobsolete cord abapically. Aperture subovate, outer lip simple.

**Discussion** – *Papuliscala presselierensis* nov. sp. is characterised by its very coarse sculpture. It differs from *P. redoniensis* nov. sp. in having even more open reticulated sculpture than that species, with fewer axial and spirals (spire whorls: 10-12 axials, 3 spirals vs. 12-14 and 4-5). Only *P. tavianii* Bouchet & Warén, 1986 from the upper Pleistocene Mediterranean has coarser sculpture still, with only two spirals per whorls. The other congeners discussed above all have finer sculpture. The protoconch also differs from that of *P. redoniensis*, which has a smaller nucleus, an extra 0.2 whorl and denser riblets on the protoconch. Finely papulose surface sculpture is well preserved in one of the specimens figured (Pl. 32, fig. 2d). We are unsure if this is a generic character as it is only seen under high SEM magnification.

It is surprising to find two species the genus *Papuliscala*, which is considered to inhabit deep-water (Bouchet & Warén, 1986) in the Assemblage I deposits, which we consider to have been deposited in shallow-water.

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

Family Hipponicidae Troschel, 1861  
Genus *Cheilea* Modeer, 1793

**Type species** (by subsequent designation, Woodring,

1928) – *Patella equestris* Linnaeus, 1758, present-day, Indian Ocean.

1793 *Cheilea* Modeer, p. 110.

1817 *Mitrularia* Schumacher, p. 183. Type species (by monotypy): *Mitrularia neptuni* Schumacher, 1817, present-day, Indian Ocean. *Mitrularia neptuni* is a substitute name for *Patella equestris* Linnaeus, 1758; *Mitrularia* is thus an objective junior synonym of *Cheilea*.

1900 *Chilea* Cossmann, p. 186. Unjustified emendation of *Cheilea*.

*Cheila* is an incorrect subsequent spelling.

### ***Cheilea equestris* (Linnaeus, 1758)**

Plate 33, figs 1-2

\*1758 *Patella equestris* Linnaeus, p. 780.

1854 *Caliptraea* [sic] *Equestroides* Millet, p. 165 (*nomen nudum*).

1865 *Caliptraea* [sic] *aequestroides* Millet, p. 598.

1964 *Cheilea equestris* Linné, 1758 – Brébion, p. 306, pl. 7, fig. 23.

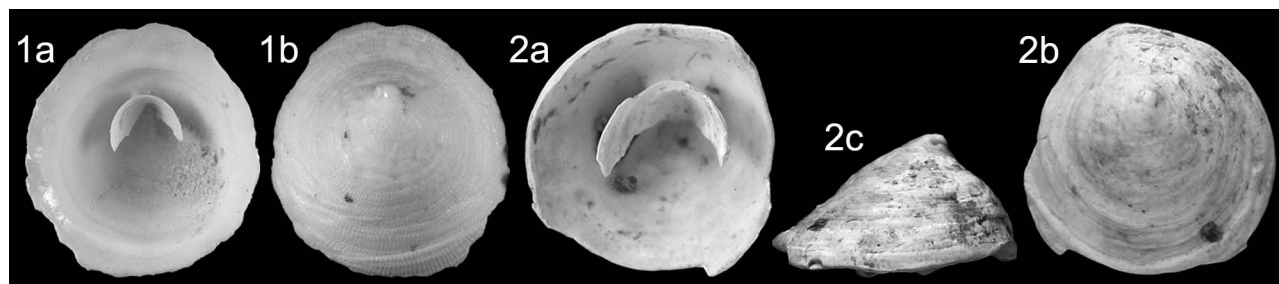
2004a *Cheilea equestris* (Linnaeus, 1758) – Landau *et al.*, p. 81, pl. 20, figs 1, 2 (*cum syn.*).

2008 *Cheilea equestris* (Linnaeus, 1758) – Chirli, p. 16, pl. 4, figs 11-15.

**Material and dimensions** – Maximum height 4.7 mm, diameter 6.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0564 (3), RGM.1347925 (1), RGM.1347945 (12 juveniles and fragments), FVD (3). **Sceaux-d'Anjou**: NHMW 2016/0103/0566 (1), NHMW 2016/0103/1418 (1), NHMW 2016/0103/0567 (8), RGM.1347928 (2), RGM.1347929 (6), RGM.1347946 (17), FVD (4). **Renaleau**: NHMW 2016/0103/0565 (27), FVD (24). **Beugnon**: RGM.1348410 (2 juveniles), RGM.1348411 (7 juveniles).

**Discussion** – *Cheilea equestris* (Linnaeus, 1758) is easily separated from other limpet-like shells by the presence of a horseshoe-shaped interior lamina. Landau *et al.* (2004a, p. 81) discussed the important difference in shell shape and sculpture that occurred with ontogeny in this species, the larger specimens becoming more flattened with rugose surface sculpture. The Assemblage I specimens are all small and similar to juvenile Pliocene specimens described from the upper Pliocene of the Estepona Basin of Spain; elevated and almost smooth. The Miocene Italian *Cheilea bredai* (Michelotti, 1847) is considered a synonym. For further discussion see Landau *et al.* (2004a, p. 81).

**Distribution** – Lower Miocene: Proto-Mediterranean, Italy (Sacco, 1896b). Middle Miocene: ?Paratethys, Poland (Bałuk, 1975), Romania (Zilch, 1934). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1896b). Lower Pliocene: central Mediterranean, Italy (Chirli, 2006). Upper



**Plate 33.** *Cheilea equestris* (Linnaeus, 1758); 1. NHMW 2016/0103/1418, height 2.5 mm, diameter 6.8 mm; 2. NHMW 2016/0103/0566, height 4.7 mm, diameter 6.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Pliocene: western Mediterranean, Estepona Basin (Landau *et al.*, 2004a); central Mediterranean, Italy (Bertarelli & Inzani, 1986). Upper Pleistocene: Red Sea, Hurghada, Egypt (NHMW coll.). Present-day: Circumglobal distribution; Indo-Pacific (Wilson, 1993), eastern Pacific (Keen, 1971); eastern Atlantic, southeastern Florida and West Indies (Abbott, 1954; Redfern, 2013), western Atlantic, Lusitanic province south to coast of West Africa (Rolán, 2005).

Superfamily Littorinoidea Children, 1834

Family Littorinidae Children, 1834

Subfamily Littorininae Children, 1834

Genus *Littorinopsis* Mörch, 1876

*Type species* (by subsequent designation, Cossmann, 1915) – *Phasianella angulifera* Lamarck, 1822, present-day, Caribbean.

1876 *Littorinopsis* Mörch, p. 135.

***Littorinopsis prevostina* (de Basterot, 1825)**

Plate 34, figs 1-2

\*1825 *Phasianella Prevostina* de Basterot, p. 38, pl. 1, fig. 18.

1845 *Phasianella Prevostina* de Bast. – Grateloup, pl. 14, figs 29-30.

1915 *Littorinopsis (Touzinia) Prevostina* Bast. – Cossmann, p. 62, pl. 3, figs 7-10.

1919 *Littorinopsis (Touzinia) Prevostina* (Basterot) – Cossmann & Peyrot, p. 637, pl. 17, figs 79-81.

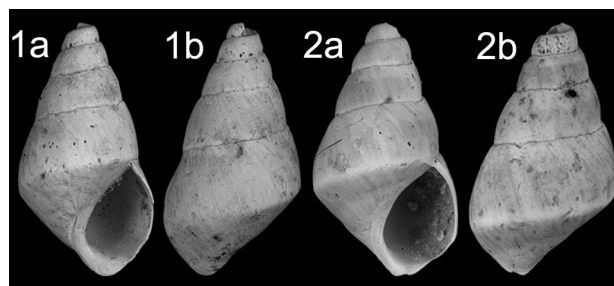
*Material and dimensions* – Maximum height 3.6 mm (incomplete), width 2.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1630-1631 (2), NHMW 2016/0103/1756 (2), LC (1).

*Discussion* – *Littorinopsis prevostina* (de Basterot, 1825) is characterised by its relatively thin shell, a generic character (Reid, 1986), but differs from most of its congeners in not having any spiral sculpture. The last whorl is sharply angled at the base. The genus is well represented in the Miocene along the eastern Atlantic frontage

by *L. grateloupi* (Deshayes, 1843) from the Aquitanian and Burdigalian Aquitaine Basin of France, which differs in having spiral sculpture and a wider apical angle (= *L. tournoueri* Cossmann, 1916 *vide* Lozouet *et al.*, 2001). In the middle Miocene Loire Basin *L. alberti* (Dujardin, 1837) occurs, which is very similar to and possibly a synonym of *L. grateloupi*, and *L. morgani* Cossmann & Peyrot, 1918, which is also smooth and sharply angled at the base, but considerably higher-spined, with slightly more convex whorls.

We note that Lozouet *et al.* (2001, p. 25) considered *Phasianella prevostina* de Basterot, 1825 simply a form of *Gibborissoia varicosa* (de Basterot, 1825). The shells illustrated here are certainly not *Gibborissoia*; there is no trace of lip varix and the shell texture is littorinid, with the classical brownish-orange colour of fossil littorinids. We are fairly certain they are conspecific with shells illustrated by Cossmann (1915) and Cossmann & Peyrot (1919) as *L. (T.) prevostina*, which are also not *Gibborissoia*. We have not found any *Gibborissoia* species in the Assemblage I fauna.

*Distribution* – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (de Basterot, 1825, Grateloup, 1845; Cossmann, 1915; Cossmann & Peyrot, 1919). Middle Miocene: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1919). Upper Miocene: Atlantic (Tortonian), NW France (this paper).



**Plate 34.** *Littorinopsis prevostina* (de Basterot, 1825); 1. NHMW 2016/0103/1630, height 3.6 mm, width 1.9 mm; 2. NHMW 2016/0103/1631, height 3.6 mm, width 2.1 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



Genus *Melarhappe* Mühlfeld in Menke, 1828

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

1828 *Melarhappe* Mühlfeld in Menke, p. 23.

For generic synonymy see Van Dingenen *et al.* (2016, p. 128).

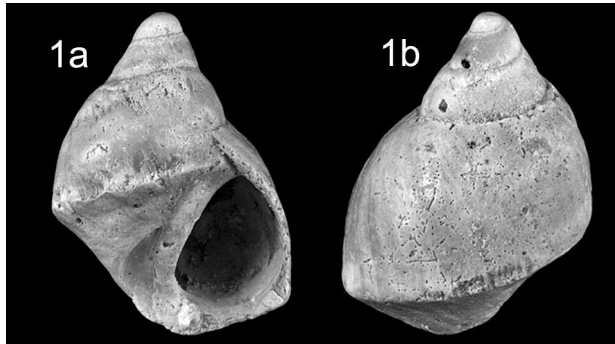
***Melarhappe gibbosa* (Etheridge & Bell, 1893)**

Plate 35, fig. 1

\*1893 *Littorina gibbosa* Etheridge & Bell in Bell, p. 630.

2016 *Melarhappe gibbosa* (Etheridge & Bell, 1893) – Van Dingenen *et al.*, p. 128, pl. 5, fig. 4 (*cum syn.*).

*Material and dimensions* – Maximum height 5.1 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0275 (1), NHMW 2016/0103/0276 (3), LC (1).



**Plate 35.** *Melarhappe gibbosa* (Etheridge & Bell, 1893); 1. NHMW 2016/0103/0275, height 3.3 mm, width 2.3 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – The shells of this tiny *Melarhappe* species from the Assemblage I locality of St-Clément-de-la-Place are identical to those of Assemblage III from Le Pigeon Blanc illustrated by Van Dingenen *et al.* (2016, pl. 10, fig. 7), which are also identical to that figured by Harmer (1921, pl. 53, fig. 24) from the Gelasian Pleistocene of St. Erth, Cornwall (England) and there is little intraspecific variability. Harmer also reported *Melarhappe gibbosa* (Etheridge & Bell, 1893) from the upper Pliocene Red Crag of eastern England and Marquet (1997a, 1998) recorded it from the Kattendijk Formation of Belgium. There is nothing to add to the description given by Harmer (1921, p. 665), nor the discussion given by Van Dingenen *et al.* (2016, p. 219).

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); NSB, Kattendijk Formation, Belgium (Marquet, 1997b; 1998). Upper Pliocene: Red Crag, England (Harmer, 1921). Lower Pleistocene: St. Erth, England (Etheridge & Bell, 1898; Bell, 1898; Harmer, 1921).

Superfamily Naticoidea Guilding, 1834

Family Naticidae Guilding, 1834

Subfamily Naticinae Guilding, 1834

*Note* – In this section we have followed Pedriali & Robba (2005) and Robba *et al.*, (2016) for our species descriptions. The shell characters are described as defined by these authors (2005, p. 111, fig. 2) and the measurements taken using their method where: DHW = diameter of first half protoconch whorl; PD = diameter of protoconch; PW = number of protoconch whorls; H = height of shell; D = maximum diameter; SH = height of spire; AH = height of aperture; AW = width of aperture; UW = width of umbilicus; WUC = width of the umbilical callus; WAB = width of the abapical sulcus; IS = inner lip slope; SA = spire angle. We have not found it easy to find the protoconch/teleoconch boundary in our material, so we have added a further measurement, which is DFW = diameter first protoconch whorl. The works of these authors have repeatedly shown the importance of the operculum as a specific character. Unfortunately, none of the Assemblage I material has an operculum *in situ*. The subfamily Polinicinae Gray, 1847 used in previous parts of this series was synonymised with Naticinae Guilding, 1834 by Bouchet & Rocroi (2017).

Genus *Cochlis* Röding, 1798

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

1798 *Cochlis* Röding, p. 146.

*Note* – *Cochlis* species, which are plentiful and diverse predators in most European Neogene assemblages (*i.e.*; Pedriali & Robba, 2005; Robba *et al.*, 2016) are remarkably scarce in the Assemblage I deposits. Naticid predation is not uncommon in Assemblage I based on the prevalence of naticid boreholes, but *Euspira* and *Payraudautia* species seem to have been the predominant predatory naticids.

***Cochlis neglecta* (Mayer, 1858)**

Plate 36, fig. 1

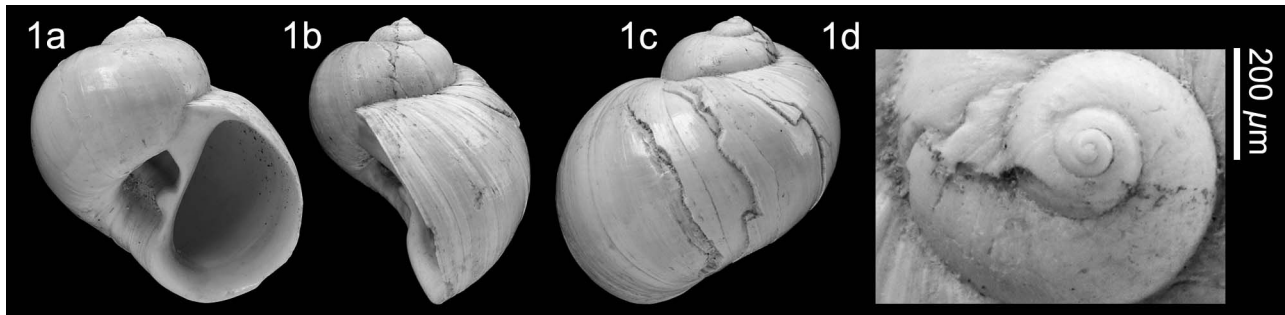
\*1858 *Natica neglecta* Mayer, p. 388, pl. 11, fig. 2.

1964 *Natica neglecta* Mayer, 1858 – Brébion, p. 339.

2016 *Cochlis neglecta* (Mayer, 1858) – Robba *et al.*, p. 131, pl. 2, figs 9-15.

*Material and dimensions* – Maximum height 24.1 mm, width 19.8 mm. **Sceaux-d'Anjou**: RGM.1348174 (50+), RGM.1348205 (18), RGM.1348210 (29), RGM.1348805 (10), RGM.1348902 (13), LC (50+), FVD (50+). **Re-nauleau**: NHMW 2016/0103/1636 (1), NHMW 2016/0103/1637 (20 juveniles).

*Discussion* – *Cochlis neglecta* (Mayer, 1858) is characterised by its multispiral protoconch of 2.5-2.75 whorls with a small nucleus, moderately elevated spire, globose last



**Plate 36.** *Cochlis neglecta* (Mayer, 1858); 1. NHMW 2016/0103/1343, height 24.1 mm, width 19.8 mm; 1d, detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorl, subquadrangular thickened parietal pad, thin to moderately thick funicle and umbilical callus separated from the parietal callus by a deep notch and a poorly differentiated basal fasciole. No colour pattern is preserved, nor enhanced under UV light.

Few adult specimens from Assemblage I are at hand, but they seem identical to the specimen illustrated by Robba *et al.* (2016, pl. 2, fig. 11) from France. The variability in the thickness of the funicle is also seen in the Assemblage I population, and it can be a little thicker than in the specimen illustrated (Pl. 36, fig. 1). The microscopic spiral striation on the last whorl described by these authors (2016, p. 131) is well preserved in the specimen here illustrated. Our only reservation is that in none of the specimens is the protoconch/teleoconch boundary well preserved and the nucleus seems a little larger than that illustrated by Robba *et al.* (2016, pl. 2, figs 12, 14).

Brébion (1964, p. 339) recorded this species from the Assemblage I localities of Thorigné and Sceaux-d'Anjou, to which we add Renauleau. He also recorded it from St-Jean-la-Poterie, which is an Assemblage IV upper Pliocene-Pleistocene locality. This seems unlikely and

we have excluded this reference pending revision.

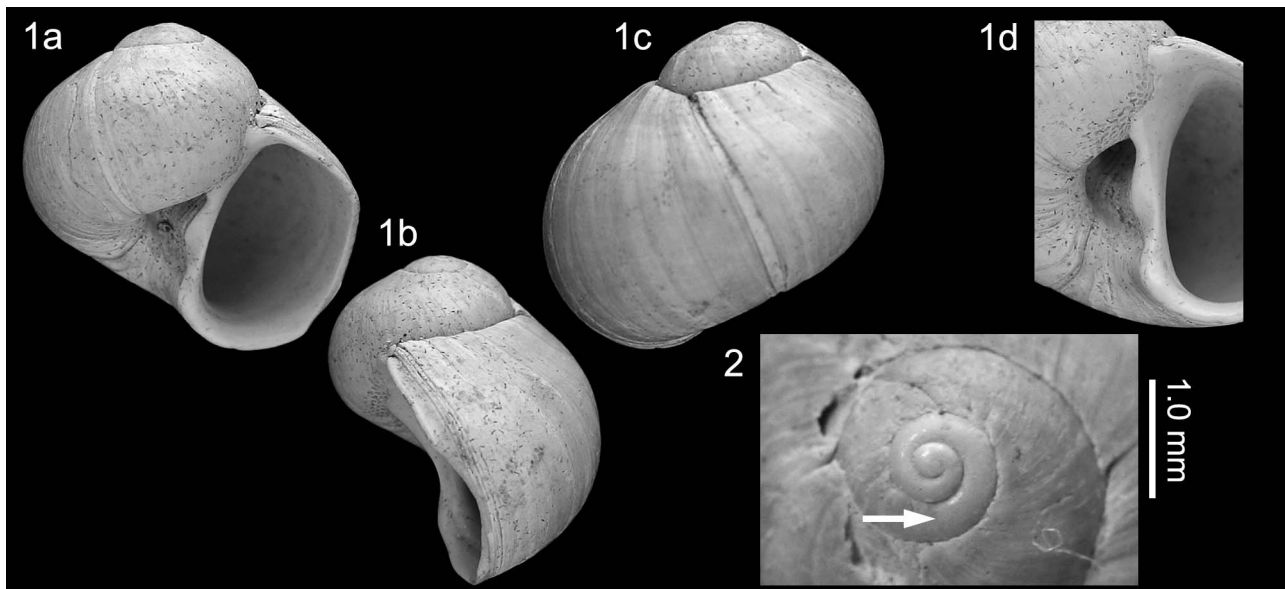
**Distribution** – Lower Miocene: Atlantic (Aquitainian and Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1919; Lozouet *et al.*, 2001); North Sea Basin, Netherlands (Nordsieck, 1972; Janssen, 1984), Belgium (Glibert, 1952b), Germany (von Koenen, 1882). Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1952a); North Sea Basin, Belgium (Glibert, 1952b), Germany (Wienrich, 2001). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964); Proto-Mediterranean, Italy (Robba *et al.*, 2016).

***Cochlis* sp.**

Plate 37, figs 1-2

**Material and dimensions** – Maximum height 12.7 mm, width 13.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1343-1344 (2), NHMW 2016/0103/1345 (1).

**Discussion** – *Cochlis* sp. is characterised by its multispi-



**Plate 37.** *Cochlis* sp.: 1. NHMW 2016/0103/1343, height 12.7 mm, width 13.1 mm; 2. NHMW 2016/0103/1344, height 8.8 mm (juvenile), detail of protoconch. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ral protoconch of 2.25 whorls with a small nucleus, low spire, depressed last whorl, with a broad subsutural ramp, narrow, weakly thickened parietal pad, broad, flattened funicle and umbilical callus separated from the parietal callus by a narrow notch, and a poorly differentiated basal fasciole. Only one adult specimen is at hand, which is small for a *Cochlis* species; the rest are juveniles. The shape of the last whorl, with its low spire and flattened subsutural ramp is reminiscent of some European *Neverita* Risso, 1826 species, but the umbilical characters are those of *Cochlis*. None of the Miocene or Pliocene *Cochlis* species reviewed by Robba *et al.* (2016) and Pedriali & Robba (2005) share this shell shape. We await further specimens to better characterise this species.

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

Genus *Tectonatica* Sacco, 1890

*Type species* (by monotypy) – *Natica tectula* Sacco, 1890, Pliocene, Italy.

1890a *Tectonatica* Sacco, p. 205 (*nomen nudum*).

1890b *Tectonatica* Sacco, p. 33.

***Tectonatica prietoi* (Hidalgo, 1873)**

Plate 38, figs 1-2

?1870 *Natica Prietoi* Hidalgo, pl. 20B, figs 2, 3.

\*1873 *Natica Prietoi* Hidalgo, p. 332.

1980b *Tectonatica astensis* (Sacco, 1891) – Pavia (*partim*), pl. 7, figs 5-7 [*non Tectonatica astensis* (Sacco, 1890)].

1992 *Natica (Tectonatica) tectula* Sacco, 1891, Bonelli m.s. – Cavallo & Repetto, p. 68, fig. 126 operculum [not shell = *Tectonatica tectula* (Sacco, 1890)].

1996 *Natica (Tectonatica) astensis* Sacco, 1891 – Pedriali (*partim*), p. 7, pl. 2, fig. 10 [*non Tectonatica astensis* (Sacco, 1890)].

1996 *Natica (Natica) adansoni* Blainville, 1825 – Gi-

annuzzi-Savelli *et al.*, p. 186, fig. 748, p. 200, fig. 810 (*non de Blainville*, 1825).

1996 *Natica (Natica) prietoi* Hidalgo, 1873 – Giannuzzi-Savelli *et al.*, p. 196, fig. 794.

1998 *Natica prietoi* Hidalgo, 1873 – Gubbioli & Nofroni, p. 21, text-figs 1, 2.

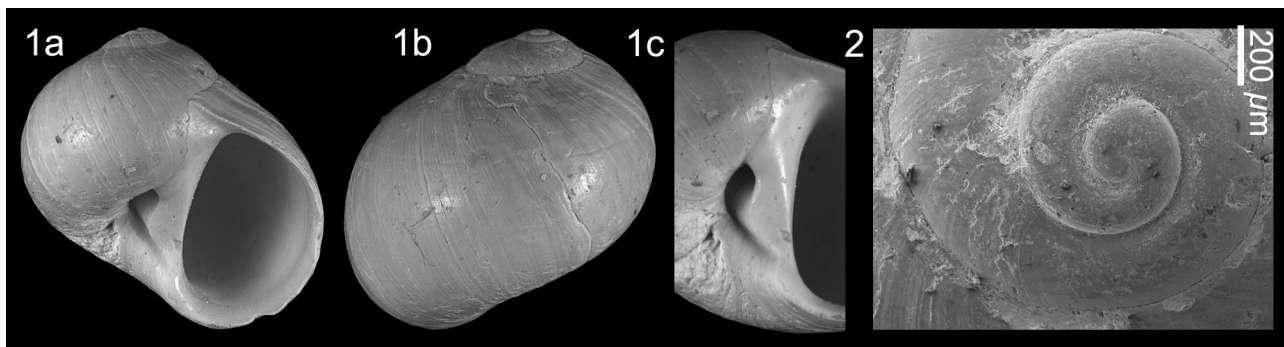
1999 *Tectonatica astensis* (Sacco, 1891) – Forli *et al.*, p. 115, pl. 2, fig. 4 [*non Tectonatica astensis* (Sacco, 1890)].

2008 *Tectonatica prietoi* (Hidalgo, 1873) – Pedriali & Robba, p. 107, pl. 2, figs 3-6, 18, pl. 3, figs 4-6, 18-21.

*Material and dimensions* – Maximum height 9.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0568-0569 (2), NHMW 2016/0103/0570 (50+), RGM.1348216 (50+), RGM.1348225 (50+), RGM.1348853 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0698 (34), RGM.1348201 (50+), RGM.1348206 (50+), RGM.1348211 (46), RGM.1348222 (23), RGM.1348806 (34), RGM.1348899 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1633 (19), RGM.1348997 (12), LC (10), FVD (3). **Beugnon**: RGM.1348463 (31), RGM.1348465 (7), RGM.1348482 (8).

*Discussion* – The specimens here identified as *Tectonatica prietoi* (Hidalgo, 1873) fit well with the description given by Pedriali & Robba (2008, p. 108); a protoconch of 2.5 whorls, the last whorl shows faint spiral sculpture adapically, the umbilicus is relatively wide open, the funicle broad and low, separated from the basal fasciole by a narrow furrow and the umbilicus large and thick, placed on the mid-abapical part of the columellar lip and bounded by a reverse S-shaped outline and merging with parietal callus at the anterior edge. As with many species in the Assemblage I deposits, the maximum height is rather smaller than that of other localities, but within the range given by Pedriali & Robba (6.1-14.2 mm; 2008, p. 110).

*Tectonatica angyglossa* (Cossmann & Peyrot, 1919) from the Burdigalian lower Miocene in the Aquitaine Basin of France is immediately separated by the shape of the funicular and parietal calluses, which are almost continuous and hardly delimited from each other.



**Plate 38.** *Tectonatica prietoi* (Hidalgo, 1873); 1. NHMW 2016/0103/0568, height 8.4 mm, width 6.5 mm; 2. NHMW 2016/0103/0569 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



This is the stratigraphically earliest record for the species, which is not reported in the Miocene of Italy (Robba *et al.*, 2016), and shows the species suffered a southwards range contraction since the late Miocene. For further discussion see Pedriali & Robba (2008).

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Pavia, 1980b; Forli *et al.*, 1999; Pedriali & Robba, 2008). Upper Pliocene: central Mediterranean, Italy (Cavallo & Repetto, 1992; Pedriali & Robba, 2008). Pleistocene: central Mediterranean, Italy (Pedriali & Robba, 2008). Present-day: eastern Atlantic south to Guinea, western Mediterranean (Pedriali & Robba, 2008).

Genus *Euspira* Agassiz in J. Sowerby, 1837

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

1837 *Euspira* Agassiz in J. Sowerby, p. 14.

For generic synonymy see Van Dingenen *et al.* (2016, p. 131).

***Euspira helicina helicina* (Brocchi, 1814)**

Plate 39, figs 1-2

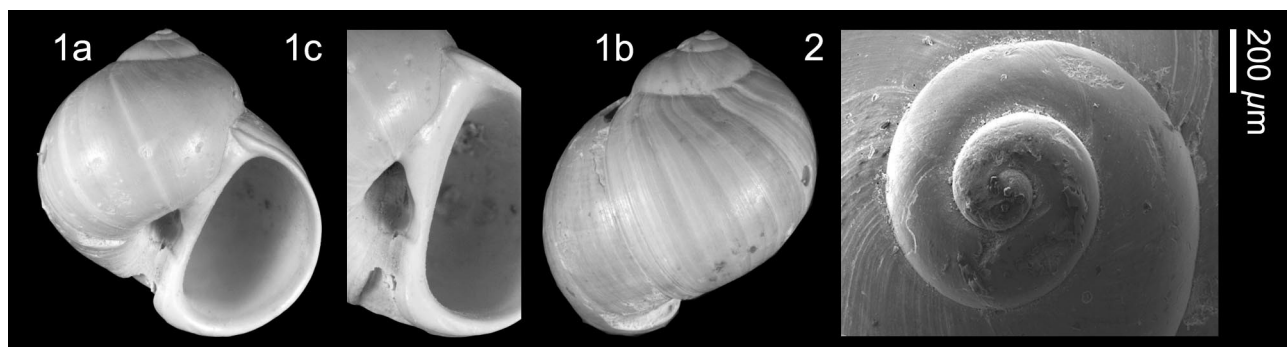
- \*1814 *Nerita helicina* Brocchi, p. 297, pl. 1, fig. 10.
- 1964 *Euspira helicina* (Brocchi, 1814) – Brébion, p. 346 (*partim*).
- 2009 *Euspira helicina helicina* (Brocchi, 1814) – Pedriali & Robba, p. 393, pl. 1, figs. 12, 13, 16-18; pl. 3, fig. 8; pl. 4, fig. 10 (*cum syn.*).
- 2013 *Euspira helicina helicina* (Brocchi, 1814) – Landau *et al.*, p. 103, pl. 11, fig. 9; pl. 12, figs. 1-3; pl. 62, figs. 6, 7 (*cum syn.*).
- 2016 *Euspira helicina helicina* (Brocchi, 1814) – Robba *et al.*, p. 168, pl. 8, figs 8-10.

**Material and dimensions** – Maximum height 10.8 mm.

**St-Clément-de-la-Place:** NHMW 2016/0103/0706-0707 (2), NHMW 2016/0103/0708 (50+), RGM.1348226 (20), RGM.1348212 (3), RGM.1348304 (1), RGM.1348851 (3), LC (30), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0709 (35), RGM.1348203 (32), RGM.1348207 (23), RGM.1348212 (23), RGM.1348221 (4), RGM.1348807 (22), RGM.1348901 (6), LC (15), FVD (23). **Renauleau:** NHMW 2016/0103/1635 (2). **Beugnon:** RGM.1348481 (8), LC (2), FVD (1).

**Discussion** – This species was fully discussed by Pedriali & Robba (2009, p. 393) and Landau *et al.* (2013, p. 103). The Assemblage I specimens are small compared with specimens from other populations [maximum height 26.3 mm, Italian Pliocene (Pedriali & Robba, 2009, p. 398); 32.0 mm middle Miocene Karaman Basin, Turkey (Landau *et al.*, 2013, p. 104)]; the small size of these NW French Tortonian populations is a recurrent theme.

**Distribution** – Lower Miocene: Atlantic (Burdigalian): Aquitaine Basin, France (Pedriali & Robba, 2009; Robba *et al.*, 2016); Proto-Mediterranean (Burdigalian): Colli Torinesi, Italy (Sacco, 1890b, 1904), (late Burdigalian): Antalya Basin, Turkey (İslamoğlu & Taner, 2003). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): ?Belgium (Glibert, 1952b), Germany (Janssen, 1969). Middle Miocene: Atlantic (Langhian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Bosnia (Atanacković, 1985), Bulgaria (Kojumdgieva & Strachimirov, 1960), Poland (Bałuk, 1970); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), Cabela Basin, Portugal (Dollfus *et al.*, 1903); Proto-Mediterranean (Tortonian): Po Basin, Italy (Sacco, 1890b, 1904; Pedriali & Robba, 2009; Robba *et al.*, 2016). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2011); western Mediterranean, Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Pelosio, 1967; Chirli, 2008; Robba *et al.*, 2016), ?Tunisia (Fekih, 1975). Lower-upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Medi-



**Plate 39.** *Euspira helicina helicina* (Brocchi, 1814); 1. NHMW 2016/0103/0706, height 9.0 mm, width 7.1 mm; 2. NHMW 2016/0103/0707 (juvenile), detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

terranean, Estepona Basin, Spain (NHMW collection); central Mediterranean, Italy (Sacco, 1890b, 1904; Palla, 1967; Mastrorilli, 1969; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992; Pedriali, 1996; Lacroce, 1997; Repetto & Lacroce, 2004; Pedriali & Robba, 2009; Sosso & Dell'Angelo, 2010; Robba *et al.*, 2016).

***Euspira varians* (Dujardin, 1837)**

Plate 40, figs 1-2

- \*1837 *Natica varians* Dujardin, p. 281, pl. 19, fig. 6.  
 1964 *Euspira varians* Dujardin, 1837 – Brébion, p. 347.  
 2016 *Euspira varians* (Dujardin, 1837) – Van Dingenen *et al.*, p. 132, pl. 6, fig. 5 (*cum syn.*).

**Material and dimensions** – Maximum height 12.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0511-0512 (2), NHMW 2016/0103/0513 (12), RGM.1348218 (4). **Sceaux-d'Anjou:** RGM.1348213 (1). **Renauleau:** NHMW 2016/0103/1634 (30), RGM.1348996 (33), LC (25), FVD (17).

**Discussion** – Based on the less well-preserved material from the lower-Pliocene Assemblage III locality of Le Pigeon Blanc in which the protoconch/teleoconch boundary is not easily seen, Van Dingenen *et al.* (2016, p. 132) described the protoconch of *Euspira varians* (Dujardin, 1837) as paucispiral with a large nucleus, composed of about 1.25 whorls (PD  $\approx$  500  $\mu$ m, DHW  $\approx$  120  $\mu$ m). The specimen illustrated here from St-Clément-de-la-Place (Pl. 40, fig. 2) is far better preserved and the protoconch/teleoconch boundary is sharp. It confirms the protoconch to be of 1.25 whorls and slightly smaller in dimensions (PD  $\approx$  440  $\mu$ m, DHW  $\approx$  100  $\mu$ m). The first protoconch whorl bears close-spaced spiral cordlets, a microsculpture seen in other *Euspira* species such as *E. pulchella* (Risso, 1826) (Pedriali & Robba, 2009, pl. 4, fig. 16), but this species differs in having a multispiral protoconch of 2.4-2.6 whorls.

*Euspira varians* is closely similar to *E. helicina* (Brocchi, 1814), from which it differs by being thicker-shelled, having a more elevated spire, and having the umbilicus

almost filled by callus (Glibert, 1952a). As noted by Cossman & Peyrot (1919), the shell adjacent to the suture is often eroded, giving the spire an exaggeratedly scalate appearance; this is not so in well-preserved specimens. Furthermore, *E. helicina* has a multispiral protoconch of 2.5-2.75 whorls, whereas *E. varians* has a paucispiral protoconch with a large nucleus.

Brébion (1964, p. 348) recorded this species from Assemblage I (Renauleau, Les Pierres Blanches, Thorigné, Contigné), to which we add St-Clément-de-la-Place, Assemblage III (Le Pigeon Blanc, Palluau, Le Girondor, La Gauvinière, La Dixmerie) and Assemblage IV (St-Jean-la-Poterie). Again, the Assemblage I specimens are small compared with those from other assemblages.

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

Genus *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, 1883

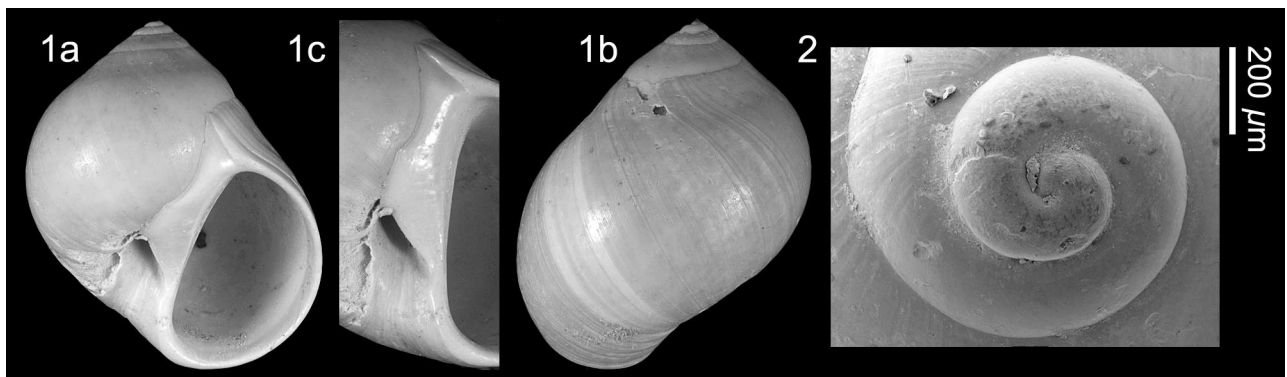
**Type species** (by original designation) – *Nerita intricata* Donovan, 1804, present-day, British Isles.

- 1883 *Payraudeautia* Bucquoy, Dautzenberg & Dollfus, pp. 137, 149.

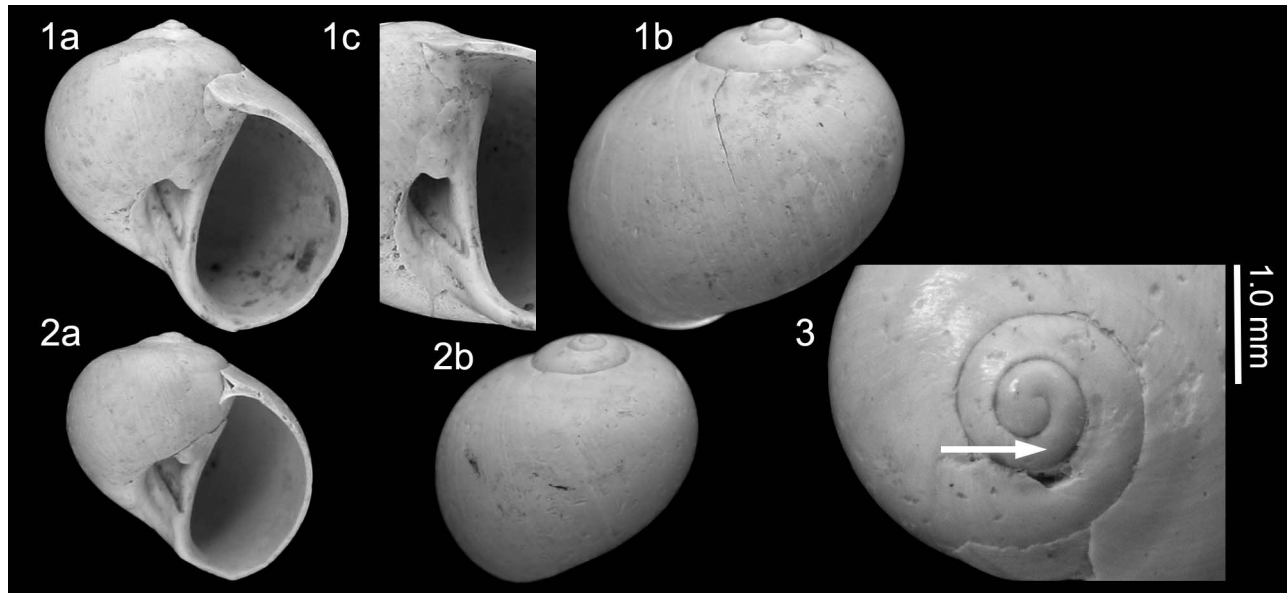
***Payraudeautia obelixi* nov. sp.**

Plate 41, figs 1-3

**Type material** – Holotype NHMW 2016/0103/0704, height 9.5 mm, width 9.5 mm; paratype 1 NHMW 2016/0103/0705, height 7.6 mm, width 7.9 mm; paratype 2 NHMW 2016/0103/1341 (juvenile); paratype 3 RGM.1348220, height 4.4 mm, width 4.7 mm (juvenile); paratype 4 RGM.1348228, height 5.6 mm, width 6.5 mm; paratype 5 RGM.1348229, height 6.7 mm, width 7.5 mm.



**Plate 40.** *Euspira varians* (Dujardin, 1837); 1. NHMW 2016/0103/0511, height 9.1 mm, width 6.5 mm; 2. NHMW 2016/0103/0512 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 41.** *Payraudeautia obelixi* nov. sp.; 1. **Holotype** NHMW 2016/0103/0704, height 9.5 mm, width 9.5 mm; 2. **Paratype 1** NHMW 2016/0103/0705, height 7.6 mm, width 7.9 mm; 3. **Paratype 2** NHMW 2016/0103/1341 (juvenile), detail of protoconch. Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Other material* – Maximum height 2.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1342 (3 juveniles), RGM.1348230 (2), RGM.1348852 (1). **Renauleau:** LC (1).

*Etymology* – Named after the heroic comic character Obelix, created by R. Goscinny and A. Uderzo, the valiant Gaul who resisted Julius Caesar from an unnamed village set not far from the study area. Obelix is a rotund character, reminiscent of the shape of this new species. *Payraudeautia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Payraudeautia* species of medium size, thin-shelled for genus, with paucispiral protoconch, globose, somewhat depressed last whorl, wide umbilicus bearing strong spiral and depressed funicle separated by groove, parietal callus poorly developed in mid-portion, anterior lobe bearing knob that overhangs umbilicus.

*Description* – Shell medium-sized, relatively thin-shelled for genus (for measurements see Table 1). Protoconch paucispiral, composed of 1.5 whorls, with large nucleus. Teleoconch globose, consisting of three whorls with broadly conical, depressed spire. Suture linear, impressed. Last whorl strongly inflated, somewhat depressed, slightly expanded toward aperture; subsutural shelf indistinct; periphery mid-whorl. Aperture D-shaped in slightly prosocline plane, length approximately 1.5 times width. Parietal callus narrowed in mid-portion (or missing), so that anterior and posterior lobes disconnected, with anterior lobe forming a rounded knob overhanging umbilicus. Umbilicus deep, very large; umbilical border narrowly rounded; umbilical wall concave, bearing prominent spiral ridge that overhangs interior of umbilicus and terminates in subtriangular, asymmetric plug on lowermost part of inner lip. Funicle broad and very depressed, separated from inner spiral ridge by groove whose abaxial side ascends to form sharp angle with top of ridge. Umbilical callus moderately thickened, narrow, demarcated from knob of anterior parietal callus by slight transverse groove. Basal fasciole poorly differentiated, rather broad and blunt. Surface with very fine growth lines.

DHW	PD	H	D	SH	AH	AW
270 $\mu$ m	820 $\mu$ m	9.5-7.6 mm	9.5-7.9 mm	2.0-1.2 mm	7.5-6.4 mm	5.4-4.4 mm
270	820	8.6	8.7	1.6	7.0	4.9
UW	WUC	WAD	WAB	IS	SA	DFW
700-550 $\mu$ m	960-940 $\mu$ m	-	280-240 $\mu$ m	21.4-22.5°	125.6-131.6°	545 $\mu$ m
625	950	-	260	22.0	129.1	545

**Table 1.** Dimensions of *Payraudeautia obelixi* nov. sp., measurements based on holotype and paratype, taken following Pedriali & Robba (2005).



*Discussion* – *Payraudeautia obelixa* nov. sp. is quite unlike its living congeners in being thinner-shelled, the globose last whorl is somewhat depressed and the anterior lobe of the parietal callus bears a distinct knob that overhangs the umbilicus. The protoconch/teleoconch boundary is not easily seen when photographed (Pl. 41, fig. 3), but is clearly delimited in the specimens at hand by a change in the shell structure at 1.5 whorls; the protoconch is translucent and highly polished, whereas the teleoconch surface is matt.

It is most similar to *P. biturberculata* Robba, Pedriali & Quagiotto, 2016, also a small species (maximum height 5.8 mm) from the upper Miocene Tortonian of Italy, with which it shares the depressed shape of the last whorl, but the Italian species differs in having a multispiral protoconch and having knobs developed on both the anterior and posterior lobes of the parietal callus.

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

***Payraudeautia pigeonblancensis* Van Dingenen, Ceulemans & Landau, 2016**

Plate 42, figs 1-3

\*2016 *Payraudeautia pigeonblancensis* Van Dingenen, Ceulemans & Landau, p. 133, pl. 12, figs 6, 7.

*Material and dimensions* – Maximum height 6.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0505-0507 (3), NHMW 2016/0103/0508 (27), RGM.1348219 (6), RGM.1348227 (7), FVD (18). **Sceaux-d'Anjou**: RGM.1348204 (12), RGM.1348208 (6), RGM.1348214 (4) RGM.1348223 (3), RGM.1348808 (1), RGM.1348900 (7).

*Discussion* – *Payraudeautia pigeonblancensis* Van Dingenen, Ceulemans & Landau, 2016 is characterised by its small size, its protoconch of 2.6 whorls, teleoconch with a slightly stepped spire, an incised suture, a wide umbilicus, a moderately depressed funicle, a short umbilical callus and a prominent umbilical rib. The protoconch of the Assemblage I specimens is similar in dimensions to

those given in the original description (St-Clément-de-la-Place: DHW = 95  $\mu\text{m}$ , PD = 870; Le Pigeon Blanc: DHW = 85  $\mu\text{m}$ , PD = 1000  $\mu\text{m}$ ).

Two *Payraudeautia* species were recognised by Pedriali & Robba (2009) in the Italian Pliocene: *P. fasciolata* (Sacco, 1890) and *P. intricata* (Donovan, 1804). *Payraudeautia pigeonblancensis* can be separated from *P. intricata* by the character of its multispiral protoconch composed of 2.6 whorls; *P. intricata* has a protoconch of 1.5-1.7 whorls. *Payraudeautia fasciolata* also has a protoconch of 2.6 whorls, but the French fossil species differs in having a slightly stepped spire, an incised suture, a wider umbilicus, a less depressed funicle, a shorter umbilical callus and, above all, the umbilical rib is much more prominent.

Brébion (1964, p. 354) recorded *P. intricata* from the upper Miocene Tortonian Assemblage I locality of Beaulieu. This record probably refers to *Payraudeautia pigeonblancensis*. Here we add the locality of St-Clément-de-la-Place. The species was originally described from the lower Pliocene Assemblage III locality of Le Pigeon Blanc (Van Dingenen *et al.*, 2016, p. 133). The Assemblage I and III populations attain a similar maximum size.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016).

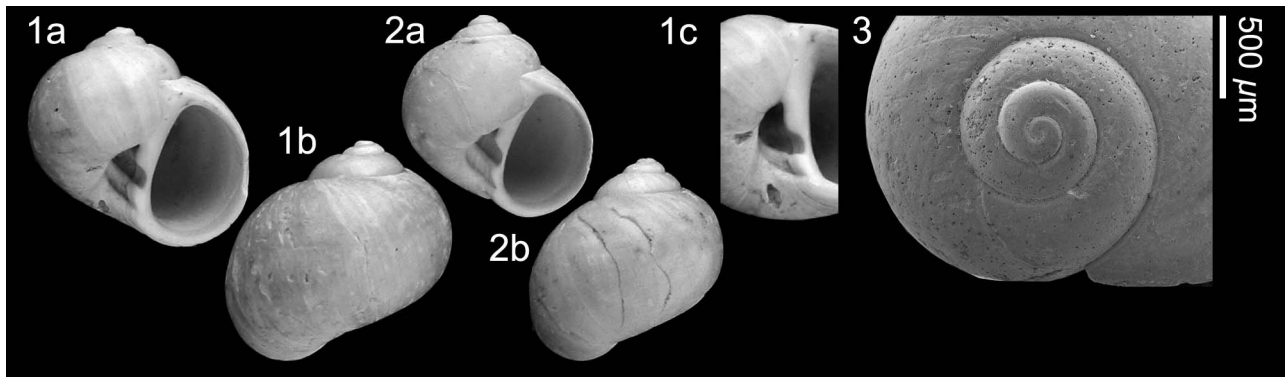
Genus *Polinices* de Montfort, 1810

*Type species* (by original designation) – *Polinices albus* de Montfort, 1810 (= *Nerita mammilla* Linnaeus, 1758), present-day, Indo-Pacific.

1798 *Albula* Röding, 1798, p. 20. Type species (by subsequent designation, Winkworth, 1945): *Nerita mammilla* Linnaeus, 1758, present-day, Indo-Pacific. Junior homonym of *Albula* Osbeck, 1762 [Pisces].

1810 *Polinices* de Montfort, p. 223.

1831 *Eucaryum* Ehrenberg, p. 46. Type species (by mo-



**Plate 42.** *Payraudeautia pigeonblancensis* Van Dingenen, Ceulemans & Landau, 2016; 1. NHMW 2016/0103/0505, height 5.0 mm, width 5.1 mm; 2. NHMW 2016/0103/0506, height 4.5 mm, width 4.5 mm; 3. NHMW 2016/0103/0507, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- notypy): *Nerita mammilla* Linnaeus, 1758, present-day, Indo-Pacific.
- 1834 *Naticina* Guilding, p. 30. Type species (by original designation): *Naticina lactea* Guilding, 1834, present-day, Caribbean.
- 1840 *Naticella* Swainson, 345. Type species (by monotypy): *Albula aurantium* Röding, 1798, present-day, Indo-Pacific.
- 1853 *Uber* Philippi, p. 497. Type species (by original designation): *Nerita mammilla* Linnaeus, 1758, present-day, Indo-Pacific.
- 1853 *Mamma* H. & A. Adams, p. 210. Type species (by subsequent designation, Kobelt, 1878): *Nerita mammilla* Linnaeus, 1758, present-day, Indo-Pacific.

### *Polinices redemptus* (Michelotti, 1847)

Plate 43, figs 1-2

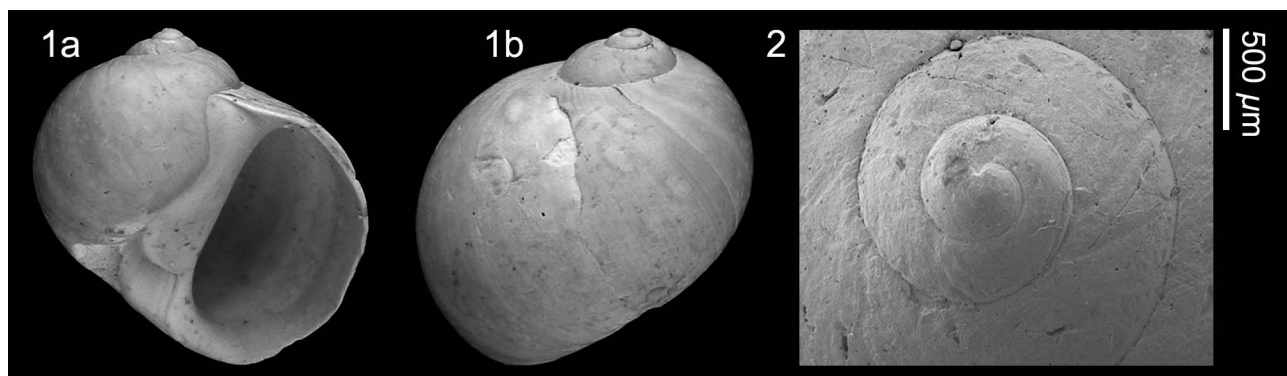
- \*1847 *Natica redempta* Michelotti, p. 157, pl. 6, figs 6, 6'.
- 2013 *Polinices redemptus* (Michelotti, 1847) – Landau *et al.*, p. 105, pl. 11, fig. 7, pl. 79, fig. 7 (*cum syn.*).
- 2016 *Polinices redemptus* (Michelotti, 1847) – Robba *et al.*, p. 199, pl. 13, figs 7-10 (*cum syn.*).

**Material and dimensions** – Maximum height 19.6 mm, width 17.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0514 (1), NHMW 2016/0103/0509 (1), NHMW 2016/0103/0510 (18), FVD (4). **Sceaux-d'Anjou**: RGM.1348200 (21), RGM.1348209 (3), RGM.1348215 (4), RGM.1348224 (4), RGM.1348809 (5), RGM.1348904 (2). **Renauleau**: NHMW 2016/0103/1632 (2). **Beugnon**: RGM.1348480 (1).

**Discussion** – Small shells attributable to the genus *Polinices* occur at St-Clément-de-la-Place, which we interpret as juvenile or dwarfed specimens of *P. redemptus* (Michelotti, 1847). Several slightly larger specimens (maximum height 19.6 mm) were found at Renauleau, but not attaining the relatively large size or solid thickness of specimens from other localities, where they can attain up to

50 mm in height. This species was recently reviewed by Landau *et al.* (2013, p. 105) and Robba *et al.* (2016, p. 199). Landau *et al.* (2013, p. 106) commented that in their material the protoconch boundary was unclear and incorrectly considered the protoconch multispiral, consisting of 2.5-3.0 whorls. Based on better preserved material, Robba *et al.* (2016, p. 200) showed the protoconch to be paucispiral, consisting of 1.75-1.9 whorls (DHW = 271-295  $\mu\text{m}$ , PD = 938-1110  $\mu\text{m}$ ). The French material seems to have the protoconch boundary at 1.7 whorls (Pl. 43, fig. 2; DHW = 270  $\mu\text{m}$ , PD = 950  $\mu\text{m}$ ), the nuclear diameter is within the range of the Italian material, the total protoconch diameter slightly smaller in size and number of whorls. The crescent-shaped colour markings typical for the species (Pl. 43, fig. 1b) are similar to those illustrated for specimens from other localities (i.e. Landau *et al.*, 2013, pl. 11, fig. 7b; Robba *et al.*, 2016, pl. 13, fig. 7b). Robba *et al.* (2016, p. 201) stated that ‘There are no reliable records of this species prior to middle Miocene and subsequent to the early Messinian.’ However, it has been reported from the Paratethyan lower Miocene (Harzhauser, 2002) and the species was illustrated by Landau *et al.* (2011, pl. 6, fig. 5) from the lower Pliocene Atlantic Guadalquivir Basin of southern Spain and it also occurs in the lower-upper Pliocene of the Estepona Basin of Spain. Therefore, the southern Iberian Atlantic and western Mediterranean seems to have acted as a refuge for the species in the Pliocene, although it did not extend its Pliocene range further into the Mediterranean, as it is unknown from the Italian Pliocene.

**Distribution** – Lower Miocene: Paratethys (Burdigalian): Austria, (Harzhauser, 2002); Proto-Mediterranean (Burdigalian): Colli Torinesi (Sacco, 1890b; Ruggieri & Davoli, 1984; Davoli, 1990; Robba *et al.*, 2016). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919; Glibert, 1963), (Langhian): Loire Basin, France (Glibert, 1952a, 1963); Paratethys (Langhian-Serravallian): Poland (Friedberg 1923; Bałuk, 1995), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1962, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz,



**Plate 43.** *Polinices redemptus* (Michelotti, 1847); 1. NHMW 2016/0103/0514, height 8.8 mm, width 9.1 mm; 2. NHMW 2016/0103/0509, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1958; Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (this paper), Cacula Basin, Portugal (Dollfus *et al.*, 1903), southern Spain (Wenz, 1942); Tethys (Tortonian and Messinian): Po Basin, Italy (Sacco, 1890b; Venzo & Pelosio, 1963; Marasti, 1973; Davoli, 1990; Caprotti, 2011; Robba *et al.*, 2016). Lower Pliocene: northeastern Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2011). Upper Pliocene: western Mediterranean, Estepona Basin (NHMW collection).

Superfamily Triphoroidea Gray, 1847  
Family Triphoridae Gray, 1847

*Note* – In triphorids with planktotrophic development (*i.e.* with multispiral protoconchs), recent authors have shown a strong correlation between the protoconch and teleoconch spirals, and therefore protoconch sculpture was considered an important character in the supraspecific classification within the family (*i.e.* Marshall, 1983; Bouchet, 1985). In species with non-planktotrophic development the protoconch is not useful at supraspecific level and can be quite variable intraspecifically (Marshall, 1983). The Triphoridae of the Assemblage I fauna show a remarkable variety in protoconch type, both in multispiral and paucispiral types, much more varied than that seen in the eastern Atlantic and Mediterranean today (Bouchet, 1985). Indeed it is similar in diversity to that seen in the Triphoridae revised by Albano & Bakker (2016) mainly from South and East Africa, the Caribbean (Rolán *et al.*, 2008) and Australia and New Zealand (Marshall, 1983). In triphorids, like in numerous other gastropod groups, planktotrophy is the ancestral condition, and all non-planktotrophic taxa are derived from planktotrophic ancestors or their non-planktotrophic descendents. The majority of species with a planktotrophic protoconch are generally more widely dispersed than their non-planktotrophic descendents. Paucispiral protoconchs are very variable in size, shape and sculpture, and similar forms have evolved repeatedly throughout the world in modern and fossil faunas (Marshall, 1983; Rolán *et al.*, 2008; Albano & Bakker, 2016; Philippe Bouchet and Bruce Marshall personal communication). Therefore, similarity of non-planktotrophic forms rarely implies phylogenetic links. Genetic evidence elucidating triphorid phylogeny is not yet available (Philippe Bouchet pers. comm.). This phenomenon is not restricted to triphorids, but also applies to cerithiopsids (Marshall, 1978). In this paper we have attempted to assign triphorid genera, but most species have been placed *incertae cedis* in *Triphora* Blainville 1828.

Genus *Inella* Bayle, 1879

*Type species* (by typification of replaced name) – *Triphora gigas* Hinds, 1843, present-day, New Guinea.

1844 *Ino* Hinds, p. 17. Type species (by subsequent designation, Gray, 1847b): *Triphora gigas* Hinds,

1843, present-day, New Guinea. Junior homonym of *Ino* Schranck, 1803 [Crustacea].

1879 *Inella* Bayle, p. 35. *Nom. nov. pro Ino* Hinds, 1843, *non* Schranck, 1803 [Crustacea].

1975 *Norephora* Gründel, 1975, p. 155. Type species (by original designation): *Triphora granulata* Strauch, 1967, Oligocene, Germany.

*Note* – The genus is used here to describe species with blunt protoconch of between two and three whorls, bearing two spiral cords per whorl and a teleoconch in which spirals 1-3 develop simultaneously, spiral 1 weaker, usually remaining weaker than spirals 2 and 3 throughout (Marshall, 1983, p. 19). Both Marshall (1983) and Rolán & Fernández-Garcés (2008) commented that the limits of the genus were uncertain.

Species of the *Inella* group have rarely been reported from European fossil assemblages. In the Neogene, Marquet (1996) described an *Inella* species from the upper Pliocene of Belgium and a second species from the lower Pliocene under the genus *Norephora* Gründel, 1975. We consider the differences given by Marquet (1996, p. 141) between *Norephora* and *Inella* insufficient to warrant separation. Lozouet (1999) described an *Inella* species from the upper Oligocene of France.

#### *Inella alia* nov. sp.

Plate 44, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1684, height 6.9 mm, width 1.6 mm, **Sceaux-d'Anjou**. Paratype 1 NHMW 2016/0103/1528, height 6.2 mm, width 1.6 mm; paratype 2 NHMW 2016/0103/1529, height 3.4 mm, width 1.0 mm, **Renauleau**.

*Other material* – Maximum height 5.2 mm. **Renauleau**: NHMW 2016/0103/1530 (4), RGM.1349026 (apical fragment).

*Etymology* – Latin '*alius, alia, aliud*', meaning different, or other, reflecting that this is the only triphorid in the assemblage in which the spirals are not strongly nodular. *Inella* gender feminine.

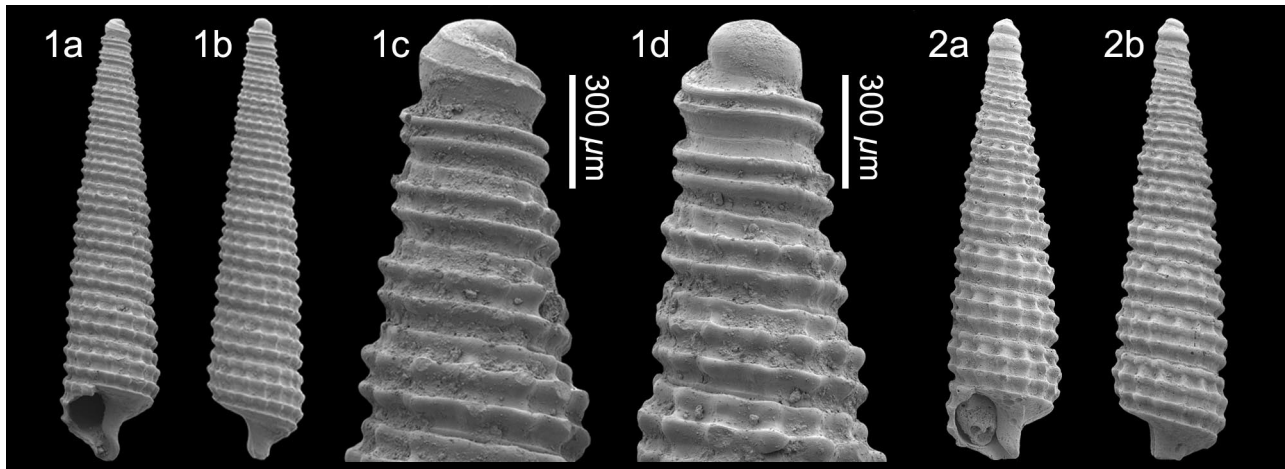
*Locus typicus* – La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Inella* species with protoconch composed of 2.5-3 whorls; Protoconch I bulbous, Protoconch II bearing two strongly elevated spiral cords, teleoconch with three tubercular cords per whorl, all three appear at teleoconch boundary, spiral 1 weaker, strengthening abapically, all cords of equal strength on later whorls, peribasal cord smooth, base smooth.

*Description* – Shell small, slender, elongate, sinistral. Protoconch multispiral, of about 2.5-3 whorls; Proto-





**Plate 44.** *Inella alia* nov. sp.; 1 **Holotype** NHMW 2016/0103/1684, height 6.9 mm, width 1.6 mm, 1c-d, detail of protoconch, La Presselière, Sceaux-d'Anjou. 2. **Paratype 1** NHMW 2016/0103/1528, height 6.2 mm, width 1.6 mm (SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

conch I bulbous, surface bearing some linear and pustular microsculpture, Protoconch II bearing two widely spaced, strongly elevated cords; adapical cord placed mid-whorl, abapical cord just above suture, tops of cords bearing fine spiral threads. Teleoconch of up to 11 flat-sided whorls separated by impressed suture, spirals 1-3 appear simultaneously at protoconch/teleoconch junction, spiral 1 weaker. Axial ribs weak, orthocone, widely spaced, about 14 on penultimate whorl, forming small tubercles at intersections with spiral sculpture. Last whorl bearing three subequal beaded primary spiral cords, smooth peribasal cord, base smooth, without cords. Aperture subquadrate, outer lip thin.

*Discussion* – *Inella alia* nov. sp. shows the characters of the genus; a protoconch with two spiral cords and teleoconch whorls with spiral 1 weaker than spirals 1 and 2. It is distinguished from all other triphorids in the Assemblage I fauna in having fewer and weaker axial ribs that do not form prominent tubercles at the intersections with the spirals and in having a smooth base, devoid of cords. *Inella rolani* nov. sp., with which it co-occurs, is immediately separated by its protoconch with sharper more elevated cords and more tubercular teleoconch sculpture. *Inella cordata* Lozouet, 1999 from the upper Oligocene Atlantic of France has half a protoconch whorls extra (3.5) than *I. alia*, and cords on the base, lacking in *I. alia*.

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

***Inella rolani* nov. sp.**

Plate 45, fig. 1

*Type material* – Holotype MNHN.F.A57727, height 7.7 mm, width 1.6 mm; paratype 1 MNHN.F.A57728, height 2.7 mm, width 1.2 mm (incomplete); paratype 2 NHMW 2016/0103/0529, height 8.8 mm, width 1.8 mm; paratype

2 NHMW 2016/0103/0530, height 5.8 mm, width 1.4 mm; paratype 3 RGM.1348322, height 3.8 mm.

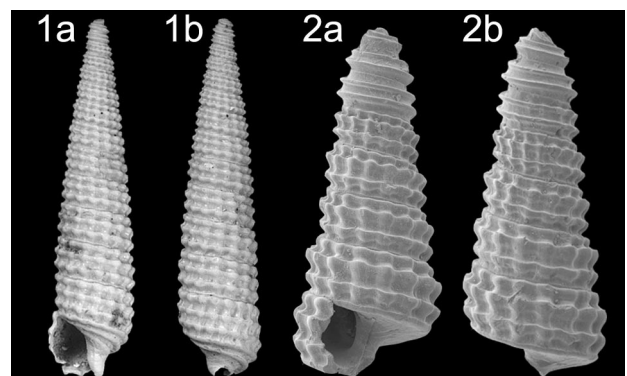
*Other material* – Maximum height 5.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0531 (5), RGM.1348710 (1 fragment).

*Etymology* – Named after Emilio Rolán of the Museo de Historia Natural de Santiago de Compostela, Spain, in recognition of his enormous contribution to gastropod systematics. *Inella* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Inella* species with multispiral protoconch bearing two strongly elevated spiral cords per whorl, three spiral cords on teleoconch whorls, spirals 2 and



**Plate 45.** *Inella rolani* nov. sp.; 1. **Holotype** MNHN.F.A57727, height 7.7 mm, width 1.6 mm; 2. **Paratype 1** MNHN.F.A57728, height 2.7 mm; width 1.2 mm (incomplete) (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

3 continuous from the two protoconch spirals, spiral 1 weaker until last two whorls, three smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral. Protoconch multispiral, two whorls preserved, bearing to two smooth, elevated spiral cords per whorl placed just above and below mid-whorl. Junction with teleoconch not sharply delimited. Teleoconch of up to 11 weakly convex to flat-sided whorls separated by impressed suture, bearing three tubercular spiral cords. Spirals 2 and 3 continue from protoconch spirals, spiral 1 weaker, appearing on first teleoconch whorl just below suture, strengthening abapically, equal in strength to spirals 2 and 3 on last two whorls. Axial ribs weak, about 14 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, three smooth cords over base. Aperture subquadrate, outer lip thin, with damaged edge.

*Discussion* – *Inella rolani* nov. sp. is most similar to *Inella pliocenica* (Marquet, 1996) from the lower Pliocene Kattendijk Formation of Belgium. Although the protoconch is incomplete in the French material at hand, it seems to have at least half a whorl more than the Belgian species and although they both bear two elevated cords, the cords are placed above and below mid-whorl in *I. rolani*, whereas in *I. pliocenica* the adapical cord is placed mid-whorl, the abapical cord just above the suture. Furthermore, the teleoconch cords in *I. pliocenica* have more crowded rounded tubercles on the spiral cords and the base bears only two smooth cords. *Inella vandermarki* Marquet, 1996 from the upper Pliocene North Sea Basin is immediately separated by having a smooth multispiral protoconch and very weak or absent axial sculpture. *Inella alia* nov. sp., also from Assemblage I (see above), is separated by its weaker protoconch cords, less strongly tuberculose spirals and smooth base. *Inella cordata* Lozouet, 1999 from the upper Oligocene Atlantic of France has more numerous protoconch whorls (3.5) than *I. rolani*.

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

Genus *Monophorus* Granata Grillo, 1877

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

1877 *Monophorus* Granata Grillo, p. 15.

1884 *Biforina* Bucquoy, Dautzenberg & Dollfus, pp. 197, 209. Type species (by monotypy): *Trochus perversus* Linnaeus, 1758, present-day, Mediterranean. Junior objective synonym of *Monophorus* Granata Grillo, 1877.

1926 *Notosinister* Finlay, pp. 384, 386. Type species (by original designation): *Triphora fascelina* Suter, 1908, present-day, New Zealand.

***Monophorus renauleauensis* nov. sp.**

Plate 46, fig. 1

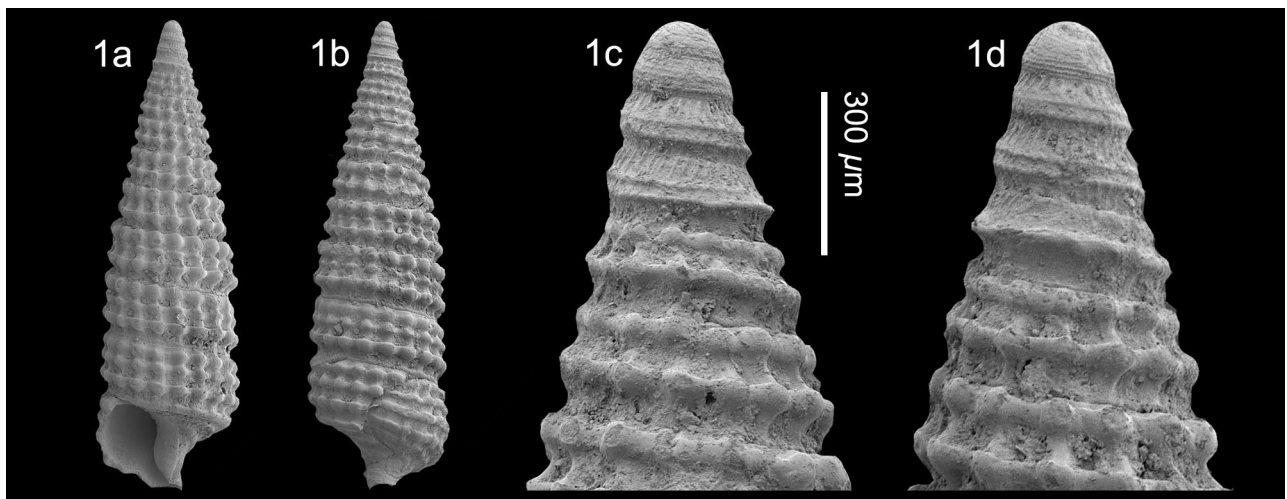
*Type material* – Holotype NHMW 2016/0103/1516, height 6.6 mm, width 1.5 mm; paratype 1 MNHN.F.A57946, height 4.0 mm, width 1.0 mm; paratype 2 NHMW 2016/0103/1517, height 5.7 mm, width 1.4 mm; paratype 3 NHMW 2016/0103/1518, height 7.9 mm, width 1.9 mm.

*Other material* – Maximum height 9.7 mm. **Renauleau:** NHMW 2016/0103/1519 (36), FVD (15), LC (17). **Sceaux-d'Anjou:** NHMW 2016/0103/1534 (3).

*Etymology* – Named after the type locality of Renauleau. *Monophorus* gender masculine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.



**Plate 46.** *Monophorus renauleauensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1516, height 6.6 mm, width 1.5 mm; 1c-d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Diagnosis** – *Monophorus* species with protoconch of four whorls; first whorl with crowded small rows of cruciform pustules, from second whorl bearing two mid-whorl cords, axial riblets above and below cords, but not in interspace between cords, teleoconch with two tubercular cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 from sixth teleoconch whorl, smooth to subobsoletely-beaded peribasal cord, two further smooth cords on base.

**Description** – Shell small, slender, elongate, sinistral. Protoconch multispiral, consisting of four whorls; first whorl bearing crowded rows of small cruciform pustules; second and third whorls bearing two cords placed either side of mid-whorl and axial ribs above and below the two cords, but not in interval between cords. Teleoconch of up to 15 flat-sided whorls separated by impressed suture, first six whorls bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 slightly weaker than 3; spiral 2 weak, delayed, appearing between spirals 1 and 3 on sixth teleoconch whorl. Axial ribs weak, orthocone, about 16 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords of roughly equal strength, smooth to subobsoletely-beaded peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin.

**Discussion** – This species fits well in the genus *Monophorus* Granata Grillo, 1877, characterised by having a multispiral protoconch in which the first whorl bears cruciform tubercles, later whorls bear spiral cords and axial riblets and three tubercular spirals on the teleoconch, of which spiral 2 is delayed (Marshall, 1983, p. 26). The type species, *M. perversus* Linnaeus, 1758, found today in the whole Mediterranean and Atlantic from north-western Spain to Angola, differs in having quite variable protoconch sculpture in which at least some surface of the protoconch above the adapical cord is smooth and the axial riblets are often interrupted (see Bouchet, 1985, figs 20-21). On the teleoconch spiral 2 appears slightly later,

on the seventh whorl. The present-day Mediterranean *M. thiriota* Bouchet, 1985 differs in having sculpture of regular ribs and cords on the later protoconch whorls that form a strong and evenly reticulated pattern. On the teleoconch, spiral two is delayed and appears on the eighth whorl.

Another extant eastern Atlantic and Mediterranean species; *M. erythrosoma* (Bouchet & Guillemot, 1978) has strong protoconch sculpture like *M. thiriota*, but the riblets are interrupted and spiral 2 on the teleoconch is even more delayed, appearing only on the tenth or eleventh whorl. *Monophorus pantherinus* Rolán & Peñas, 2001 from the Canary Islands has a strongly and evenly sculptured protoconch, like *M. thiriota*, but spiral 2 is more delayed, appearing on the ninth whorl. *Monophorus alboranensis* Rolán & Peñas, 2001 from the Alboran Sea has a similar protoconch, but spiral 2 is less delayed, appearing on the sixth teleoconch whorl. The differences between these *Monophorus* species are summarised in Table 2.

The lower Miocene Atlantic Aquitanian *Triphora papaveracea* (Benoist, 1874) might also be a *Monophorus* species, although in the small area of early protoconch whorl in which the pustules are preserved in the specimen figured by Lozouet *et al.* (2001, pl. 21, fig. 2) the micro-pustules are very small and do not seem to be cruciform. The later teleoconch whorls have the two mid-whorl cords wider spaced than in *M. renauleauensis* nov. sp., the riblets are stronger and continuous in the interspace between the cords, forming a more prominent reticulated pattern. Like in *M. renauleauensis*, spiral 2 appears on the sixth teleoconch whorl (Lozouet *et al.*, 2001, pl. 20, fig. 4). *Triphora nodosoplicata* (Benoist, 1874), also from the French Atlantic Aquitanian lower Miocene has similar protoconch sculpture to *T. papaveracea*, but the two spiral cords mid-whorl on the protoconch are closer set than in *T. papaveracea*, but not as close set as in *M. renauleauensis*, and the ribs are present in the interspaces between these ribs, absent in *M. renauleauensis*. Spiral 2 also appears on the sixth teleoconch whorl. The surface of the early protoconch whorls is worn in the specimen illustrated by Lozouet *et al.* (2001, pl. 21, fig. 3), so we

species	later protoconch whorls	spiral 2 on teleoconch
<i>Monophorus renauleauensis</i> nov. sp.	axial riblets above and below mid-whorl cords, not between; cords very closely spaced	appears 6 <sup>th</sup> whorl
<i>M. perversus</i> (Linnaeus, 1758)	interrupted weak sculpture, with smooth parts	appears 7 <sup>th</sup> whorl
<i>M. thiriota</i> Bouchet, 1985	strong uninterrupted reticulated pattern	appears 8 <sup>th</sup> whorl
<i>M. erythrosoma</i> (Bouchet & Guillemot, 1978)	strong interrupted reticulated pattern	appears 10-11 <sup>th</sup> whorl
<i>M. pantherinus</i> Rolán & Peñas, 2001	strong uninterrupted reticulated pattern	appears 9 <sup>th</sup> whorl
<i>M. alboranensis</i> Rolán & Peñas, 2001	strong uninterrupted reticulated pattern	appears 6 <sup>th</sup> whorl
<i>Triphora papaveracea</i> (Benoist, 1874)	strong uninterrupted reticulated pattern; cords widely spaced	appears 6 <sup>th</sup> whorl
<i>Triphora nodosoplicata</i> (Benoist, 1874)	strong uninterrupted reticulated pattern; cords relatively closely spaced	appears 6 <sup>th</sup> whorl

**Table 2.** Comparison of most important diagnostic protoconch and teleoconch characters in European *Monophorus* and *Triphora* species.



cannot comment on its sculpture.

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

Genus *Obesula* Jousseau, 1897

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

1897 *Obesula* Jousseau, p. 75.

***Obesula marshalli* nov. sp.**

Plate 47, figs 1-2

*Type material* – Holotype MNHM.F.A66692, height 3.8 mm, width 1.1 mm; paratype 1 MNHM.F.A66693, height 3.6 mm, width 1.1 mm; paratype 2 NHMW 2016/0103/1520, height 4.2 mm, width 1.2 mm; paratype 3 NHMW 2016/0103/1521, height 4.0 mm, width 1.1 mm, **Renauleau**. Paratype 4 RGM.1348466, height 8.5 mm, width 1.9 mm; paratype 5 RGM.1348467, height 6.2 mm, width 1.4 mm, **Beugnon**.

*Other material* – Maximum height 5.6 mm. **St-Clément-de-la-Place**: RGM.1347965 (1). **Renauleau**: NHMW 2016/0103/1522 (50+), RGM.1349027 (10), FVD (50+), LC (50+). **Beugnon**: RGM.1348468 (10 fragments).

*Etymology* – Named after Bruce A. Marshall of the National Museum of New Zealand, Wellington, in recognition of his enormous contribution to triphorid taxonomy. *Obesula* gender feminine.

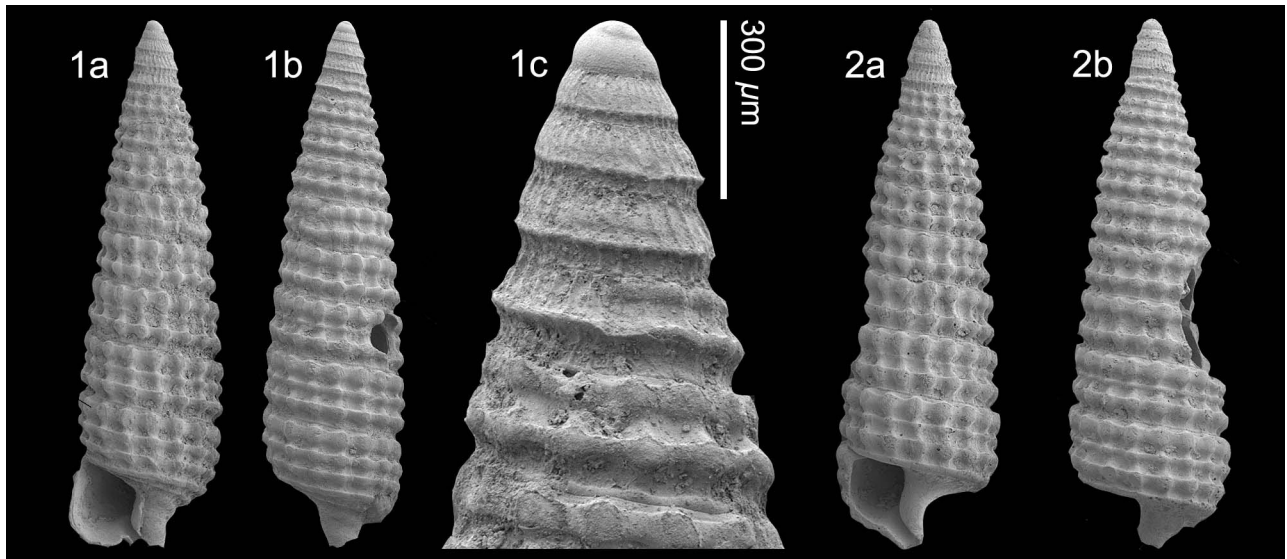
*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Obesula* species with multispiral protoconch of five whorls; first whorl bearing crowded rows of micropustules; from second whorl bearing single cord placed below mid-whorl and continuous axial ribs, teleoconch with two tubercular cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 from sixth or seventh teleoconch whorl, smooth peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral. Protoconch multispiral, consisting of five whorls; first whorl bearing crowded rows of micropustules; from second whorl bearing single cord placed below mid-whorl and continuous axial ribs which cross, but do not strengthen over cord. Teleoconch of up to eight flat-sided whorls separated by impressed suture, first six whorls bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 slightly weaker than 3; spiral 2 weak, only appearing between spirals 1 and 3 on sixth or seventh teleoconch whorl. Axial ribs weak, orthocline, about 16 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, spiral 2 weaker, smooth peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin.

*Discussion* – This species fits well in the genus *Obesula* Jousseau, 1897, characterised by having a multispiral protoconch with one spiral thread and uninterrupted axial riblets, and three tubercular spirals on the teleoconch, of which spiral 2 is delayed (Marshall, 1983, p. 69). Only one species is known from the present-day European fauna; *Obesula marisnostris* Bouchet, 1985 from the Mediterranean differs in having 2 spiral cords on the second



**Plate 47.** *Obesula marshalli* nov. sp.; 1. **Holotype** MNHM.F.A66692, height 3.8 mm, width 1.1 mm; 1c, detail of protoconch (SEM image); 2. **Paratype 1** MNHM.F.A66693, height 3.6 mm, width 1.1 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

species	protoconch whorls	Spiral 2 on teleoconch
<i>Obesula marshalli</i> nov. sp.	multispiral; all whorls 1 cord	appears 6 <sup>th</sup> -7 <sup>th</sup> whorl
<i>O. marisnostris</i> Bouchet, 1985	multispiral; second whorl 2 cords, later whorls 1 cord	appears 5 <sup>th</sup> whorl
<i>O. protopaucispirata</i> Landau, La Perna and Marquet, 2006	paucispiral	appears 3 <sup>rd</sup> whorl
<i>O. scaldensis</i> Marquet, 1996	paucispiral	appears 4-6 <sup>th</sup> whorl

**Table 3.** Comparison of most important diagnostic protoconch and teleoconch characters in European *Obesula* species.

protoconch whorl and spiral 2 on the teleoconch is less delayed, appearing on the fifth whorl. Landau *et al.* (2006) described a species from the upper Pliocene of southern Spain; *O. protopaucispirata* Landau, La Perna and Marquet, 2006, which differs in having a smooth paucispiral protoconch, with spiral 2 appearing on the third teleoconch whorl. *Obesula scaldensis* Marquet, 1996 from the upper Pliocene North Sea Basin of Belgium is another species with a paucispiral protoconch in which spiral 2 appears between the fourth and sixth whorls. These last two species both differ from *Obesula marshalli* nov. sp. in having a paucispiral protoconch. The differences between these *Obesula* species are summarised in Table 3. We note that Marshall also described an *Obesula* species with a paucispiral protoconch (*O. profundior* Marshall, 1983, p. 71, figs 30A-D).

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

Genus *Triphora* de Blainville, 1828

*Type species* (by monotypy) – *Triphora gemmata* de Blainville, 1828, present-day, Mauritius.

1828 *Triphora* de Blainville, p. 344.

*Note* – As discussed above, we do not offer a generic synonymy for *Triphora* de Blainville, 1828, as we use it in a broad sense until molecular data reveals phylogenetic relationships within the group.

***Triphora buscheri* nov. sp.**

Plate 48, fig. 1

*Type material* – Holotype NHMW 2016/0103/1509, height 6.6 mm, width 1.5 mm.

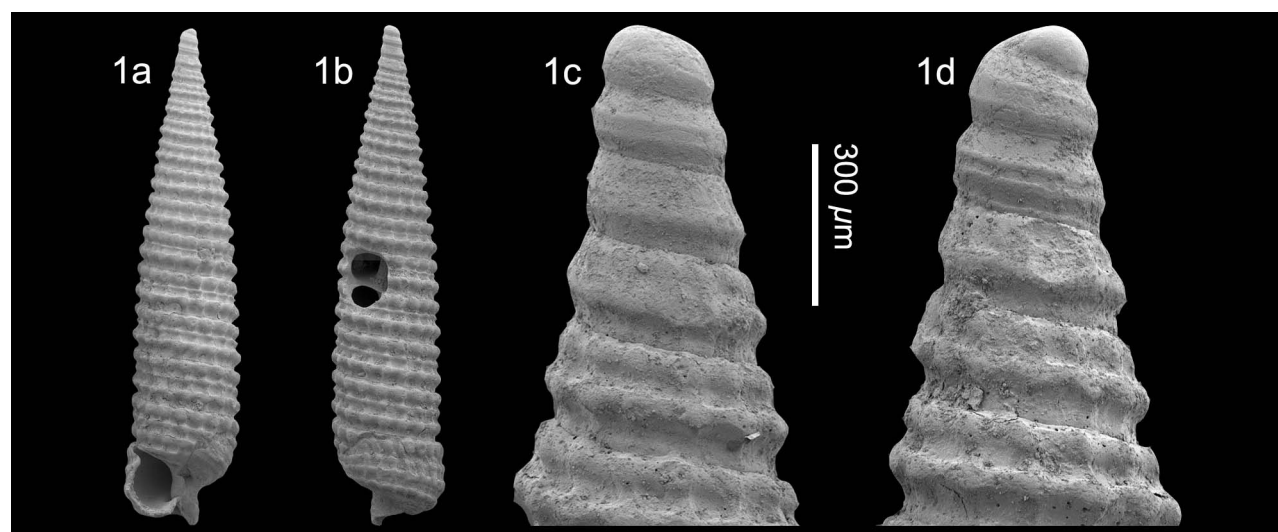
*Other material* – Maximum height 5.0 mm (incomplete). **St-Clément-de-la-Place:** NHMW 2016/0103/1532 (3 fragments), LC (1).

*Etymology* – Named after Dr H.N. Büscher, Belgian gastroenterologist and researcher in European Clausiliidae. *Triphora* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Triphora* species with protoconch of 3.5 whorls; from second whorl bearing two mid-whorl cords



**Plate 48.** *Triphora buscheri* nov. sp.; 1. **Holotype** NHMW 2016/0103/1509, height 6.6 mm, width 1.5 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

and third cord just above suture, surface micropustular, teleoconch with two tubercular cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 from seventh teleoconch whorl, prominent subobsoletely-beaded peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral. Protoconch multispiral, consisting of 3.5 whorls; first whorl elevated, bulbous, later whorls bearing two cords placed either side of mid-whorl and one weaker cord just above suture; surface finely pustular. Teleoconch of 12 flat-sided whorls separated by impressed suture, first six whorls bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 slightly weaker than 3; spiral 2 weak, only appearing between spirals 1 and 3 on seventh teleoconch whorl. Axial ribs weak, orthocone, about 16 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, spiral 2 weaker, subobsoletely-beaded peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin.

*Discussion* – *Triphora buscheri* nov. sp. is characterised by its multispiral protoconch bearing two cords mid-whorl and a further cord above the suture, covered in micropustules and its teleoconch sculpture of two strongly tuberculate spiral cords, with spiral 2 delayed, appearing from the seventh teleoconch whorl, strengthening abapically, but never equalling spirals 1 and 3. This type of protoconch has not been reported from any Neogene or present-day European species. Rolán & Fernández-Garcés (2008) described several present-day Caribbean triphorids with this sort of protoconch like *Inella pseudolongissima* Rolán & Fernández-Garcés, 2008 and *I. apexbilirata* Rolán & Fernández-Garcés, 2008. We have not placed this species in the genus *Inella* Bayle, 1879 as the order of appearance of the teleoconch spirals is not that of the genus, in which spirals 1-3 develop simultaneously,

spiral 1 weaker, usually remaining weaker than spirals 2 and 3 throughout.

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

***Triphora chauvereauensis* nov. sp.**

Plate 49, fig. 1

*Type material* – Holotype NHMW 2016/0103/1511, height 6.2 mm, width 1.5 mm.

*Other material* – Known only from holotype.

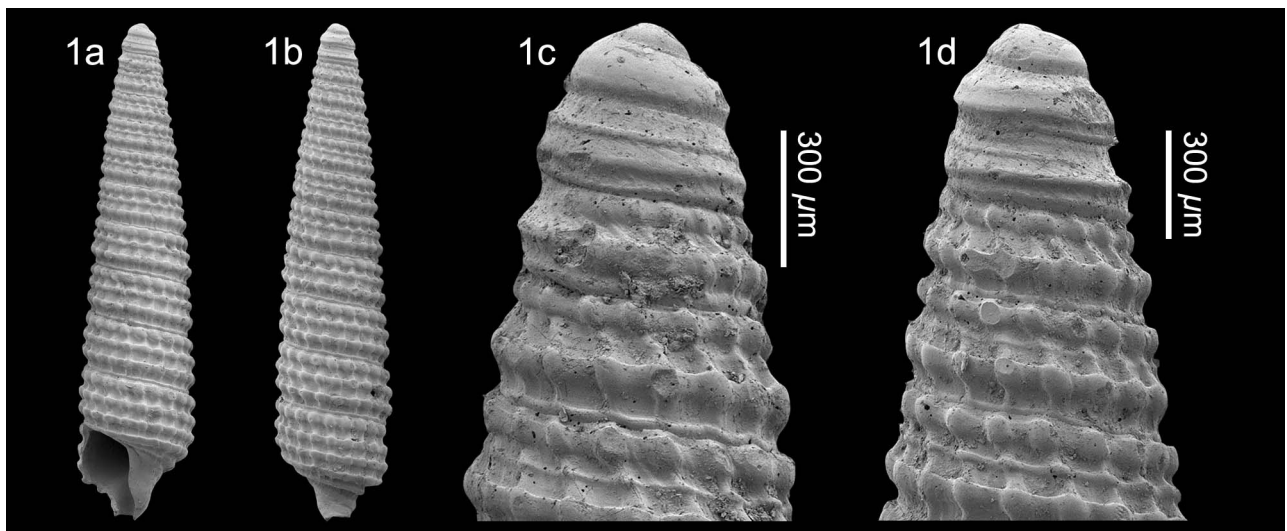
*Etymology* – Named after the farm of Le Grand Chauvereau, where the type locality is found. *Triphora* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Triphora* species with protoconch of 3.5 whorls bearing three spiral cords, mid-whorl cord strongest, teleoconch with two tubercular cords on first whorl, with spiral 2 appearing between spirals 1 and 3 from second teleoconch whorl, prominent subobsoletely-beaded peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral. Protoconch dome-shaped, multispiral, composed of 3.5 whorls, bearing three spiral cords, middle cord strongest; surface smooth. Teleoconch of ten flat-sided whorls separated by impressed suture, first whorl bearing two tubercular spiral cords and single fine suprasutural thread. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 slightly weaker than 3; spi-



**Plate 49.** *Triphora chauvereauensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1511, height 6.2 mm, width 1.5 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



species	protoconch	Spiral 2 on teleoconch
<i>Triphora buscheri</i> nov. sp.	3.5 whorls; two mid-whorl spirals and third just above suture	appears 7 <sup>th</sup> whorl
<i>T. chauvereauiensis</i> nov. sp.	3 whorls; 3 spirals, mid-whorl strongest	appears 2 <sup>nd</sup> whorl
<i>T. fernandezgarcesi</i> nov. sp.	3 whorls; 3 spiral, 2 placed abapically	appears 4 <sup>th</sup> whorl
<i>T. lherbetteorum</i> nov. sp.	2 whorls; 1 <sup>st</sup> bulbous, 2 <sup>nd</sup> strongly carinate mid-whorl	last whorl
<i>T. miopygmaea</i> nov. sp.	2 whorls; 1 <sup>st</sup> whorl large, 2 <sup>nd</sup> carinate mid-whorl	appears 4 <sup>th</sup> whorl
<i>T. sancticlementensis</i> nov. sp.	2.5 whorls; 1 <sup>st</sup> bulbous, 2 <sup>nd</sup> bearing 2 cords mid-whorl, riblets above and below	appears 4 <sup>th</sup> or 5 <sup>th</sup> whorl

**Table 4.** Comparison of most important diagnostic protoconch and teleoconch characters in Assemblage I *Triphora* species.

ral 2 appears between spirals 1 and 3 on second teleoconch, strengthening abapically, so that on later whorls spiral 1 is slightly stronger than spirals 2 and 3, which are of equal strength. Axial ribs weak, orthocline, about 20 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, spiral 1 strongest, weakly beaded peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin.

**Discussion** – *Triphora chauvereauiensis* nov. sp. is characterised by its multispiral protoconch, bearing three spiral cords, mid-cord strongest, a teleoconch with two tubercular cords on the first whorl, spiral 2 only slightly delayed, appearing between spirals 1 and 3 from the second teleoconch whorl. *Triphora chauvereauiensis*, like *T. buscheri* nov. sp., *T. fernandezgarcesi* nov. sp. and *T. lherbetteorum* nov. sp. has a protoconch with spiral sculpture, but it is dome shaped, whereas in the other three species the first protoconch whorl is bulbous or elevated. It also differs in having spiral 2 less delayed, appearing on the second teleoconch whorl. (seventh in *T. buscheri* nov. sp.; fourth in *T. fernandezgarcesi* nov. sp.; last whorl in *T. lherbetteorum*; see Table 4).

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

***Triphora fernandezgarcesi* nov. sp.**

Plate 50, fig. 1

**Type material** – Holotype NHMW 2016/0103/1510, height 5.0 mm, width 1.5 mm.

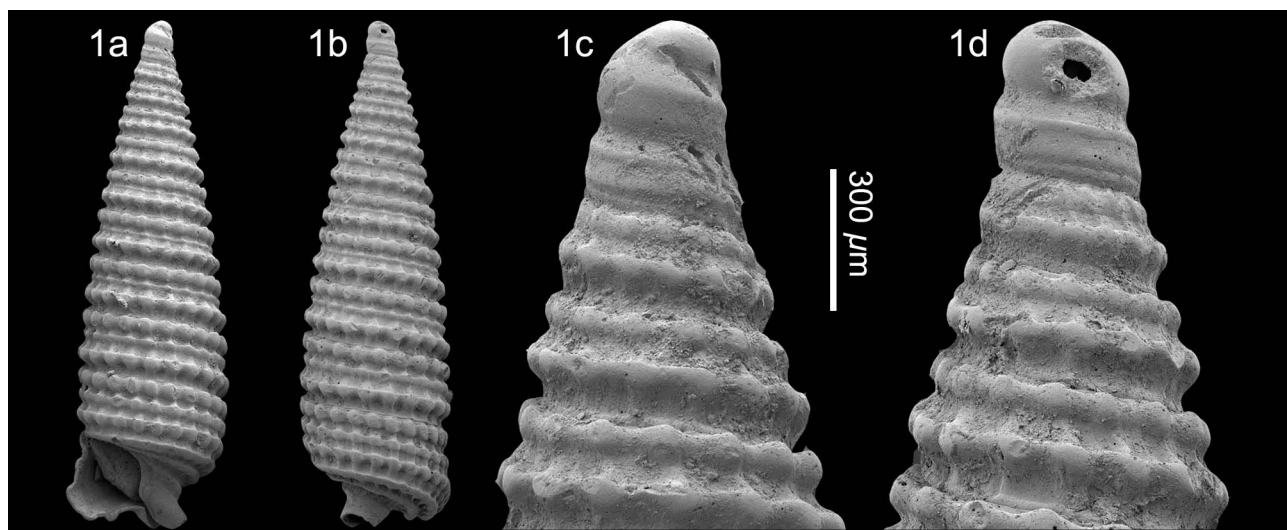
**Other material** – Known only from holotype.

**Etymology** – Named after the Dr Raúl Fernández-Garcés of the Centro de Estudios Ambientales de Cienfuegos (CEAC), Cuba, in recognition of his contributions on triphorid systematics. *Triphora* gender feminine.

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

**Stratum typicum** – Tortonian, upper Miocene.

**Diagnosis** – *Triphora* species with protoconch of three whorls; first whorl bulbous, later whorls bearing two widely spaced cords placed some distance from mid-



**Plate 50.** *Triphora fernandezgarcesi* nov. sp.; 1. **Holotype** NHMW 2016/0103/1510, height 5.0 mm, width 1.5 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorl and one weaker cord just above suture running close to lower of two primary cords, surface micropustular, teleoconch with two tubercular spiral cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 from fourth teleoconch whorl, smooth peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral. Protoconch multispiral, of three whorls; first whorl bulbous, later whorls bearing two widely spaced cords placed some distance from mid-whorl and one weaker cord just above suture running close to lower of two primary cords; surface abraded. Teleoconch of ten flat-sided whorls separated by impressed suture, first four whorls bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 slightly weaker than 3; spiral 2 weak, only appearing between spirals 1 and 3 on fifth teleoconch whorl. Axial ribs weak, orthocone, about 19 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing three beaded primary spiral cords, spiral 2 weaker, smooth peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin.

*Discussion* – *Triphora fernandezgarcesi* nov. sp. is characterised by its multispiral protoconch bearing two widely spaced cords mid-whorl and a further cord above the suture, and its teleoconch sculpture of two strongly tuberculate spiral cords, with spiral 2 appearing late, from the fifth teleoconch whorl, strengthening abapically, but never equalling spirals 1 and 3. It is similar to *Triphora buscheri* nov. sp., but differs in that the mid-whorl cords on the protoconch are more widely spaced, so that in *T. fernandezgarcesi* the third cord above the suture is separated from the lower primary cord by a fine groove and in having spiral 2 less delayed, appearing on the fifth teleoconch whorl as opposed to the seventh as in *T. buscheri* (see Table 4).

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

***Triphora lherbetorum* nov. sp.**

Plate 51, fig. 1

*Type material* – Holotype NHMW 2016/0103/1507, height 4.7 mm, width 1.4 mm; paratype 1 NHMW 2016/0103/1508, height 5.0 mm, width 1.2 mm; paratype 2 NHMW 2016/0103/1527, height 5.2 mm, width 1.3 mm; paratype 3 RGM.1348323, height 5.1 mm; paratype 4 RGM.1348324, height 5.2 mm.

*Other material* – Maximum height 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1531 (5), RGM.1348325 (1 fragment), RGM.1348711 (1).

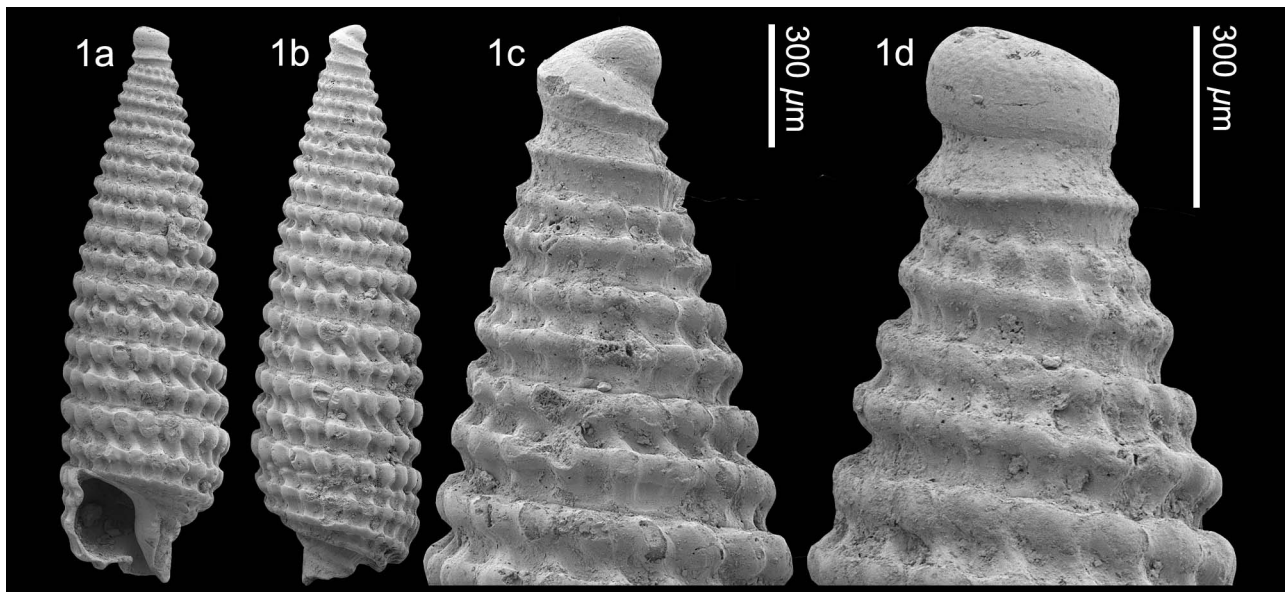
*Etymology* – Named after the Mr and Mrs Lherbette, owners of the farm Le Grand Chauvèreau in recognition of their permission and support during our research. *Triphora* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Triphora* species with protoconch of two whorls; first whorl bulbous, bearing rows of micropustules, second whorl strongly carinate mid-whorl, teleoconch with two tubercular spiral cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 on last half whorl, prominent subobsoletely-beaded peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, elongate, sinistral.



**Plate 51.** *Triphora lherbetorum* nov. sp.: 1. **Holotype** NHMW 2016/0103/1507, height 4.7 mm, width 1.4 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Protoconch of two whorls; first whorl bulbous, bearing rows of micropustules, second whorl strongly carinate mid-whorl. Junction with teleoconch sharply delimited. Teleoconch of up to nine flat-sided whorls separated by impressed suture, bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, of equal strength; spiral 2 weak, only appearing between spirals 1 and 3 on last half whorl. Axial ribs weak, prosocline, about 18 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl bearing two beaded primary spiral cords, peribasal cord, two smooth cords over base. Aperture subquadrate, outer lip thin, with damaged edge.

*Discussion* – *Triphora lherbetorum* nov. sp. is characterised by its protoconch made of two whorls; the first bulbous, covered in micropustules, the second strongly carinate mid-whorl and its teleoconch sculpture of two strongly tuberculate spiral cords, with spiral 2 appearing very late, only on the last half whorl. This type of protoconch has not been reported from any Neogene or present-day European species. For a summary of the key diagnostic shell characters compared with its congeners from Assemblage I, see Table 4.

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

***Triphora miopygmaea* nov. sp.**

Plate 52, figs 1-3

*Type material* – Holotype MNHN.F.A57944, height 2.3 mm, width 0.9 mm; paratype 1 MNHN.F.A57945, height 3.1 mm, width 1.1 mm; paratype 2 NHMW 2016/0103/1512, height 1.6 mm, width 0.8 mm; paratype 3 NHMW 2016/0103/1513, height 2.4 mm, width 0.8 mm; paratype 4 NHMW 2016/0103/1514, height 2.3 mm, width 0.8 mm; paratype 5 RGM.1348712, height 3.0 mm; paratype 6 RGM.1348713, height 2.7 mm.

*Other material* – Maximum height 2.2 mm. **St-Clément-**

**de-la-Place:** NHMW 2016/0103/1515 (11). **Sceaux-d'Anjou:** RGM.1348641 (2 apical fragments).

*Etymology* – Named reflecting the Miocene time in which they occurred and their small size Latin, ‘*Pygmaei*’ a mythical race of pygmies. *Triphora* gender feminine.

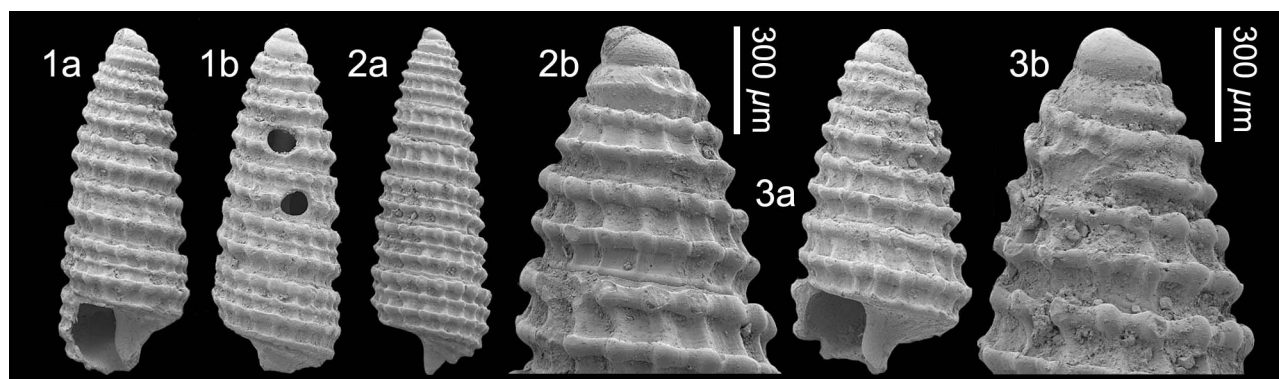
*Locus typicus* – Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Triphora* species with a squat shell, protoconch of two whorls; first whorl large, bearing rows of micropustules, second whorl carinate mid-whorl, teleoconch with two equal tubercular cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 on fourth whorl, prominent subobsoletely-beaded peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, squat, sinistral. Low paucispiral protoconch of two whorls; first whorl large, bearing rows of micropustules, second whorl carinate mid-whorl. Junction with teleoconch sharply delimited. Teleoconch of up to six flat-sided whorls separated by impressed suture, bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, of equal strength; spiral 2 weak, only appearing between spirals 1 and 3 on fourth whorl. Axial ribs weak, orthocline, about 16 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl spirals 1 and 3 beaded, equal in strength, spiral 2 weaker, peribasal cord smooth, two smooth cords over base. Aperture subquadrate, outer lip thin, with damaged edge.

*Discussion* – *Triphora miopygmaea* nov. sp. is characterised by its protoconch made of two whorls; the first bulbous, covered in micropustules, the second carinate mid-whorl and its teleoconch sculpture of two equal tuberculate spiral cords, with spiral 2 delayed, appearing on the fourth teleoconch whorl. This type of protoconch



**Plate 52:** *Triphora miopygmaea* nov. sp.; 1. **Holotype** MNHN.F.A57944, height 2.3 mm, width 0.9 mm; 2. **Paratype 1** MNHN.F.A57945, height 3.1 mm, width 1.1 mm; 2b, detail of protoconch; 2. **Paratype 2** NHMW 2016/0103/1512, height 1.6 mm, width 0.8 mm; 3b, detail of protoconch (all SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



has not been reported from any Neogene or present-day European species, but was reported by Albano & Bakker (2016) in the South African species *T. brevis* Thiele, 1925, which is also remarkably similar in shape, but differs in that spiral 2 is less delayed and becomes as strong as spirals 1 and 3 on later whorls.

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

***Triphora sancticlementensis* nov. sp.**

Plate 53, figs 1-3

*Type material* – Holotype MNHN.F.A66694, height 5.2 mm, width 1.6 mm; paratype 1 NHMW 2016/0103/1523, height 2.9 mm, width 1.0 mm; paratype 2 NHMW 2016/0103/1524, height 3.0 mm, width 1.0 mm; paratype 3 NHMW 2016/0103/1525, height 4.6 mm, width 1.2 mm; paratype 4 RGM.1348715, height 3.8 mm, width 1.2 mm; paratype 5 RGM.1348716, height 2.8 mm, width 0.9 mm.

*Other material* – Maximum height 5.8 mm. **St-Clément-**

**de-la-Place:** NHMW 2016/0103/1526 (15), RGM.1348717 (5), LC (4), FVD (2). **Sceaux-d’Anjou:** NHMW 2016/0103/1533 (2).

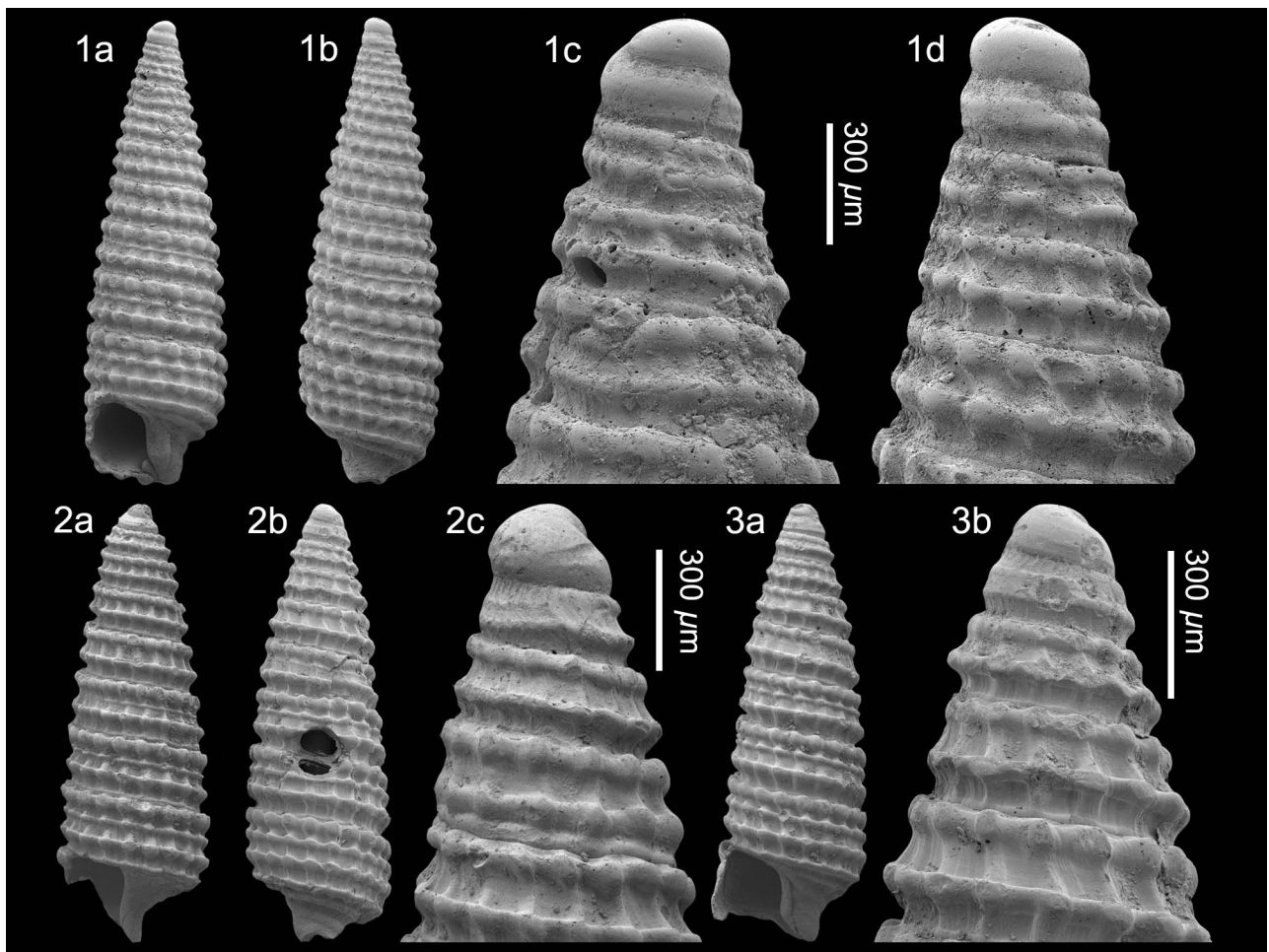
*Etymology* – Named after the type locality of St-Clément-de-la-Place. *Triphora* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Triphora* species with a protoconch composed of 2-2.25 whorls; first whorl large, bulbous, covered in micropustules, second whorl bearing two cords mid-whorl, with weak riblets above and below cords, teleoconch with two equal tubercular spiral cords per whorl, with weaker spiral 2 appearing between spirals 1 and 3 on fourth or fifth whorl, smooth peribasal cord, two further smooth cords on base.

*Description* – Shell small, slender, squat, sinistral. Protoconch composed of 2-2.25 whorls; first whorl large,



**Plate 53.** *Triphora sancticlementensis* nov. sp.; 1. **Holotype** MNHN.F.A66694, height 5.2 mm, width 1.6 mm; 1c-d, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1523, height 2.9 mm, width 1.0 mm; 2c, detail of protoconch; 3. **Paratype 2** NHMW 2016/0103/1524, height 3.0 mm, width 1.0 mm; 3b, detail of protoconch (all SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

bulbous, covered in micropustules, second whorl bearing two cords mid-whorl, with weak riblets above and below cords. Junction with teleoconch sharply delimited. Teleoconch of up to 11 flat-sided whorls separated by impressed suture, bearing two tubercular spiral cords. Spirals 1 and 3 appear simultaneously at protoconch/teleoconch junction, of equal strength; spiral 2 weak, only appearing between spirals 1 and 3 on fourth or fifth whorl. Axial ribs weak, orthocline, about 18 on penultimate whorl, forming strong tubercles at intersections with spiral sculpture. Last whorl spirals 1 and 3 beaded, equal in strength, spiral 2 weaker, peribasal cord smooth, two smooth cords over base. Aperture subquadrate, outer lip thin, edge damaged.

*Discussion* – *Triphora sancticlementensis* nov. sp. is characterised by its protoconch and its teleoconch sculpture of two equal tuberculate spiral cords, with spiral 2 delayed, appearing on the fourth or fifth teleoconch whorl. It is similar to *Triphora miopygmaea* nov. sp., but differs in its protoconch; *T. miopygmaea* has a lower protoconch of only two whorls, the last whorl bearing a single carina or cord and devoid of axial riblets.

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

Subfamily Metaxiinae Marshall, 1977  
Genus *Metaxia* Monterosato, 1884

*Type species* (by subsequent designation, Bouchet & Rocco, 2017) – *Murex metaxa* Delle Chiaje, 1828, present-day, Mediterranean.

1884b *Metaxia* Monterosato, p. 125.

### ***Metaxia metaxa* (Delle Chiaje, 1828)**

Plate 54, figs 1-3

- \*1828 *Murex Metaxa* Delle Chiaje, p. 222, pl. 49, figs 29-31.
- ?1848 *Cerithium metaxa* (?) Delle Chiaje – Wood, p. 71, pl. 8, fig. 6.
- ?1912 *Cerithiopsis (Metaxia) rugulosa* Sow. – Cerulli-Irelli, p. 336, pl. 23, fig. 52.
- ?1914 *Cerithiopsis metaxa* della [sic] Chiaje – Friedberg, p. 309, pl. 18, figs 20-21.
- ?1918 *Cerithiopsis Metaxae* – Harmer, p. 422, pl. 41, figs 16-19.
- ?1954 *Cerithiopsis rugulosa metaxa* Chiaje – Strausz, p. 18, pl. 2, fig. 30.
- ?1966 *Cerithiopsis (Metaxia) rugulosa metaxae* Chiaje, 1826 [sic] – Strausz, p. 167, pl. 8, fig. 21.
- 1975 *Cerithiopsis (Metaxia) metaxa* (Delle Chiaje, 1828) – Bahuk, p. 160, pl. 19, figs 15, 16.
- 1988 *Metaxia incerta* Fernandes & Rolán, 21, pl. 1 fig. 10, pl. 3, figs 11, 14.
- ?1996 *Metaxia* aff. *metaxae* (Delle Chiaje, 1828) – Mar-

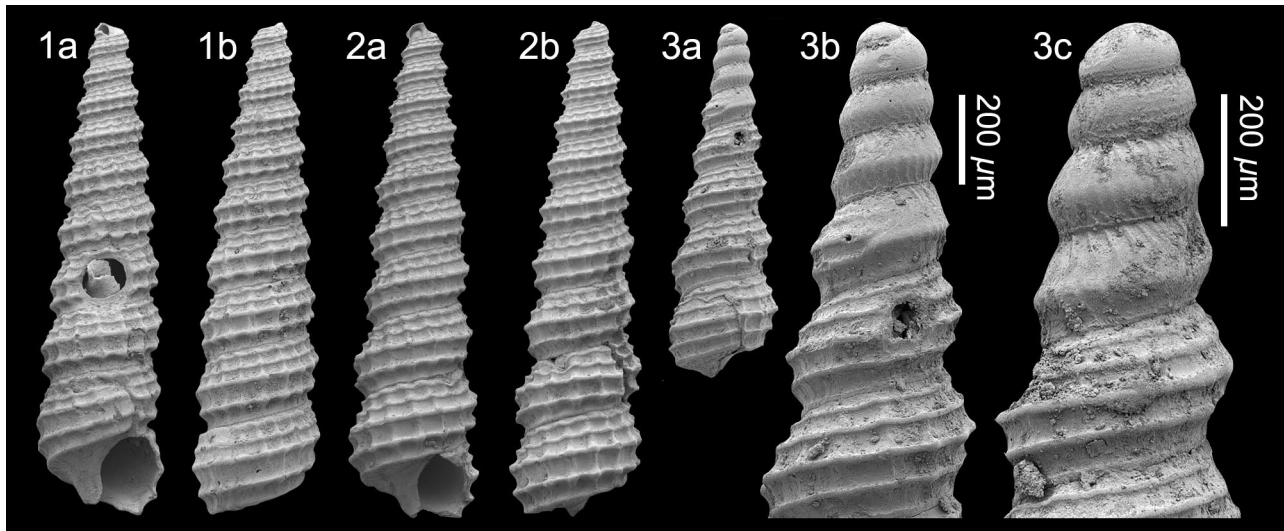
quet, p. 144, pl. 2, fig. 3.

- 1998 *Metaxia metaxae* (Delle Chiaje, 1828) – Van der Linden, p. 116, figs 1-3.
- ?1998 *Metaxia* cfr. *metaxae* (Delle Chiaje, 1828) – Marquet, p. 105, fig. 79.
- ?2001 *Metaxia* sp. – Silva, p. 309.
- ?2006 *Metaxia* aff. *metaxae* (Delle Chiaje, 1828) – Landau *et al.*, p. 7, pl. 2, fig. 1 (*cum syn.*).
- 2009 *Metaxia metaxae* (Delle Chiaje, 1828) – Chirli, p. 21, pl. 9, figs 3-10.
- 2018 *Metaxia metaxae* (Delle Chiaje, 1828) – Menkhurst & Wesselingh, p. 50, figs 40-41.

*Material and dimensions* – Maximum height 7.3 mm (fragment). **St-Clément-de-la-Place**: NHMW 2016/0103/0633-0634 (2), NHMW 2016/0103/1535 (1), NHMW 2016/0103/0635 (12), RGM.1348534 (2), RGM.1348718 (9). **Sceaux-d'Anjou**: NHMW 2016/0103/0677 (4), RGM.1348232 (1 fragment), RGM.1348243 (1 fragment). **Re-nauleau**: NHMW 2016/0103/0640 (47), RGM.1349016 (8), LC (35), FVD (31). **Beugnon**: RGM.1348439 (1).

*Discussion* – The genus *Metaxia* Monterosato, 1884 is represented in the Assemblage I localities mainly by apical or teleoconch fragments. The protoconch is tall, multispiral, composed of four whorls; the first two whorls convex, bearing zigzag spiral threads, the last two whorls carinate mid-whorl, bearing continuous axial riblets. This is similar to the protoconch of the present-day Moroccan specimen illustrated by Van der Linden (1998, p. 117, fig. 3), who regarded the number of whorls to be rather variable (between 3.5-almost 5). This broader species concept led Van der Linden to consider *M. incerta* Fernandes & Rolán, 1988 from the Cape Verde Islands a synonym. This type of protoconch was also illustrated in lower Pliocene Italian specimens (Chirli, 2009, pl. 9, figs 5, 6).

Van der Linden (1998) showed the genus to be more speciose in the eastern Atlantic than previously thought. The teleoconch sculpture is rather conservative, composed of axial ribs and four spiral cords, tubercles variably developed at the intersections depending on the species. However, the small number of European present-day species can immediately be separated based on protoconch type and sculpture. Glibert (1949) recorded two species in the middle Miocene Loire Basin of France; *M. turonensis* (Glibert, 1949) and *M. quadrilineata* (Mayer-Ehmar in Ivolas & Peyrot, 1900). The protoconch of neither of these French fossil species has been described. As the protoconch is so important, we hesitate to comment as to the validity of these middle Miocene taxa. We have included specimens in the fossil literature illustrating the teleoconch, but not the protoconch, with a question mark. They are probably this species, although without the protoconch we cannot be certain (*i.e.* Marquet, 1998, p. 105, fig. 79; Landau *et al.*, 2006, pl. 2, fig. 1). Marquet (1996, p. 143) recorded *M. degrangei* (Cossmann & Peyrot, 1922) from the lower Miocene of Belgium and separated it from *M. metaxa* based mainly on having a greater number of protoconch whorls (5.5). At the time *M. metaxa* was con-



**Plate 54.** *Metaxia metaxa* (Delle Chiaje, 1828); 1. NHMW 2016/0103/0633, height 7.3 mm, width 2.3 mm; 2. NHMW 2016/0103/0634, height 5.4 mm, width 1.8 mm; 3. NHMW 2016/0103/1535, height 1.9 mm; 3b-c, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

sidered to have only 4.5 (Fretter & Graham, 1982, p. 370) or 3.5 protoconch whorls (Bouchet, 1985, p. 16). If Van der Linden's (1998) interpretation is correct, these middle Miocene forms may also fall into synonymy, but we provisionally exclude them, as the protoconch has even more whorls than the maximum given by Van der Linden. The specimens from the Paratethys of Poland described by Bałuk (1975, p. 160) are probably *M. metaxa*. The protoconch is not illustrated, but the description of it fits *M. metaxa*, although it does not mention the microsculpture, which is often worn.

If all these records are indeed *M. metaxa*, this is a relatively long-lived and widely distributed species in the European fossil and extant faunas.

**Distribution** – Middle Miocene: Paratethys: Poland (Friedberg, 1914; Bałuk, 1975), ?Hungary (Strausz, 1954, 1966). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: ?North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1918), Kattendijk Formation, Belgium (Marquet, 1996, 1998); central Mediterranean, Italy (Chirli, 2009). Upper Pliocene: ?North Sea Basin, Red Crag, England (Harmer, 1918); ?Atlantic, Pombal Basin, Portugal (Silva, 2001; NHMW coll.); ?western Mediterranean, southern Spain (Landau *et al.*, 2006). Lower Pleistocene: ?central Mediterranean, Italy (Cerulli-Irelli, 1912). Pleistocene-Holocene: North Sea Basin, Netherlands (Menkhorst & Wesselingh, 2018). Present-day: southwestern British Isles to West Africa, Mediterranean.

Family Cerithiopsidae H. & A. Adams, 1853  
Subfamily Cerithiopsinae H. & A. Adams, 1853  
Genus *Cerithiopsis* Forbes & Hanley, 1850

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

- 1850 *Cerithiopsis* Forbes & Hanley, pl. OO.
- 1956a *Conciliopsis* Laseron, 164. Type species (by original designation): *Conciliopsis carrota* Laseron, 1956, present-day, Queensland, Australia.
- 2010 *Nanopsis* Cecalupo & Robba, p. 53. Type species (by original designation): *Cerithiopsis nana* Jeffreys, 1867. Junior homonym of *Nanopsis* Freytag, 1974 [Homoptera].

**Note** – The species included in this genus are probably not all congeneric and we have compared some of the species to types of other similar antipodean cerithiopsid genera, but for the present prefer to keep them provisionally under the genus *Cerithiopsis*, except for two species we place in the genus *Cerithiopsidella* Bartsch, 1911.

#### ***Cerithiopsis barleei* Jeffreys, 1867**

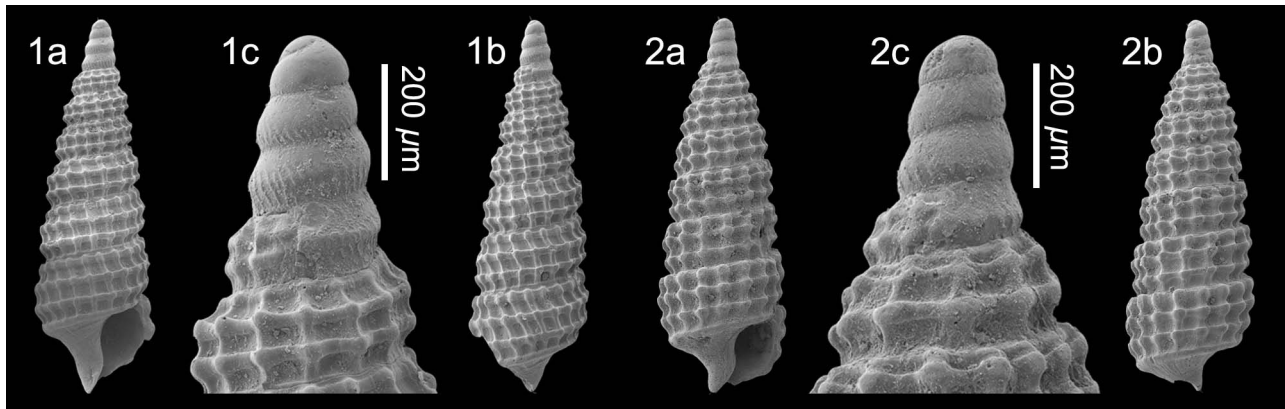
Plate 55, figs 1-2

- \*1867 *Cerithiopsis barleei* Jeffreys, p. 267.
- 2006 *Cerithiopsis* (*s.l.*) *barleei* Jeffreys, 1867 – Landau *et al.*, p. 12, pl. 3, fig. 2 (*cum syn.*).
- 2009 *Cerithiopsis barleei* Jeffreys, 1867 – Chirli, p. 4, pl. 1, figs 8-15.
- 2010 *Prolixodens barleei* (Jeffreys, 1867) – Cecalupo & Robba, p. 61, figs 2A-C, 5J, K.

**Material and dimensions** – Maximum height 2.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0364-0365 (2), NHMW 2016/0103/0366 (3), RGM.1348706 (1). **Renauveau:** NHMW 2016/0103/1495 (24), LC (5), FVD (2). **Begnon:** RGM.1348508 (1).

**Discussion** – *Cerithiopsis barleei* Jeffreys, 1867 is characterised by its multispiral protoconch in which Protoconch I is covered in micropustules and Protoconch II is





**Plate 55.** *Cerithiopsis barleei* (Jeffreys, 1867); 1. NHMW 2016/0103/0364, height 2.9 mm, width 1.8 mm; 1c, detail of protoconch; 2. NHMW 2016/0103/0365, height 2.5 mm, width 1.8 mm; 2c detail of protoconch (all SEM images). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

composed of rounded whorls with micropustules on the adapical portion and axial riblets below. The micropustules cannot be seen in the specimens illustrated from St-Clément-de-la-Place (Pl. 55, figs 1, 2), but the protoconchs are slightly abraded.

The teleoconch has two primary cords on the first whorl, three on later whorls, with tubercles developed at the intersections, similar to that of many of its congeners, but differs from species like *C. tubercularis* (Montagu, 1803) in having a smooth base, without spiral cords. Landau *et al.* (2013, pl. 63, figs 1, 2) figured a species from the middle Miocene eastern Proto-Mediterranean of Turkey as *C. cf. barleei* Jeffreys, 1867, which differs from the typical form in that the last protoconch whorl is carinate. We note that Cecalupo & Robba (2010, p. 61) placed this species in the genus *Prolixodens* Marshall, 1978, an antipodean genus. We provisionally prefer to keep it in *Cerithiopsis* pending genetic data confirming them to be monophyletic.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1918), Kattendijk Formation, Belgium (Marquet, 1997b, 1998); western Mediterranean: Italy (Chirli, 2009). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1918); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2006). Present-day: Atlantic, south western England to Mediterranean (Fretter & Graham, 1982).

***Cerithiopsis cerithiopsoides* nov. sp.**

Plate 56, figs 1-2

**Type material** – Holotype MNHN.F.A66695, height 5.2 mm, width 1.5 mm; paratype 1 MNHN.F.A66696, height 4.1 mm, width 1.3 mm; paratype 2 NHMW 2016/0103/0636, height 5.6 mm, width 1.6 mm; paratype 3 NHMW 2016/0103/0637, height 5.0 mm, width 1.3 mm; paratype 4 NHMW 2016/0103/0638, height 7.1 mm, width 1.8 mm, **Renauleau**; paratype 5 RGM.1348346, height 7.4 mm, width 2.1 mm; paratype 6 RGM.1348535, height

height 7.2 mm, width 2.0 mm, **St-Clément-de-la-Place**.

**Other material** – Maximum height 7.1 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1664 (6), LC (4). **Renauleau**: NHMW 2016/0103/0639 (50+), RGM.1349012 (10), LC (50+), FVD (50+). **Beugnon**: RGM.1348472 (1).

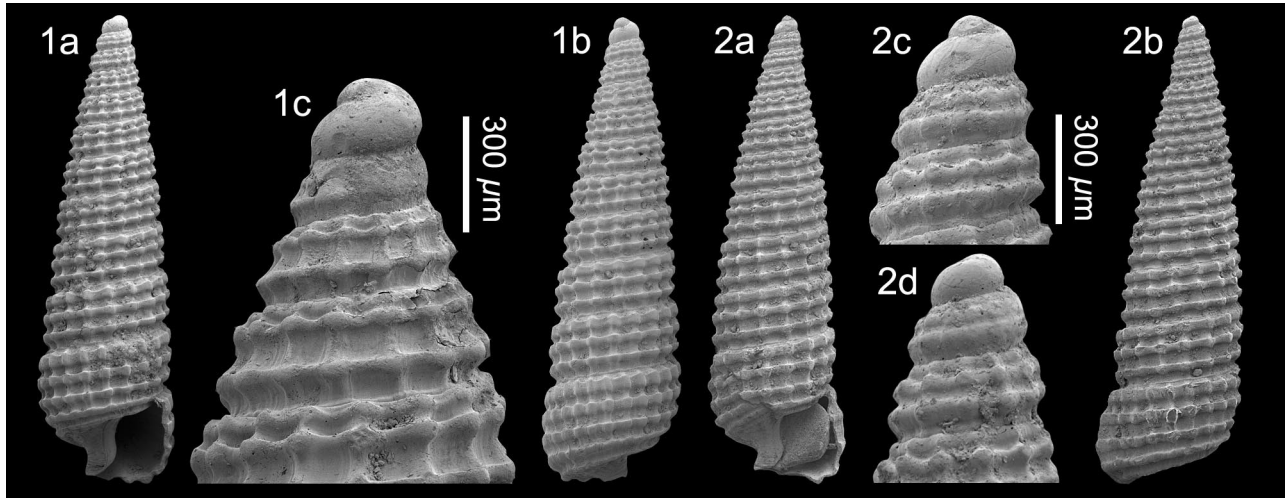
**Etymology** – Name reflecting the teleoconch shell being similar, but not typical, for the genus *Cerithiopsis*. *Cerithiopsis* gender feminine.

**Locus typicus** – Renauleau, Maine-et-Loire, NW France.

**Stratum typicum** – Tortonian, upper Miocene.

**Diagnosis** – *Cerithiopsis* species with small slender shell, protoconch of two smooth whorls, straight-sided teleoconch whorls bearing three spiral cords; spirals 2 and 3 appear at start of teleoconch, spiral 1 on second whorl, close-set axial ribs forming tubercular sculpture, two prominent, smooth peribasal cords, smooth base.

**Description** – Shell small, slender, elongate. Protoconch consisting of two smooth whorls with medium-sized nucleus. Teleoconch of up to 11 straight-sided whorls separated by deeply impressed suture. Sculpture of three spiral cords; spirals 2 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 develops on second whorl, rapidly strengthening abapically to become equal in strength to other spirals by fourth teleoconch whorl. Spirals 1 and 2 closer spaced than spiral 3. Axial sculpture of about 16 orthocone ribs, roughly aligned along length of teleoconch, forming regular, slightly horizontally-elongated reticulated surface pattern, with strong, rounded tubercles formed at sculptural intersections. Last whorl weakly convex; two prominent smooth peribasal cords delimiting concave base, adapical peribasal cord weakly tubercular in some specimens, base smooth, devoid of cords. Aperture small, outer lip simple, columella weakly excavated, columellar and parietal callus sharply delimited, weakly thickened, adherent, forming narrow callus margin.



**Plate 56.** *Cerithiopsis cerithiopsoides* nov. sp.; 1. **Holotype** MNHN.F.A66695, height 5.2 mm; width 1.5 mm; 1c, detail of protoconch; 2. **Paratype 2** NHMW 2016/0103/0636, height 5.6 mm, width 1.6 mm; 2c-d, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – The teleoconch of *Cerithiopsis cerithiopsoides* nov. sp. differs from that typical for the genus *Cerithiopsis* in having a spiral cord on the base (or two peribasal cords). *Cerithiopsis* species have a smooth base (Marshall, 1978, p. 81). Bouchet & Warén (1993) placed cerithiopsids with two peribasal cords in the genus *Krachia* Baluk, 1975, but Bruce Marshall (personal communication to BL, 2018) suspects that the modern species referred to *Krachia* by Bouchet & Warren are related to *Ataxocerithium* and thus likely to be newtoniellids. The protoconch of *C. cerithiopsoides* is non-planktotrophic and thus not useful in assigning the species to a cerithiopsid genus, but there are similarities with the antipodean genus *Mendax* Finlay, 1927. *Cerithiopsis nana* (Wood, 1848) from the North Sea Basin Pliocene has a similar paucispiral protoconch, but differs in having spirals 1-3 present at the protoconch/teleoconch boundary and in

having a single peribasal cord; typical of *Cerithiopsis*.

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

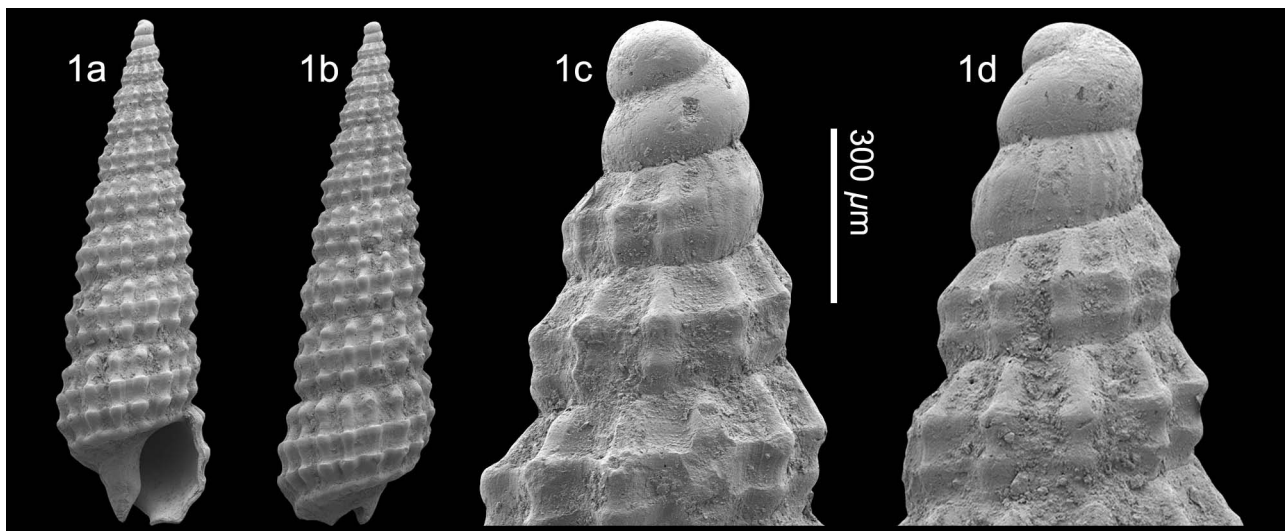
***Cerithiopsis esterae* nov. sp.**

Plate 57, fig. 1

*Type material* – Holotype NHMW 2016/0103/1540, height 6.6 mm, width 2.0 mm.

*Other material* – Known only from holotype.

*Etymology* – Name after Ester Camacho Matias, first granddaughter of the first author. *Cerithiopsis* gender feminine.



**Plate 57.** *Cerithiopsis esterae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1540, height 6.6 mm; width 2.0 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Cerithiopsis* species with convex whorls, protoconch of 2.2 whorls; nucleus large, axial riblets on last half protoconch whorl, teleoconch whorls bearing three spiral cords; spirals 2 and 3 appear at start of teleoconch, spiral 1 on fifth whorl, axial ribs forming tubercular sculpture, single peribasal cord, smooth base.

**Description** – Shell small, slender, elongate. Protoconch consisting of 2.2 whorls with large nucleus; first whorl smooth (possibly micropustules present near suture) with strongly oblique suture; second whorl bearing fine orthocone axial riblets on last half whorl. Teleoconch of nine convex whorls separated by impressed suture. Sculpture of three evenly spaced spiral cords; spirals 2 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 develops on fifth whorl, strengthening abapically to become equal in strength to other spirals on last whorl. Axial sculpture of 14 orthocone ribs, roughly aligned along length of teleoconch, forming regular reticulated surface pattern, with strong, rounded tubercles formed at sculptural intersections. Teleoconch microsculpture present consisting of spiral rows of micropustules. Last whorl convex, single prominent tubercular peribasal cords delimiting concave base, base smooth, devoid of cords. Aperture small, outer lip simple, columella excavated, columellar and parietal callus weakly developed, forming narrow callus margin.

**Discussion** – Although represented by a single specimen, it is perfectly preserved and exhibits characters that separate it from its congeners, and therefore warrants description. The protoconch of *Cerithiopsis esterae* nov. sp., with its big nucleus and riblets on the last half whorl, is typically non-planktotrophic and very similar to that of the present-day eastern Atlantic *Krachia cossmanni* (Dautzenberg & Fischer, 1896) (see Bouchet & Warén, 1993, p. 607, fig. 1345). However, the character of non-planktotrophic protoconchs in cerithiopsids is not useful

for supraspecific classification (Marshall, 1978). *Krachia* species have two peribasal cords. The teleoconch whorls are more convex than in most European *Cerithiopsis* species and the teleoconch micropustular spiral sculpture is not a cerithiopsid feature known to the authors. *Cerithiopsis esterae* is reminiscent of the present-day New Zealand species *Specula retifera* (Suter, 1908).

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

### *Cerithiopsis minima* (Brusina, 1865)

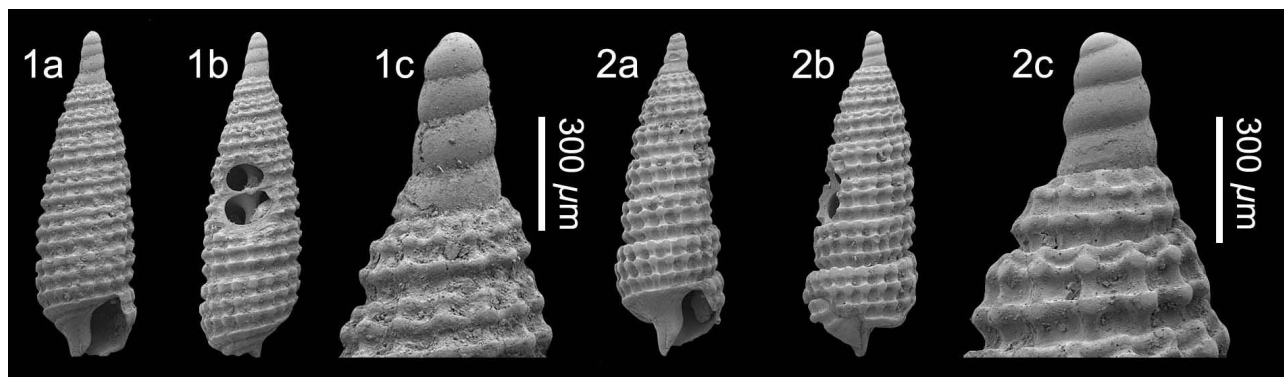
Plate 58, figs 1-2

- \*1865 *Cerithium minimum* Brusina, p. 17.
- 1999 *Cerithiopsis minima* (Brusina, 1865) – Giannuzzi-Savelli *et al.*, p. 36, figs 47-49.
- 2009 *Cerithiopsis minima* (Brusina, 1865) – Chirli, p. 8, pl. 3, figs 6-15.

**Material and dimensions** – Maximum height 3.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1543 (1), NHMW 2016/0103/1544 (2), RGM.1348707 (1). **Sceaux-d'Anjou:** NHMW 2016/0103/1665 (6). **Renauleau:** NHMW 2016/0103/1541 (1), NHMW 2016/0103/1542 (8), LC (10).

**Discussion** – This species is characterised by its tall, smooth, protoconch composed of about four convex whorls and its rather pupoid teleoconch, with spirals 2 and 3 developing at the protoconch/teleoconch junction and spiral 1 slightly delayed, appearing on the second half of the first whorl. One of the figured specimens has a weak basal cord (Pl. 58, fig. 1), whereas the other has a smooth base (Pl. 58, fig. 2).

Several similar pupoid species with a multispiral protoconch have been described in the European faunas. *Cerithiopsis nana* Jeffreys, 1867 differs in having small axial riblets on the adapical portion of the later protoconch whorls, a feature for which Cecalupo & Robba (2010) erected the genus *Nanopsis*. *Cerithiopsis jeffreysi* Watson, 1885 differs in having a sharper lattice-like teleoconch sculpture



**Plate 58.** *Cerithiopsis minima* (Brusina, 1865); 1. NHMW 2016/0103/1541, height 2.9 mm, width 0.9 mm, 1c detail of protoconch. Renauleau. 2. NHMW 2016/0103/1544, height 3.0 mm, width 1.1 mm, 2c detail of protoconch (all SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



with weaker tubercles developed at the intersections.

*Cerithiopsis minima* has been recorded from the lower Pliocene Coralline Crag of England (Harmer, 1918, p. 423, pl. 41, figs 22, 23) and the Pleistocene of the Balearic Islands (Cuerda Barceló, 1987, p. 237, pl. 18, figs 32, 33), but these and other references in which the protoconch is not figured have been excluded from the chresonymy and distribution pending confirmation.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: western Mediterranean: Italy (Chirli, 2009). Present-day: European Atlantic frontage and Mediterranean (Chirli, 2009).

***Cerithiopsis mira* nov. sp.**

Plate 59, fig. 1

*Type material* – Holotype NHMW 2016/0103/1539, height 4.5 mm, width 1.4 mm.

*Other material* – Known only from holotype.

*Etymology* – Latin from ‘*mirus*, -a, -um’, adjective, meaning wonderful, strange, remarkable, reflecting the unusual protoconch shape and sculpture for the genus. *Cerithiopsis* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Cerithiopsis* species with a small slender shell, protoconch of 2.5 weakly angular whorls covered in fine spiral threads, straight-sided teleoconch whorls bearing three spiral cords; spirals 2 and 3 appear at start of teleoconch, spiral 1 on second whorl, close-set axial ribs forming tubercular sculpture, two prominent, smooth peribasal cords, smooth base.

*Description* – Shell small, slender, elongate. Proto-

conch consisting of 2.5 weakly angular whorls covered in crowded, regular, fine spiral threads. Junction with teleoconch sharply delimited by change in sculpture. Teleoconch of eight straight-sided whorls separated by deeply impressed suture. Sculpture of three spiral cords; spirals 2 and 3 appear simultaneously at protoconch/teleoconch junction, spiral 1 develops on second whorl, rapidly strengthening abapically to become equal in strength to other spirals by fourth teleoconch whorl. Spirals 1 and 2 closer spaced than spiral 3. Axial sculpture of 16 orthocline, non-aligned ribs, forming regular, slightly horizontally-elongated reticulated surface pattern, with strong, rounded tubercles formed at sculptural intersections. Last whorl weakly convex, spirals of equal strength and evenly spaced; two prominent smooth peribasal cords delimiting concave base, base smooth, devoid of cords. Aperture small, outer lip simple, columella weakly excavated, columellar and parietal callus sharply delimited, weakly thickened, adherent, forming narrow callus margin.

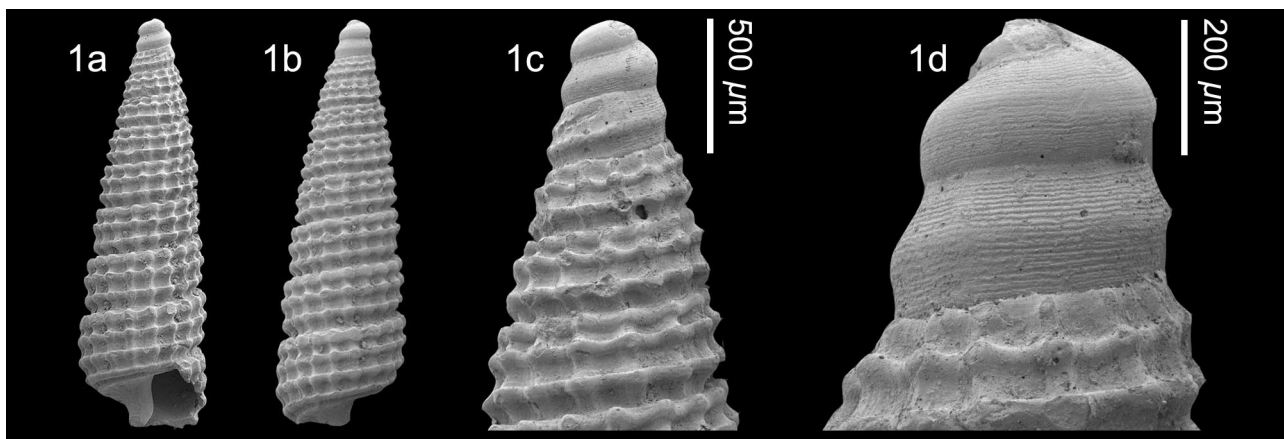
*Discussion* – This is yet another unusual species in the Assemblage I fauna that although represented by a single specimen, merits description. The teleoconch characters are similar to those of *Cerithiopsis cerithiposoides* nov. sp. with three primary spirals and two smooth, or almost so, peribasal cords. However, we have not seen the protoconch shape and sculpture of *Cerithiopsis mira* nov. sp. in any other *Cerithiopsis* species, at least not any European Neogene or extant species. The protoconch composed of 2.5 weakly angular whorls covered in fine spiral threads immediately separate it from any of its congeners.

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

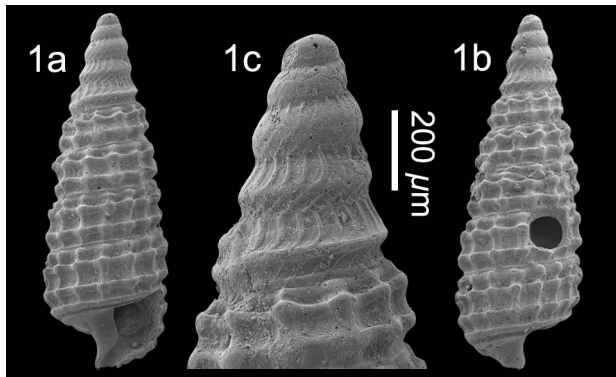
***Cerithiopsis* sp.**

Pl. 60, fig. 1

*Material and dimensions* – Maximum height 5.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0362 (1), NHMW 2016/0103/0363 (7), RGM.1348708 (1).



**Plate 59.** *Cerithiopsis mira* nov. sp.; 1. **Holotype** NHMW 2016/0103/1539, height 4.5 mm, width 1.4 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 60.** *Cerithiopsis* sp.; 1. NHMW 2016/0103/0362, height 4.5 mm, width 1.6 mm; 1c detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Description** – Shell small, solid. Protoconch multispiral, of 4.5 whorls, with a narrow rounded apex; Protoconch I about 1.5 whorls, sculpture abraded; on middle whorls Protoconch II sculptured with fine, sharp, evenly spaced opisthocline collabral riblets that extend between sutures, and relatively closely-spaced, regular, diagonally reticulating prosocline riblets over abapical half, last whorl strongly carinate just below mid-whorl, with comma-shaped collabral riblets above and fine, strongly opisthocline ribs below carina. Sinusigera sinus deep, rather broad, opisthocline. Teleoconch of 4.5 weakly convex whorls, separated by weakly impressed suture, sculptured by three spiral cords; adapical cord weaker, strengthening abapically but remaining weaker than other two cords and closer spaced to mid-cord; cords overrun axial ribs, forming rounded tubercles at intersections. Last whorl with fourth cord emerging from insertion of outer lip; base strongly contracted, bearing one smooth spiral. Aperture subquadrate. Columella smooth. Siphonal canal moderately well developed, somewhat produced, open, sharply inclined away from aperture.

**Discussion** – This species is characterised by its richly sculptured multispiral protoconch, consisting of 4.5 whorls. The last two protoconch whorls are carinate, the last strongly so, the sculpture on the abapical half netted on the penultimate whorl, but bearing only axial riblets below the carina on the last whorl. Teleoconch sculpture consists of three spiral cords, the adapical cord weaker, but present from the first whorl. The cords overrun 13-14 axial ribs, forming tubercles at the intersections.

The protoconch type and sculpture is reminiscent to that seen in the genus *Cerithiopsidella* Bartsch, 1911 (see below), but that genus has non-commarginal ribs abapically. The presence of strong commarginal ribs adapically, however, might suggest that the two groups may be related. This might be an ancestor of *Mendax* Finlay, 1927, which has very similar teleoconch, but unfortunately there is no way of telling as the type species of *Mendax* is non-planktotrophic (Bruce Marshall personal communication, 2018).

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

Genus *Cerithiopsidella* Bartsch, 1911

**Type species** (by original designation) – *Cerithiopsis cosmia* Bartsch, 1907, present-day, California.

1911 *Cerithiopsidella* Bartsch, p. 329.

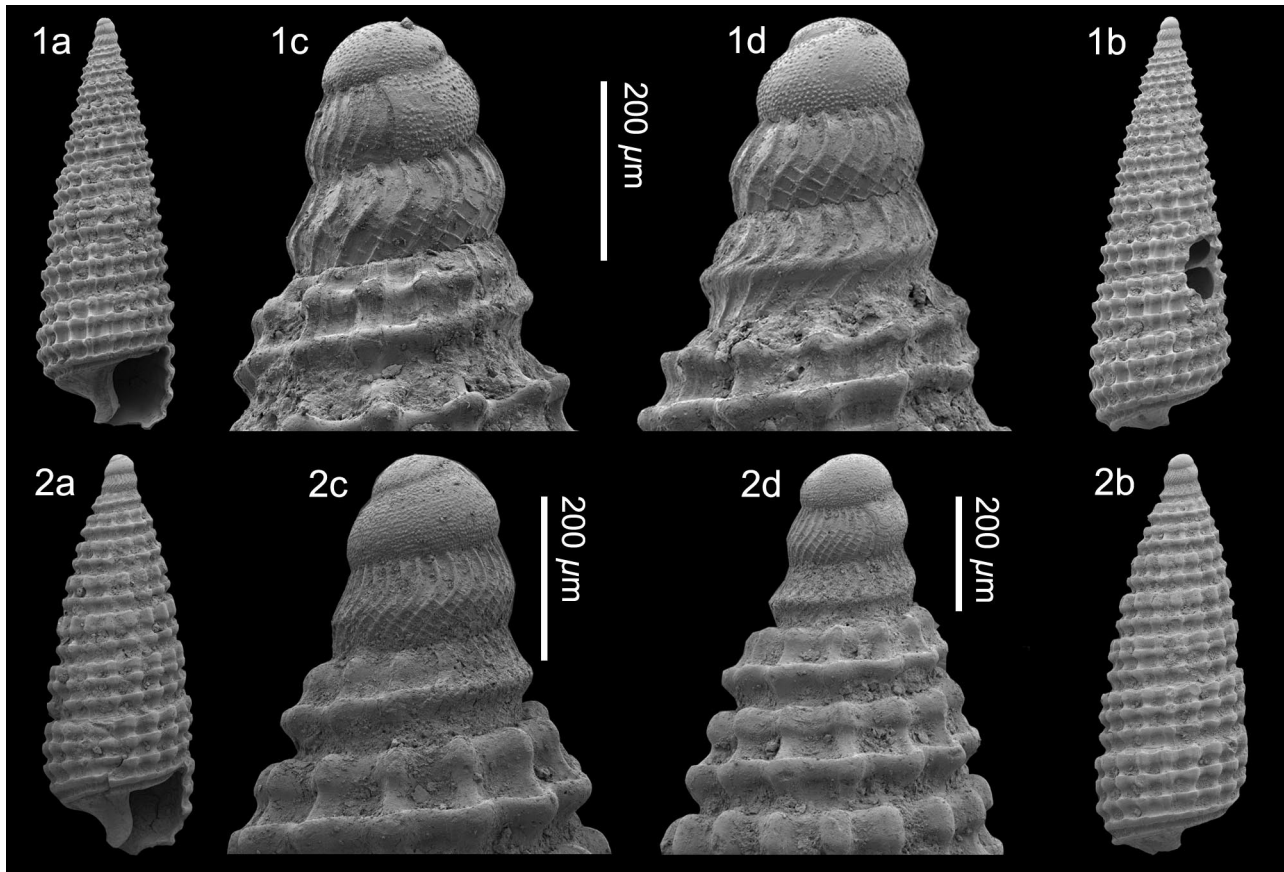
### *Cerithiopsidella* sp. 1

Pl. 61, fig.1

**Material and dimensions** – Maximum height 4.8 mm. **Renauleau:** NHMW 2016/0103/1722 (1), NHMW 2016/0103/1748 (24).

**Description** – Shell small, solid. Protoconch multispiral, of 3.5 whorls, with a broad rounded apex; Protoconch I 1.5 whorls, sculptured by micropustules throughout; Protoconch II sculptured with fine, sharp, evenly spaced opisthocline collabral riblets that extend between sutures, and relatively widely-spaced, irregular diagonally reticulating prosocline riblets over abapical half. Sinusigera sinus deep, rather broad, opisthocline. Teleoconch of up to nine almost flat-sided whorls separated by weakly impressed suture, sculptured by two spiral cords on first two whorls, third appearing at below suture on third whorl, cords equally spaced on last two whorls; cords overrun axial ribs, forming rounded tubercles at intersections. Last whorl with fourth cord emerging from insertion of outer lip; base strongly contracted, bearing one smooth spiral. Aperture subquadrate. Columella strongly excavated adapically. Siphonal canal rather short, open, sharply inclined away from aperture.

**Discussion** – The presence in the European Neogene of cerithiopsids belonging within the genus *Cerithiopsidella* Bartsch, 1911 has been widely reported in the literature (Marquet, 1998; Landau *et al.*, 2006, 2013; Chirli, 2009). These have usually been ascribed to *Cerithiopsis subulata* (Wood, 1848), originally described from the North Sea Basin lower Pliocene Coralline Crag of England, but this is incorrect and they represent several species. In the Assemblage I fauna *Cerithiopsidella* sp. 1 differs from *Cerithiopsidella* sp. 2 in having half a protoconch whorl less, the diagonally reticulating prosocline riblets over the abapical half of the later protoconch whorls are more widely spaced and sometimes absent, making the reticulation somewhat irregular. The formation of the third spiral cord differs; in *Cerithiopsidella* sp. 1 it appears below the suture on the third teleoconch whorl, whereas in *Cerithiopsidella* sp. 2 the adapical cord broadens on the second whorl and then divides on the fourth whorl. The specimen from the lower Piacenzian upper Pliocene of the Estepona Basin illustrated by Landau *et al.* (2006, p. 14, pl. 4, fig. 1) differs from both of the Assemblage I species in having a protoconch of at least four whorls



**Plate 61.** 1. *Cerithiopsidella* sp. 1, NHMW 2016/0103/1722, height 4.8 mm, width 1.7 mm; 1c, d, detail of protoconch; 2. *Cerithiopsidella* sp. 2, NHMW 2016/0103/1747, height 2.9 mm, width 1.1 mm; 2c, d, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

and the third spiral appears below the suture much later, only on the penultimate whorl. The species discussed and illustrated by Marquet (1998, p. 109, fig. 83) has an incomplete protoconch with only the last whorl preserved; the sculpture is similar to that of *Cerithiopsidella* sp. 1, but the adapical spiral cord appears, albeit weaker, from the protoconch/teleoconch junction. The specimens discussed and illustrated by Landau *et al.* (2013, p. 137, pl. 63, figs 4, 5), from the Serravallian middle Miocene of the Karaman Basin of Turkey, differ from both of the Assemblage I species in having a protoconch of at least four whorls and the weaker third spiral appears below the suture from the first teleoconch whorl. The species from the lower Pliocene of Italy figured by Chirli (2009, pl. 4, figs 11-15) have a finely reticulated protoconch similar to that seen in *Cerithiopsidella* sp. 1, but differ in the formation of the third spiral cord. It is not clear from Chirli's illustrations exactly when the third cord develops; possibly on the third teleoconch whorl, but it appears below the suture rather than by division of the adapical cord. We refrain from formally describing these species, which would be best done with more comparative material at hand, and by a cerithiopsid expert.

We note that *Cerithiopsis subulata* (Wood, 1848) is a secondary homonym of *Cerithiopsis subulata* (Montagu, 1808) (Porter & Wolfe, 1971), originally described in the

genus *Murex*. However this is a *taxon inquirendum*. If Montagu's species should turn out to be valid and belong within the genus *Cerithiopsis*, it would take precedence.

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

#### *Cerithiopsidella* sp. 2

Pl. 61, fig. 2

*Material and dimensions* – Height 2.9 mm. **Renauleau:** NHMW 2016/0103/1747 (1).

*Description* – Shell small, solid, somewhat pupoid. Protoconch multispiral, of three whorls, with a broad rounded apex; Protoconch I 1.5 whorls, sculptured by micro-pustules throughout; Protoconch II sculptured with fine, sharp, evenly spaced opisthocline collabral riblets that extend between sutures, and relatively closely-spaced, regular, diagonally reticulating prosocline riblets over abapical half. Sinusigera sinus deep, rather broad, opisthocline. Teleoconch of seven almost flat-sided whorls separated by weakly impressed suture, sculptured by two spiral cords on first three whorls, adapical cord broadens and divides into two on fourth whorl, only separating completely on



penultimate whorl and migrating abapically so that cords equally spaced on last whorl; cords overrun axial ribs, forming spirally-elongated rounded tubercles at intersections. Last whorl with fourth cord emerging from insertion of outer lip; base strongly contracted, bearing one smooth spiral. Aperture subquadrate. Columella strongly and deeply excavated adapically. Siphonal canal rather short, open, sharply inclined away from aperture.

*Discussion* – See above under *Cerithiopsidella* sp. 2.

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

Genus *Dizoniopsis* Sacco, 1895

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

1895a *Dizoniopsis* Sacco, p. 67.

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

***Dizoniopsis bilineata* (Hörnes, 1848)**

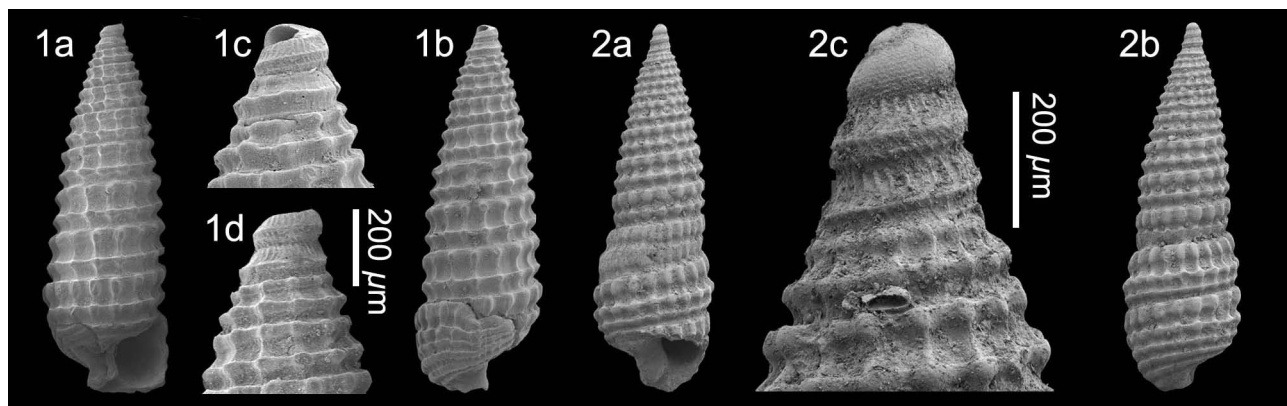
Plate 62, figs 1-2

\*1848 *Cerithium bilineatum* Hörnes, p. 21.

- 1964 *Cerithiopsis (Dizoniopsis) bilineata* Hörnes, 1856 [sic] – Brébion, p. 247.
- non 1968 *Cerithiopsis (Dizoniopsis) bilineata* (Hörnes) – Nordsieck, p. 70, pl. 11, fig. 43.10 [= *Dizoniopsis coppolae* (Aradas, 1870)].
- non 1976 *Cerithiopsis (Dizoniopsis) bilineata* (Hörnes, 1856 [sic]) – Nordsieck, p. 7, fig. 12, p. 18, unnumbered fig. [= *Dizoniopsis concatenata* (Conti, 1864)].
- non 1980 *Dizoniopsis bilineata* (Hörnes, 1848)? – Gründel, p. 229, figs 14-15 [= *Dizoniopsis coppolae* (Aradas, 1870)].
- non 1999 *Dizoniopsis bilineata* (Hörnes, 1848) – Giannuzzi-Savelli *et al.*, p. 44, fig. 76 [= *Dizoniopsis concatenata* (Conti, 1864)].
- 2006 *Cerithiopsis (s. lat.) bilineata* (Hörnes, 1848) – Landau *et al.* p. 14, text-fig. 1, figs 1-3.
- 2009 *Dizoniopsis bilineata* (Hörnes, 1848) – Chirli, p. 14, pl. 7, figs 1-12.

*Material and dimensions* – Maximum height 5.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0526 (1), NHMW 2016/0103/0527 (19), LC (1). **Sceaux-d’Anjou**: NHMW 2016/0103/1663 (7), RGM.1348327 (2), RGM.1348619 (2). **Renauleau**: NHMW 2016/0103/1729 (1), NHMW 2016/0103/0528 (31), LC (5), FVD (2). **Beugnon**: RGM.1348471 (8).

*Discussion* – At species level, identification is not possible without the protoconch. As the protoconch of *Cerithium bilineatum* Hörnes, 1848 was not known, Landau *et al.* (2006) designated a lectotype from the middle Miocene Paratethys of Steinebrunn (Austria). The protoconch is incomplete, but shows it to be multispiral bearing two spiral cords on the penultimate whorl, a single raised carina on the last half whorl and comma-shaped axial riblets in the interspaces. We have one specimen from Renauleau with a complete protoconch (Pl. 62, fig. 2). The last two protoconch whorls are identical to those of the lectotype from Steinebrunn. We therefore consider the upper Miocene Atlantic specimens from NW France to be conspecific with those from the Paratethys. *Dizoniopsis bilineata* has been reported widely in both the



**Plate 62.** *Dizoniopsis bilineata* (Hörnes, 1848); 1. NHMW 2016/0103/0526, height 3.3 mm, width 1.1 mm; 1c-d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/1729, height 4.4 mm, width 1.4 mm; 2c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fossil and present-day literature, usually without details of the protoconch. Bouchet *et al.* (2010) reviewed the extant Mediterranean species of *Dizoniopsis*; they all differ from *Dizoniopsis bilineata* in protoconch character, none have two spiral cords on the penultimate whorl, nor do they bear regular axial riblets. Of the fossil records we restrict the synonymy and distribution to ones in which the protoconch is known and note that both the stratigraphical and geographical distribution may be much wider.

Brébion (1964, p. 248) recorded this species from Assemblage I localities (Renauleau, St-Clément-de-la-Place, St-Michel), Assemblage II (Apigné, Le Temple du Cerisier) and Assemblage III (Palluau, Le Girondor) to which Van Dingenen *et al.* (2016, p. 163) added *Dizoniopsis cf. bilineata* from Le Pigeon Blanc. Only the Assemblage I specimens are placed in the distribution. We have included the lower Pliocene Mediterranean specimens recently figured by Chirli (2009, pl. 7, figs 1-12), as the protoconch fragment illustrated is similar to that recognised here for the species.

**Distribution** – Middle Miocene: Paratethys, Austria (Hörnes, 1848; Landau *et al.*, 2006). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Mediterranean, Italy (Chirli, 2009).

***Dizoniopsis boucheti* nov. sp.**

Plate 63, fig. 1

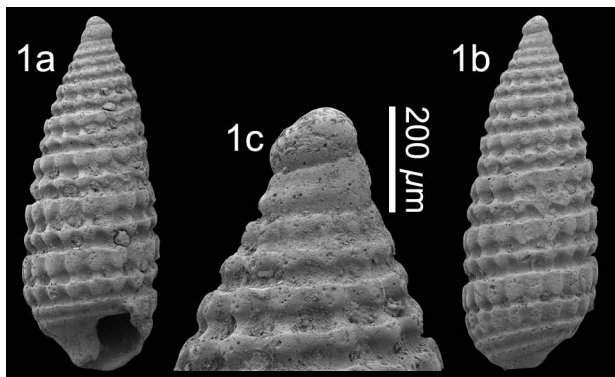
**Type material** – Holotype NHMW 2016/0103/1727, height 2.5 mm, width 0.9 mm.

**Other material** – Renauleau: LC (2).

**Etymology** – Named after Philippe Bouchet of the MNHN (Paris) for his support in this project and in recognition of his work with the genus. *Dizoniopsis* gender feminine.

**Locus typicus** – Renauleau, Maine-et-Loire, NW France.

**Stratum typicum** – Tortonian, upper Miocene.



**Plate 63.** *Dizoniopsis boucheti* nov. sp.; 1. **Holotype** NHMW 2016/0103/1727, height 2.5 mm, width 0.9 mm; 1c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Diagnosis** – *Dizoniopsis* species with pupoid shell shape, low paucispiral protoconch composed two whorls, large nucleus, strong single keel below mid-whorl on last half whorl, teleoconch with adapical cord dominant, two smooth peribasal cords, smooth concave base.

**Description** – Shell small, solid, pupoid. Protoconch paucispiral, smooth, consisting of two low whorls with large nucleus, last half whorl bearing single broad keel placed below mid-whorl. Teleoconch boundary not sharply delimited. Teleoconch of 6.5 whorls sculptured by two spiral cords separated by interspace roughly equal in width to cords. Abapically upper cord gains strength; almost twice width of lower cord on last two whorls. Axial ribs cut cords deeply forming distinct squarish beading. Last whorl convex, beads axially elongated. Base slightly concave, smooth, delimited by two smooth peribasal cords. Aperture ovate, outer lip damaged.

**Discussion** – Three specimens of a *Dizoniopsis* species with a paucispiral protoconch are present from the Renauleau deposits. The protoconch is rather low, composed of about two whorls, with a large nucleus and the surface appears smooth, although it might be abraded. There is a broad carina below mid-whorl on the last half whorl.

The genus in the present-day Mediterranean was recently reviewed by Bouchet *et al.* (2010) and several European species with a paucispiral protoconch have been described. *Dizoniopsis concatenata* (Conti, 1864) from the lower Pleistocene to present-day Mediterranean has a similar protoconch with a large nucleus, but the protoconch is taller and the last half whorl has two cords or keels. The adapical cord on the last teleoconch whorl tends to divide into two rows of closely placed beads in *D. concatenata*, a feature not seen in *Dizoniopsis boucheti* nov. sp. and the adapical peribasal cord is beaded, whereas in the French shell both peribasal cords are smooth. *Dizoniopsis aspicienda* Bouchet, Gofas & Warén, 2010 from the present-day Mediterranean differs from *D. boucheti* and *D. concatenata* in having a cyrtoconoid rather than pupoid teleoconch. The protoconch has a more bulbous first whorl and a weaker cord just above mid-whorl on the last half protoconch whorl, plus a row of pustules on the shoulder. *Dizoniopsis abylenis* Bouchet, Gofas & Warén, 2010 from the present-day Strait of Gibraltar has a protoconch with a bulbous first whorl, two cords on the last half whorl. Like the French fossil species it has a smooth concave base delimited by a single peribasal cord as opposed to two in *D. boucheti*. In the fossil record *D. brevicaput* Lozouet, Lesport & Renard, 2001 from the lower Miocene Aquitanian of the Aquitaine Basin, France has a paucispiral protoconch with axial riblets on the last half whorl and on the last teleoconch whorl the base is delimited by a beaded cord with two further cords running over the base. According to Lozouet *et al.* (2001, p. 49) the sympatric *D. aquitaniensis* (Cossmann & Peyrot, 1922) has a multispiral protoconch.

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

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

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

1861 *Seila* A. Adams, p. 131.

For generic synonymy see Van Dingenen *et al.* (2016, p. 163).

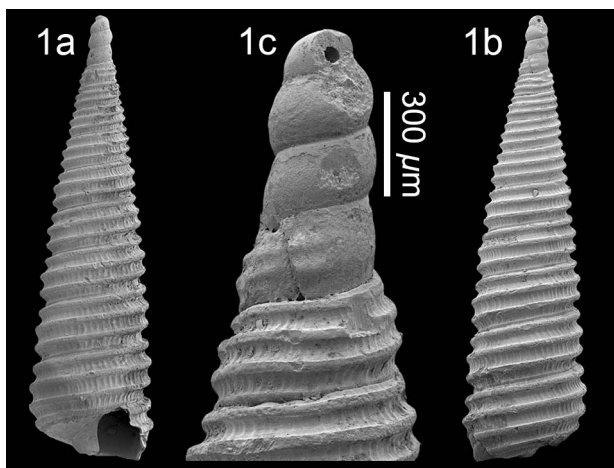
***Seila cf. carinata* (Smith, 1871)**

Plate 64, fig. 1

- cf. \*1871 *Cerithium (Cerithiopsis) carinatum* Smith, p. 736.  
cf. 1990b *Seila carinata* (E.A. Smith, 1871) – Rolán & Fernandes, p. 20, figs 1, 20.  
cf. 2006 *Seila carinata* (E.A. Smith, 1871) – Rolán & Pe-lorce, p. 74, figs 5-7.

*Material and dimensions* – Maximum height 6.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1538 (1).

*Discussion* – One *Seila* specimen from St-Clément-de-la-Place has a tall multispiral protoconch comprising four elevated, rounded whorls. The surface and apex are abraded. At the protoconch/teleoconch boundary spirals 2 and 3 appear first, rapidly followed by spiral 1, and a fourth weaker spiral develops just above the suture. These shell characters are similar to those of *S. carinata* (Smith, 1871) from present-day West Africa. We hesitate to say they are conspecific, as Rolán & Fernandes (1990b, p. 22) describe spiral 2 to be the first to appear, whereas in the shell from St-Clément-de-la-Place spirals 2 and 3 appear simultaneously. Nevertheless, the tall protoconch and the presence of a weak spiral 4 at the



**Plate 64.** *Seila cf. carinata* (Smith, 1871); 1. NHMW 2016/0103/1538, height 6.3 mm, width 1.7 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

suture are common to both.

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

***Seila petasa* nov. sp.**

Plate 65, fig. 1

*Type material* – Holotype NHMW 2016/0103/1536, height 3.7 mm, width 1.6 mm, **Le Grand Chauvreaux**. Paratype 1 NHMW 2016/0103/1605, height 8.8 mm, width 2.1 mm; Paratype 2 NHMW 2016/0103/1606, height 3.0 mm (apical fragment) **Renauleau**.

*Other material* – **Renauleau**: NHMW 2016/0103/1607 (3 apical fragments), LC (5). **Beugnon**: RGM.1348494 (1 apical fragment).

*Etymology* – Latin from ‘*petasus*, -i’, noun, a broad-brimmed travelling hat, reflecting the shape of the protoconch. *Seila* gender feminine.

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

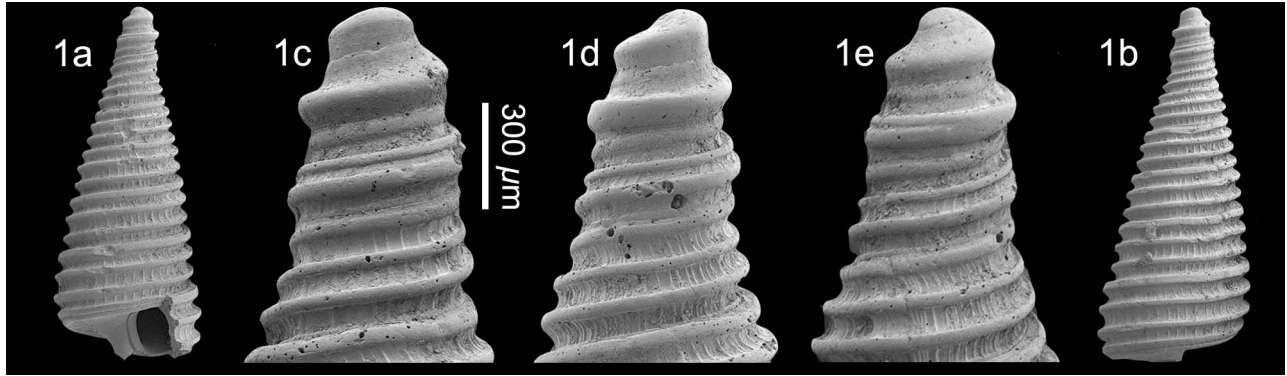
*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Seila* species with relatively wide apical angle, protoconch of just over two whorls; first whorl smooth, broadly and roundly carinate; on second whorl carina strap-like, second weak cord below suture, teleoconch of six straight sided whorls, bearing three equal, narrow, elevated spirals with small axial riblets in interspaces, bifid peribasal cord.

*Description* – Shell small, with relatively wide apical angle for genus. Protoconch consisting of just over two whorls; first whorl smooth, broadly and roundly carinate; second whorl carina placed below mid-whorl, becomes strap-like, broad, elevated, second weak cord develops below suture. Junction with teleoconch not sharply delimited, marked by division of band into spirals 2 and 3 of teleoconch. Teleoconch of six straight sided whorls, separated by superficial suture, bearing three equal, narrow, elevated spirals with small axial riblets in interspaces. Last whorl broad for genus, bearing bifid peribasal cord, base smooth. Aperture damaged.

*Discussion* – Although represented by few specimens, *Seila petasa* nov. sp. has such an unusual protoconch that it merits formal description. The elevated, strap-like cord on the second protoconch is a feature we have not seen in any European fossil species. The protoconch could place it in the subgenus *Lyroseila* Finlay, 1928 (type species *Seila chathamensis* Suter, 1908, Pleistocene to present-day, New Zealand) characterised by its heavy, broadly-conical, non-planktotrophic protoconch, which can be carinate (Marshall, 1978, p. 95), as it is in





**Plate 65.** *Seila petasa* nov. sp.; 1. **Holotype** NHMW 2016/0103/1536, height 3.7 mm, width 1.6 mm; 1c-e, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

this species.

*Seila deaurata* Rolán & Fenandes, 1990 from Angola does have a weakly carinate protoconch, but it does not develop into a strap-like cord and it has more numerous protoconch whorls. We note that some New Zealand species included in the subgenus *Lyroseila* Finlay, 1928 by Marshall (*i.e.*, *Seila (Lyroseila) dilecta* Marshall, 1978) have a similar protoconch. However, *Lyroseila* is considered a synonym of *Seila* by Marshall & Rosenberg (2015; WoRMS). The holotype of *S. petasa* may not be fully grown, but does seem to be complete, as the last whorl has a bifid peribasal cord.

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

***Seila sancticlementi* Marquet, 2001**

Plate 66, fig. 1

\*2001 *Seila (Hebeseila) sancticlementi* Marquet, p. 202, pl. 1, fig. 7, pl. 2, fig. 1.

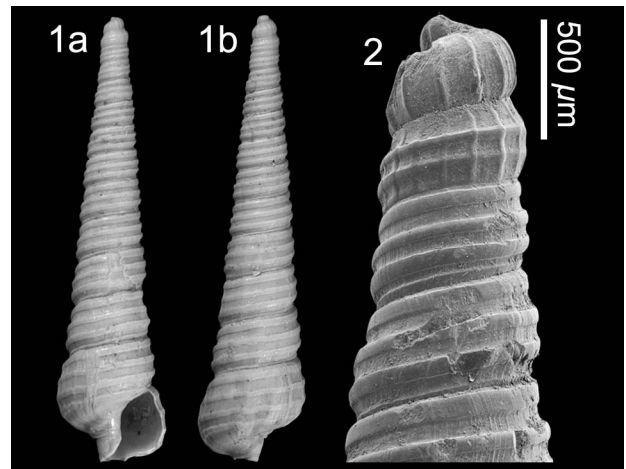
**Material and dimensions** – Maximum height 11.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0327-0328 (2), NHMW 2016/0103/0329 (33), RGM.1348536 (4 with protoconch + 33 fragments without), RGM.1348838 (1), LC (8), FVD (14). **Sceaux-d’Anjou:** RGM.1348291 (1 complete adult), RGM.1348928 (1), LC (1). **Renauleau:** LC (1).

**Discussion** – ‘*Seila* (H.) *sancticlementi* *n. sp.* differs clearly from *S.* (C.) *trilineata* (Philippi, 1836) and the other *Seila* (*Seila*) and *Seila* (*Cinctella*) species by its axially sculptured angular protoconch and the absence of axial ornament on the teleoconch. *S. sancticlementi* *n. sp.* differs from *S. suttonensis* *n. sp.* by possessing a carinate protoconch and by the absence of teleoconch axial sculpture’ (Marquet, 2001, p. 202). This is the most abundant *Seila* species in the Assemblage I fauna and is easily separated from its congeners by its greater size, protoconch sculpture and also by having far broader strap-like spirals on the teleoconch.

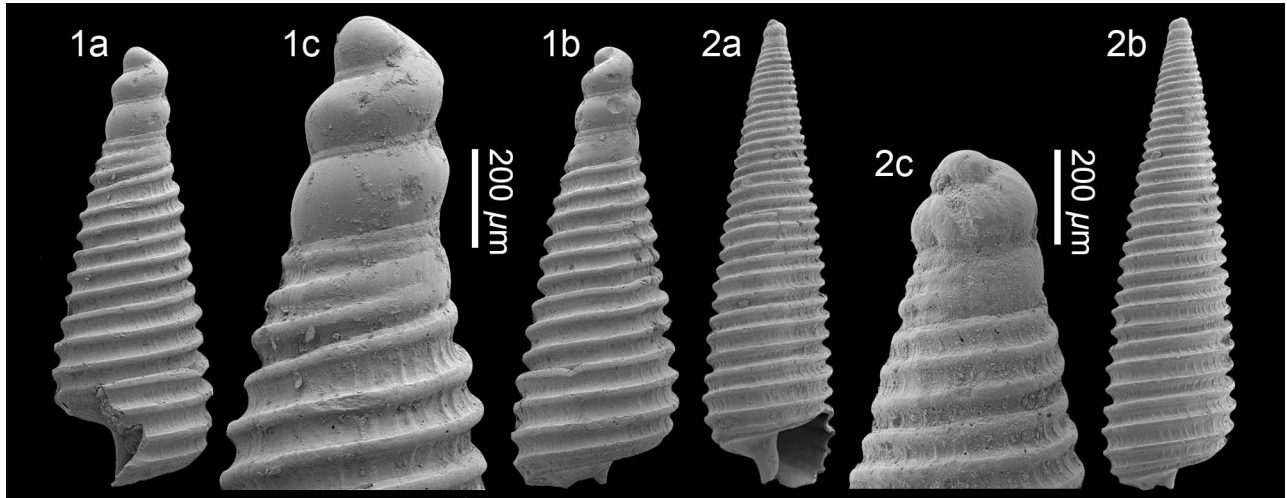
*Seila sancticlementi* Marquet, 2001 is closely similar to *Seila suttonensis* Marquet, 2001 from the lower Pliocene Assemblage III localities of northwestern France, but differs in having a carinate protoconch and lacking axial sculpture on the teleoconch. These two species are quite different from other Atlantic or Mediterranean Neogene or present-day *Seila* species and should probably be placed in a separate genus, but whether they form a monophyletic group with the antipodean species placed in *Hebeseila* Finlay, 1926, as suggested by Marquet (2001, p. 201), is doubtful. In any case, we note that *Hebeseila* is synonymised with *Seila* by Marshall & Rosenberg (2015; WoRMS).

Marquet (2001, p. 199) recorded this species from Assemblage I localities (St-Clément-de-la-Place, Sceaux-d’Anjou).

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (Marquet, 2001).



**Plate 66.** *Seila sancticlementi* Marquet, 2001; 1. NHMW 2016/0103/0327, height 8.0 mm, width 1.9 mm; 2. NHMW 2016/0103/0328, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 67:** 1. *Seila trilineata andegavensis* Marquet, 2001; NHMW 2016/0103/1537, height 2.3 mm, width 900 µm; 1c, detail of protoconch (SEM image); 2. *Seila cf. trilineata andegavensis* Marquet, 2001, NHMW 2016/0103/0322, height 6.1 mm, width 1.7 mm; 2c, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Seila trilineata andegavensis* Marquet, 2001**

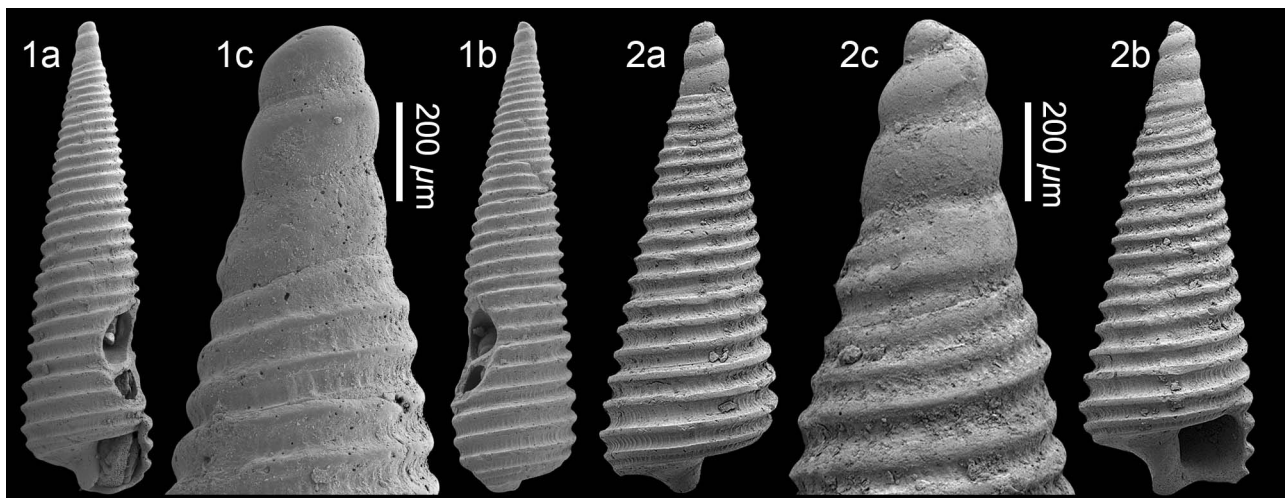
Plate 67, fig. 1

- 1949 *Seila (Seila) trilineata* Philippi, 1836 – Glibert, p. 155, pl. 10, fig. 10 [*non Seila trilineata* (Philippi, 1836)].
- 1964 *Seila trilineata* Philippi, 1836 – Brébion (*partim*), p. 250 [*non Seila trilineata* (Philippi, 1836)].
- \*2001 *Seila (Cinctella) trilineata andegavensis* Marquet, p. 198, pl. 1, fig. 2.

**Material and dimensions** – Maximum height 10.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0322 (1), NHMW 2016/0103/1537 (1), NHMW 2016/0103/0323 (4), RGM.1348537 (1). **Sceaux-d’Anjou:** NHMW 2016/0103/0325 (17), LC (X), FVD (12). **Renauleau:** NHMW

2016/0103/0324 (24), LC (7), FVD (5). **Beugnon:** NHMW 2016/0103/0326 (5).

**Discussion** – ‘*Seila* (C.) *trilineata andegavensis n. subsp.* is very similar to *S. (C.) t. trilineata (Philippi, 1836)*, but has a slightly larger protoconch. The teleoconch sculpture, however, differs in the new subspecies: the spirals are broader, the axials weaker and the first spiral to appear is the abapical instead of the middle one’ (Marquet, 2001, p. 200). In the specimen figured (Pl. 69, fig. 1) the protoconch is composed of about 2.5 whorls. The protoconch is slightly larger than the living subspecies (dp = 310 µm, hp = 430 µm vs. dp = 300 µm, hp. 350 µm; measured from Rolán & Fernandes, 1990b, p. 23, fig. 22). It also shows the weak sutural cord figured by Rolán & Fernandes (1990b, p. 23, fig. 22) for *S. trilineata*



**Plate 68.** *Seila* sp.; 1. NHMW 2016/0103/0330, height 5.1 mm, width 1.4 mm; 1c, detail of protoconch; 2. NHMW 2016/0103/0331, height 3.0 mm, width 1.2 mm; 2c, detail of protoconch (all SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



(Philippi, 1836). All three cords are present at the protoconch/teleoconch boundary, although the abapical is the most strongly developed and there are rather fewer axial riblets in the interspaces than seen in the present-day *S. trilineata*. The second specimen illustrated above as *Seila* cf. *trilineata andegavensis* has a somewhat lower protoconch with one whorl less. We are unsure whether they are conspecific.

Marquet (2001, p. 199) recorded this subspecies from Assemblage I localities St-Clément-de-la-Place and Sceaux-d'Anjou, to which we add Beugnon and Renauleau.

**Distribution** – Middle Miocene: Atlantic, Loire Basin, France (Marquet, 2001). Upper Miocene: Atlantic (Tortonian), NW France (Marquet, 2001).

***Seila* sp.**

Plate 68, figs 1-2

**Material and dimensions** – Maximum height 8.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0330-0331 (2).

**Discussion** – A few specimens from St-Clément-de-la-Place represent a further *Seila* species with a protoconch consisting of at least three tall slender whorls. The protoconch is worn in all specimens. Like *S. carinata* (Smith, 1871), spirals 2 and 3 appear first, simultaneously, at the protoconch/teleoconch boundary, but this species has a less elevated protoconch than *S. carinata* with one whorl less, and there is no fourth spiral on the teleoconch whorls. Some of the West African species revised by Rolán & Pelorce (2006) have similar protoconch characters, but we await further material to formally identify this species.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (Marquet, 2001).

Family Newtoniellidae Korobkov, 1955  
Subfamily Ataxocerithiinae Ludbrook, 1957  
Genus *Ataxocerithium* Tate, 1894

**Type species** (by original designation) – *Cerithium serotinum* A. Adams in G.B. Sowerby II, 1855, present-day, Tasmania, Australia.

1894 *Ataxocerithium* Tate, p. 179.

**Note** – Van Dingenen *et al.* (2016, p. 110) discussed the inclusion of certain NW French Miocene and Pliocene cerithiid-like shells within the genus *Colina* H. Adams & A. Adams 1854, as done by Brébion (1964), and expressed their scepticism as to this placement. No protoconch material was available to the authors at the time. However, the resemblance to the *Colina* species reviewed by Houbrick (1990) is superficial. The protoconch of the type species of *Colina*, *Cerithium macrostoma* Hinds, 1844 from present-day Indonesia is smooth, comprising one whorl and indicative of direct development (Hou-

brick, 1990, p. 48).

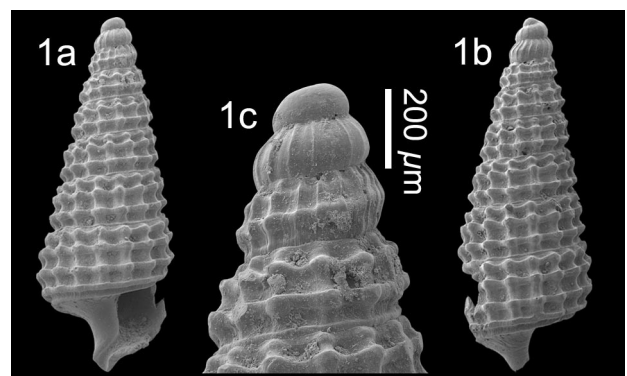
The upper Miocene Assemblage I material from NW France is far better preserved. Most specimens within this group are decollate, but the few shells with the protoconch preserved show it to be sculptured by strong axial ribs and supports placement within the Newtoniellidae Korobkov, 1955, genus *Ataxocerithium* Tate, 1894. The genus is known from the Eocene and Oligocene of Europe (Cossmann, 1906; Gründel, 1980), the lower Miocene Atlantic of the Aquitaine Basin of France (Cossmann & Peyrot, 1921) and the middle Miocene of the North Sea Basin (Marquet, 1997c) and the Paratethys (Boettger, 1902). *Cerithium puymoriae* Mayer, 1862 from the middle Miocene of the Loire Basin probably also belongs in this section, although we have not seen its protoconch. This is the latest stratigraphical record of the genus, which today is found in the western Pacific and Australia. Bouchet & Warén (1993) placed cerithiopsids with two peribasal cords in the genus *Krachia* Bałuk, 1975, but Bruce Marshall (personal communication to BL, 2018) suspects that the modern species referred to *Krachia* by Bouchet & Warén are related to *Ataxocerithium* and thus likely to be newtoniellids.

***Ataxocerithium cylindratum* (Jeffreys, 1885)**

Plate 69, fig. 1

- \*1885 *Cerithium cylindratum* Jeffreys, p. 112.
- 1985 *Cerithiopsis uruoi* Hallgass, p. 11, figs 1-3.
- 1999 *Krachia cylindrata* (Jeffreys, 1885) – Giannuzzi-Savelli *et al.*, p. 44, figs 72-75.
- 2006 *Krachia cylindrata* (Jeffreys, 1885) – Peñas *et al.*, p. 84, figs 121-124.
- 2009 *Krachia cylindrata* (Jeffreys, 1885) – Chirli, p. 3, pl. 1, figs 1-7.

**Material and dimensions** – Maximum height 2.6 mm, width 1.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1545-1546 (2). **Renauleau:** NHMW 2016/0103/1608 (5), LC (5).



**Plate 69.** *Ataxocerithium cylindratum* (Jeffreys, 1885); 1. NHMW 2016/0103/1545, height 2.4 mm, width 1.0 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Discussion** – Represented by a few specimens, the protoconch fits within the range for the extant (Giannuzzi-Savelli *et al.*, figs 73; Peñas *et al.*, p. 84, figs 123-124) and fossil (Chirli, pl. 1, figs 4, 5) specimens figured in the literature. In all specimens spiral 1 is delayed, appearing on the third teleoconch whorl. Another extant Mediterranean species, *A. tiara* (Monterosato, 1874) has an extra protoconch whorl.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli, 2009). Present-day: Mediterranean (Peñas *et al.*, 2006).

### *Ataxocerithium jucundum* (Millet, 1865)

Plate 70, figs 1-3

- 1854 *Cerithium Jucundum* Millet, p. 163 (*nomen nudum*).  
 \*1865 *Cerithium jucundum* Millet, p. 594.  
 1964 *Colina jucunda* Millet, 1854 – Brébion, p. 236, pl. 6, figs 13-14.  
 2016 *Colina jucunda* (Millet, 1865) – Van Dingenen *et al.*, p. 111, pl. 1, figs 4-7.

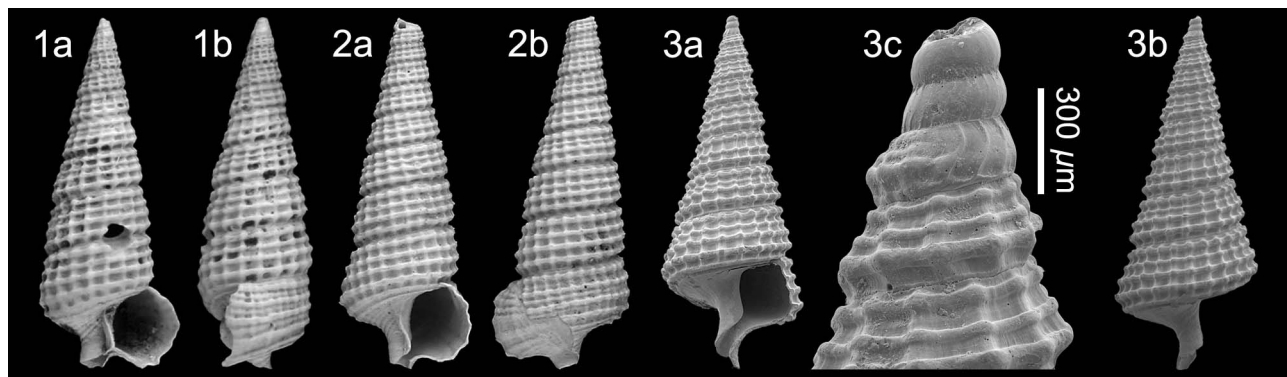
**Type material** – Syntypes: Sceaux-d'Anjou, Thorigné and Renauleau, Musée d'Angers, France (*vide* Brébion, 1964, p. 237).

**Material and dimensions** – Maximum height 18.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0499-0501 (3), NHMW 2016/0103/0502 (50+), RGM.1348525 (9 fragments), RGM.1348531 (6), RGM.1348532 (39 juveniles), RGM.1348547 (41 fragments), RGM.1348629 (50+ fragments), RGM.1348664 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0503 (9), RGM.1348582 (28), RGM.1348653 (5), RGM.1348660 (20), RGM.1348663 (50+ fragments), RGM.1348684 (35 fragments), RGM.1348780 (17), LC (20), FVD (14). **Renauleau**: NHMW 2016/0103/0504 (50+), RGM.1349000 (18), LC (50+), FVD (50+). **Beugnon**: RGM.1348476 (1), RGM.1348477 (40 fragments), RGM.1348507 (7), LC (5).

**Discussion** – *Ataxocerithium jucundum* (Millet, 1865) is characterised by having flat-sided whorls, spiral sculpture consisting of three spiral cords on the early teleoconch whorls, four or rarely five subequal spiral cords on later whorls and 17-19 axial ribs, roughly equal in strength to the cords forming a horizontally-elongated reticulated sculpture. Small tubercles develop at the sculptural intersections. The last two adult whorls become strongly varicose, and in some specimens inflated. The base is delimited by two smooth peribasal cords. The material from St-Clément-de-la-Place has the protoconch preserved and shows it to be newtoniellid in type, composed of 2.5 bulbous whorls, the last 1.5 whorls bearing strong orthocone ribs. The juvenile specimen figured (Pl. 71, fig. 3), has a multispiral protoconch of which only the last three whorls are preserved. The first preserved whorl (probably the second protoconch whorl) has micropustules on the abapical half, strengthening towards the suture. The second and third preserved whorls bear sinuous axial riblets fusing with a narrow suprasutural cord on the last whorl.

*Ataxocerithium jucundum* differs from *A. puymoriae* (Mayer, 1862), from the middle Miocene Loire Basin of France, in having flatter sided whorls, finer sculpture, with four or more cords on intermediate spire whorls, whereas in *A. puymoriae* only the penultimate and last whorl have four cords. In both species the fourth cord appears between the first and second cord. The specimen of *A. puymoriae* figured by Glibert (1949, pl. 9, fig. 9) does not show any varices. The two North Sea Basin middle Miocene species illustrated by Marquet (1997c) *A. christinae* (Boettger, 1902) and *A. asperatum* (Cossman & Peyrot, 1922) both differ in having a far higher multispiral protoconch composed of more numerous whorls. The early teleoconch sculpture of *A. asperatum* is similar to that of *A. jucundum*, with three primary spiral cords (see Marquet, 1997c, p. 28, fig 2d).

Millet (1865, p. 595) recorded this species from from Assemblage I (Renauleau, Sceaux-d'Anjou, Thorigné). Brébion (1964, p. 238) added several further Assemblage I localities (St-Michel, les Pierres Blanches, Chalonnès, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné, Le Temple du Cerisier, Moulin de Carcé) and



**Plate 70.** *Ataxocerithium jucundum* (Millet, 1865); 1. NHMW 2016/0103/0499, height 8.6 mm, width 3.4 mm; 2. NHMW 2016/0103/0500, height 8.9 mm, width 3.6 mm; 3. NHMW 2016/0103/0501, height 3.2 mm, width 1.2 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Assemblage III (Le Pigeon Blanc, Le Girondor, La Gauvinière, La Dixmerie, Palluau).

*Distribution* – Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016).

***Ataxocerithium petitianum* (Millet, 1865)**

Plate 71, figs 1-3

- 1854 *Cerithium Petitianum* Millet, p. 164 (*nomen nudum*).  
 \*1865 *Cerithium Petitianum* Millet, p. 595.  
 1964 *Colina petitiana* [sic] Millet, 1854 – Brébion, p. 235, pl. 6, figs 11-12.  
 2016 *Colina petitiana* (Millet, 1865) – Van Dingenen *et al.*, p. 111, pl. 1, fig. 8.

*Type material* – Syntypes: Sceaux-d'Anjou, Thorigné, Renauleau and St-Michel, Musée d'Angers, France (*vide* Brébion, 1964, p. 235).

*Material and dimensions* – Maximum height 20.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0493-0496 (4), NHMW 2016/0103/0497 (50+), RGM.1348533 (14 juveniles), RGM.1348548 (3 + 9 fragments), RGM.1348639 (50+), RGM.1348661 (26 fragments), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0498 (17), NHMW 2016/0103/1685 (1), RGM.1348576 (46), RGM.1348585 (2), RGM.1348656 (50+), RGM.1348659 (50+), RGM.1348662 (31 fragments), RGM.1348685 (50+), RGM.1348709 (40 fragments), RGM.1348765 (40 fragments), RGM.1348781 (50+), RGM.1348799 (13 fragments), RGM.1348917 (50+ fragments), LC (50+), FVD (50+). **Renauleau:** LC (1?).

*Discussion* – The Assemblage I specimens of *Ataxocerithium petitianum* (Millet, 1865) are characterised by having spiral sculpture consisting of five or six spiral cords on each whorl, the two adapical cords are usually fused to form a broader subsutural cord, below which are 1-2 weaker cords placed mid-whorl. The two abapi-

cal cords are more strongly developed and have prominent tubercles formed at the sculptural intersections. The strength of these abapical cords is highly variable, as can be seen in the series illustrated (Pl. 71, figs 1-3). They differ slightly from the lower Pliocene Assemblage III specimen illustrated by Van Dingenen *et al.* (2016, pl. 1, fig. 8) in that the Pliocene forms have 3-4 weaker adapical cords, often alternate in strength, and lacks the fused subsutural cord. The protoconch (Pl. 71, fig. 4), is multispiral, composed of just over four whorls. The first whorl is covered in micropustules, abapically prominent sinuous opisthocline ribs develop, fusing with a narrow suprasutural cord on the last whorl. This protoconch is very similar to that of *A. jucundum* (Millet, 1865), but seems to have three ribbed whorls instead of two.

*Ataxocerithium petitianum* is similar in sculpture to *A. christinae* (Boettger, 1902) recorded from the middle Miocene Paratethys of Romania and the middle Miocene North Sea Basin of Belgium (Marquet, 1997c). Both species have the lower two spiral cords on each whorl swollen, but the protoconch in *A. christinae* is comprised of fewer whorls, sculptured with more widely spaced ribs. Millet (1865, p. 595) recorded this species from from Assemblage I (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel). Brébion (1964, p. 238) added several further Assemblage I localities (les Pierres Blanches, St-Clément-de-la-Place). Van Dingenen *et al.* (2016) added Assemblage III (Le Pigeon Blanc).

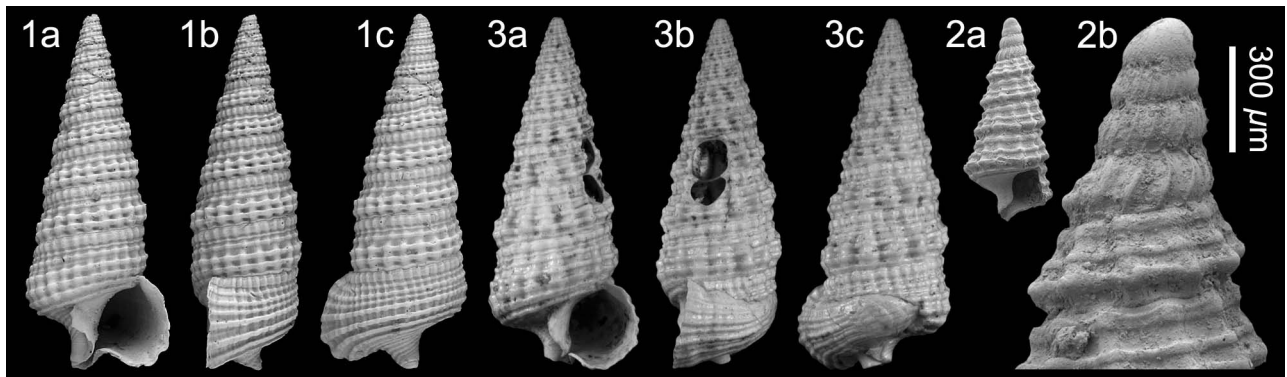
*Distribution* – Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016).

***Ataxocerithium turbineum* nov. sp.**

Plate 72, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1547, height 5.5 mm, width 2.3 mm; paratype 1 NHMW 2016/0103/1548, height 6.5 mm, width 2.4 mm.

*Other material* – Known only from type series.



**Plate 71.** *Ataxocerithium petitianum* (Millet, 1865); 1. NHMW 2016/0103/0493, height 11.9 mm, width 4.8 mm; 2. NHMW 2016/0103/0496; 4b, detail of protoconch (SEM image); Le Grand Chauvère, St-Clément-de-la-Place. 3 NHMW 2016/0103/1685, height 12.8 mm, width 5.7 mm; La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Etymology* – Latin from ‘*turbineus, -a, um*’, adjective, meaning gyrating like a spinning top, reflecting the shape of the protoconch. *Ataxocerithium* gender neuter.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Ataxocerithium* species with relatively broad shell, protoconch of 2.5 whorls; first whorl bulbous, smooth, second whorl bearing regular axial ribs, straight-sided teleoconch whorls bearing three spiral cords on first 3-4 whorls; appearing in order spiral 3, 4, 1; spiral 2 appearing on later teleoconch whorls, so that last whorl bears four equal, evenly spaced cords, close-set axial ribs forming weakly tubercular sculpture, two smooth peribasal cords of which abapical is weaker, smooth base.

*Description* – Shell small, with relatively broad apical angle, elongate. Protoconch consisting of 2.5 convex whorls with medium-sized nucleus; first whorl bulbous, smooth, second whorl bearing regularly placed orthocline axial ribs. Junction delimited by beginning of adult sculpture. Teleoconch of up seven straight-sided whorls separated by impressed suture. Sculpture of four spiral cords; spiral 3 appears at protoconch/teleoconch junction, rapidly followed by spiral 4 and spiral 1, so that first 3-4 whorls have three spirals. Spiral 2 appears on third to fourth whorl, rapidly strengthening abapically to become equal in strength to other spirals and evenly spaced on last whorl. Axial sculpture of about 18-20 weak ribs, forming horizontally elongated reticulated surface pattern, with small tubercles formed at sculptural intersections. Last whorl weakly convex; two smooth peribasal cords delimiting concave base, abapical peribasal cord weaker, base smooth, devoid of cords. Aperture small, outer lip simple, columella hardly excavated, columellar and parietal callus hardly developed.

*Discussion* – *Ataxocerithium turbineum* nov. sp. differs from all its Assemblage I congeners in having a broad-

er apical angle and four spirals on the later teleoconch whorls. Spiral 2 is delayed, only appearing on the third to fourth teleoconch whorl. The first protoconch whorl is bulbous, larger than the second whorl, similar to that of *A. cossmanni* (Dautzenberg & Fischer, 1896) from the eastern European Atlantic, but that species differs in having more convex teleoconch whorls bearing three spirals; Spiral 1 weakest. *Ataxocerithium obeliscoides* (Jeffreys, 1885) from the Atlantic of southwestern Europe, North Africa and the Azores also has a large first protoconch whorl, but differs in having more convex whorls, four thinner spirals developed earlier on the teleoconch, and more numerous thinner spirals on the last whorl.

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

#### *Ataxocerithium turgidulum* (Millet, 1865)

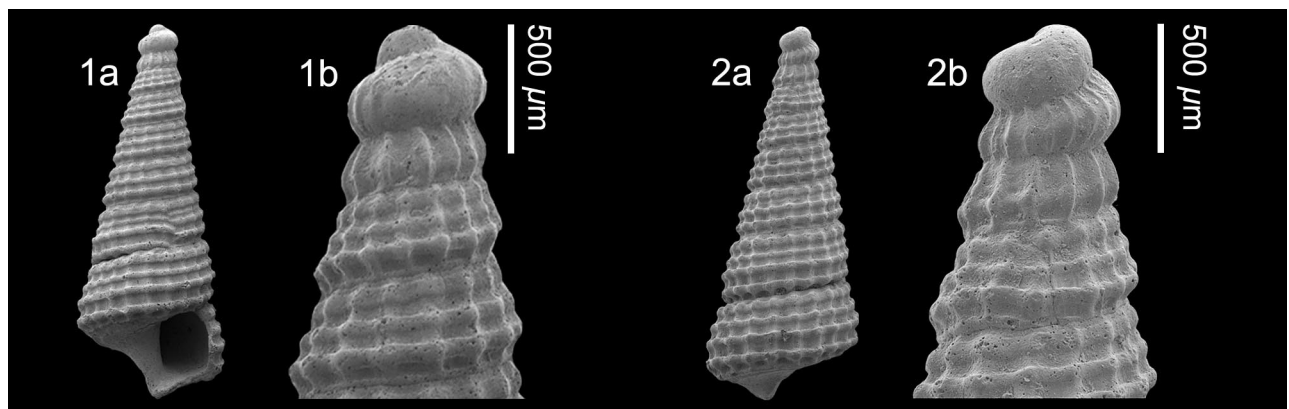
Plate 73, figs 1-4

- 1854 *Cerithium Turgidulum* Millet, p. 164 (*nomen nudum*).  
 \*1865 *Cerithium turgidulum* Millet, p. 595.  
 1964 *Colina turgidula* [sic] Millet, 1854 – Brébion, p. 238, pl. 6, fig. 15.

*Type material* – Syntypes: Sceaux-d’Anjou, Thorigné and Renauleau, Musée d’Angers, France (*vide* Brébion, 1964, p. 239).

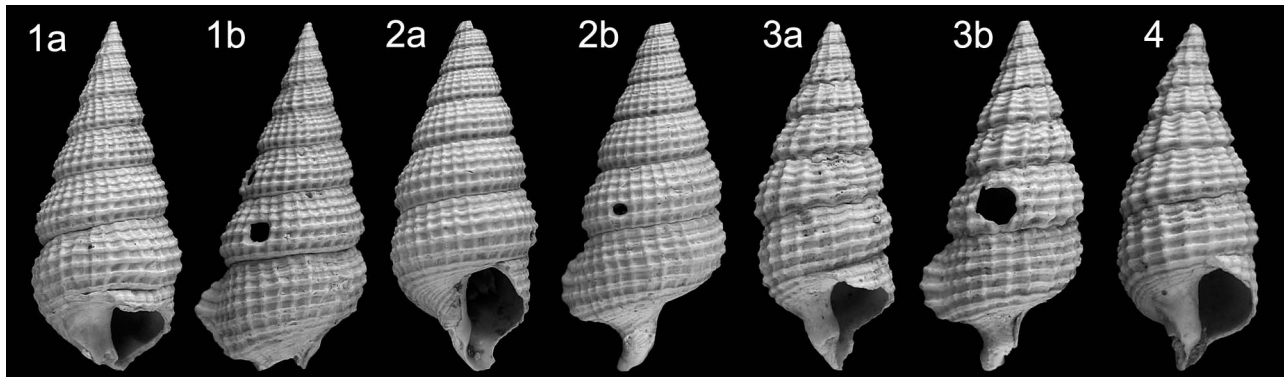
*Material and dimensions* – Maximum height 13.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0488-0489 (2), RGM.1348549 (1), LC (3). **Sceaux-d’Anjou:** NHMW 2016/0103/0490-0491 (2), NHMW 2016/0103/0492 (1), RGM.1348420575 (5), RGM.1348665 (1), RGM.1348686 (4), RGM.1348782 (3), RGM.1348800 (2), LC (4). **Renauleau:** LC (8?).

*Discussion* – *Ataxocerithium turgidulum* (Millet, 1865) is characterised by its inflated shell shape. The protoconch is incomplete in all the material at hand, but the last protoconch whorl is preserved on one specimen



**Plate 72.** *Ataxocerithium turbineum* nov. sp.; 1. **Holotype** NHMW 2016/0103/1547, height 5.5 mm, width 2.3 mm; 2. **Paratype 1** NHMW 2016/0103/1548, height 6.5 mm; width 2.4 mm; 1b, 2b, detail of protoconch (all SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.





**Plate 73.** *Ataxocerithium turgidulum* (Millet, 1865); 1. NHMW 2016/0103/0488, height 13.4 mm, width 5.9 mm; 2. NHMW 2016/0103/0489, height 13.5 mm, width 5.8 mm. Le Grand Chauvère, St-Clément-de-la-Place; 3. NHMW 2016/0103/0489, height 13.4 mm, width 5.9 mm; 3. NHMW 2016/0103/0490, height 12.7 mm, width 5.5 mm; 4. NHMW 2016/0103/0491, height 9.5 mm, width 4.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

and shows axial ribs similar to those of the other species included in this section. The teleoconch consists of 7-8 weakly convex whorls, bulging just above the deeply impressed suture. The number of axial ribs differs between the specimens from St-Clément-de-la-Place ( $\approx 40$ ; Pl. 73, figs 1-2) and those from Sceaux d'Anjou (18-20; Pl. 73, figs 3-4). This difference might warrant separation at specific level, but the shell shape and number of spiral cords is the same, which has led us to a conservative approach to this species. All specimens have five spiral cords crossing the axial ribs, forming small tubercles at the intersections. Like other species included here in *Ataxocerithium*, the penultimate or last whorl can be gibbose and strongly varicose. The base is delimited by two peribasal cords, the axial sculpture stopping abruptly at the adapical peribasal cord. Further weaker smooth cords cover the base. The aperture and protoconch is damaged in all specimens. *Ataxocerithium turgidulum* is separated from its congeners by its broad shell shape.

Millet (1865, p. 595) recorded this species from from Assemblage I (Renauleau, Sceaux-d'Anjou, Thorigné). Brébion (1964, p. 238) added the Assemblage I locality of St-Clément-de-la-Place, and doubtfully from Assemblage II (Apigné).

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

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

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

1843 *Petalococonchus* H.C. Lea, p. 162.

For generic synonymy see Van Dingenen *et al.* (2016, p. 155).

### *Petalococonchus intortus* (Lamarck, 1818)

Plate 74, fig. 1

- \*1818 *Serpula intorta* Lamarck, p. 365.
- 1964 *Petalococonchus intortus* var. *woodi* Mörch, 1861 – Brébion, p. 209.
- 2004a *Petalococonchus glomeratus* (Linnaeus, 1758) – Landau *et al.*, p. 27, pl. 3, figs 15, 16 (*cum syn.* – fossil references only) [*non Petalococonchus glomeratus* Linnaeus, 1758)].
- 2011 *Petalococonchus glomeratus* (Linnaeus, 1758) – Landau *et al.*, p. 13, pl. 4, fig. 1 [*non Petalococonchus glomeratus* Linnaeus, 1758)].
- 2013 *Petalococonchus intortus* (Lamarck, 1818) – Landau *et al.*, p. 65, pl. 5, fig. 15.
- 2016 *Petalococonchus intortus* (Lamarck, 1818) – Van Dingenen *et al.*, p. 155, pl. 13, fig. 7.

**Material and dimensions** – Maximum height 15.5 mm.

**St-Clément-de-la-Place:** NHMW 2016/0103/0689 (1), NHMW 2016/0103/0690 (50+), RGM.1347857 (37), RGM.1347868 (50+), RGM.1347962 (19 juveniles), RGM.1348630 (8), LC (50+), FVD (50+). **Sceaux d'Anjou:** NHMW 2016/0103/0691 (30), RGM.1347869 (50+), RGM.1347870 (50+), RGM.1347873 (25), RGM.1347914 (24), RGM.1347932 (50+), RGM.1347985 (50+), RGM.1348069 (50+), RGM.1348927 (13), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1404 (50+), RGM.1348979 (42), LC (50+), FVD (50+). **Beugnon:** RGM.1348398 (50+), RGM.1348378430 (2), RGM.1348470 (50+), LC (10).

**Discussion** – As discussed by Landau *et al.* (2013, p. 65), Scuderi (2012) considered the fossil European Neogene species *Petalococonchus intortus* (Lamarck, 1818) to be distinct from the present-day species *P. glomeratus* (Linnaeus, 1758), the fossil species differing from the extant one in details of the protoconch. Whilst both have a protoconch consisting of about 2.5 whorls, that of the fossil species is smaller ( $0.65 \times 0.4$  mm, vs.  $1.1 \times 0.7$  mm), and there is a basal cord on the protoconch in the fossil spe-

cies that is absent in *P. glomeratus*. Again, we accept this distinction, although we do not have a specimen with a protoconch from the Assemblage I material.

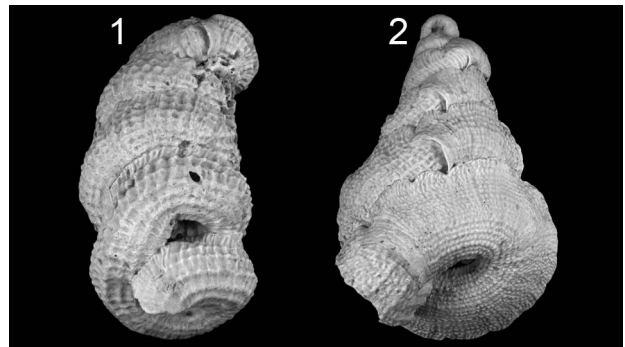
This species is common in the NW French Assemblage I deposits. The specimens are much smaller than those from some other fossil assemblages, such as the middle Miocene of the Karaman Basin, Turkey, where specimens can reach over 40 mm in height (Landau *et al.*, 2013, p. 65). It is quite possible that these fossil forms represent a species complex rather than a single species, but until protoconch material from different populations is compared, we consider them all *P. intortus*.

Brébion (1964, p. 210) recorded this species from Assemblage I (Renauleau, Sceaux-d'Anjou, Thorigné, St. Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu), Assemblage II (Apigné) and Assemblage III (Le Pigeon Blanc, Le Girondor, La Gauvinière, Palluau) and Assemblage IV (St-Jean-la-Poterie).

**Distribution** – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964; Moths, 1989), Netherlands (Janssen, 1984). Middle Miocene: Atlantic (Aquitainian-Serravallian): Aquitaine Basin, (Cossmann & Peyrot, 1924; Lozouet *et al.*, 2001), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1914; Bałuk, 1970, 1975), Vienna Basin, Austria (Hörnes, 1856; Tejkal *et al.*, 1967; Schultz, 1998), Bulgaria (Kojumdzieva & Strachimirov, 1960), Hungary (Strausz, 1966), Romania (Moisescu, 1955; Stancu & Andreescu, 1968); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentoz, 1958). Upper Miocene: northeastern Atlantic (Tortonian and Messinian), NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1896b), Tunisia (Stchepinsky, 1938). Lower Pliocene: North Sea Basin, England (Wood, 1848; Harmer, 1918), Belgium (Glibert, 1958; Marquet, 1997b); Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016), Guadalquivir Basin, Spain (González-Delgado, 1986; Landau *et al.*, 2011), Morocco (Lecointre, 1952); western Mediterranean, northeastern Spain, (Martiniell & Domènech, 1984; Solsona, 1998), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974; Anfossi *et al.*, 1983; Baroncelli, 2001); Tunisia (Fekih, 1975). Lower-upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); western Mediterranean, Estepona Basin (Landau *et al.*, 2004a); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912; Taviani *et al.*, 1998).

Genus *Thylacodes* Guettard, 1770

*Type species* (by subsequent designation, Keen, 1961) –



**Plate 74.** 1. *Petalocochus intortus* (Lamarck, 1818), NHMW 2016/0103/0689, height 11.2 mm, width 6.2 mm. 2. *Thylacodes arenarius* (Linnaeus, 1758), 2016/0103/0692, height 13.0 mm, width 8.3 mm. Le Grand Chauverau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Serpulorbis polyphragma* Sassi, 1827, present-day, Mediterranean.

1770 *Thylacodes* Guettard, p. 143.

For generic synonymy see Van Dingenen *et al.* (2016, p. 156).

#### ***Thylacodes arenarius* (Linnaeus, 1758)**

Plate 74, fig. 2

- \*1758 *Serpula arenaria* Linnaeus, p. 1266.
- 1854 *Serpula Dentifera*? Lamk. – Millet, p. 153 [*non Thylacodes dentiferus* (Lamarck, 1818)].
- 1964 *Lemintina arenaria* Linné, 1766 [*sic*] – Brébion, p. 211.
- 2013 *Thylacodes* [*sic*] *arenarius* (Linnaeus, 1758) – Landau *et al.*, p. 65, pl. 5, fig. 16 (*cum syn.*).
- 2016 *Thylacodes arenarius* (Linnaeus, 1758) – Van Dingenen *et al.*, p. 156, pl. 13, fig. 8.

**Material and dimensions** – Maximum height 30.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0692 (1), NHMW 2016/0103/0693 (15), RGM.1347858 (3), RGM.1347867 (41), RGM.1348631 (2), LC (20), FVD (17). **Sceaux d'Anjou:** NHMW 2016/0103/0694 (30), RGM.1347871 (11), RGM.1347876 (50+), RGM.1347931 (2), RGM.1347984 (5), RGM.1348070 (35), LC (15), FVD (10). **Renauleau:** NHMW 2016/0103/1405 (20), RGM.1348990 (12), LC (22). **Beugnon:** RGM.1348399 (17).

**Discussion** – *Thylacodes arenarius* (Linnaeus, 1758) was fully discussed by Landau *et al.* (2013, p. 65). The specimens from Assemblage I are relatively small in size compared to those found in other localities, although fragments of fairly large individuals occur at St-Clément-de-la-Place.

Brébion (1964, p. 211) recorded this species from As-

semblage I (Renauleau, Sceaux-d'Anjou, Thorigné, St. Michel, St-Clément-de-la-Place, les Cléons, Beaulieu), Assemblage II (Apigné) and Assemblage III (Le Pigeon Blanc, Le Girondor) and Assemblage IV (Gourbesville).

**Distribution** – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Netherlands (Janssen, 1984). Middle Miocene: Atlantic (Aquitanian-Serravallian): Aquitaine Basin, (Cossmann & Peyrot, 1924), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1914, 1938; Bałuk, 1975), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Csepregy-Meznerics, 1954; Strausz, 1966), Romania (Moisescu, 1955; Stancu & Andreescu, 1968), Bosnia (Atanacković, 1969; Eremija, 1971), Ukraine (Zelinskaya *et al.*, 1968); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016), Guadalquivir Basin, Spain (González-Delgado, 1986; Landau *et al.*, 2011), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a), northeastern Spain, (Solsona, 1998), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974; Anfossi *et al.*, 1983); Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1912). Present-day: north-eastern Atlantic, Iberian Peninsula, Morocco, Mediterranean (Poppe & Goto, 1991).

Subfamily Dendropomatinae Bandel & Kowalke, 1997  
Genus *Dendropoma* Mörch, 1861

**Type species** (by subsequent designation, Keen, 1961) – *Siphonium lituella* Mörch, 1861, present-day, California, USA.

- 1842 *Bivonia* Gray, pp. 62, 90. Type species (by subsequent designation, Gray, 1847b): *Vermetus glomeratus* Bivona-Bernardi, 1832, present-day, Mediterranean. Junior homonym of *Bivonia* Cocco, 1832 [Crustacea].
- 1850 *Siphonium* Gray, p. 82. Junior homonym of *Siphonium* Link, 1807 [Cephalopoda].
- 1861 *Dendropoma* Mörch, p. 153.
- 1937 *Veristoa* Iredale, p. 254. Type species (by original designation): *Veristoa howensis* Iredale, 1937, present-day, Lord Howe Island, Australia.

***Dendropoma cristatum* s. l. (Biondi, 1859)**

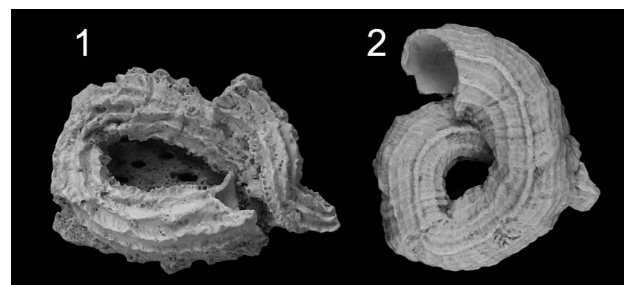
Plate 75, figs 1-2

- 1832 *Vermetus glomeratus* Bivona-Bernardi, p. 7, pl. 2, fig. 7 (*non* Linnaeus, 1758).
- \*1859 *Vermetus cristatus* Biondi, p. 120, pl. 1, fig. 5.
- 1884b *Bivonia petraea* Monterosato, p. 81.
- 1884 *Vermetus panormitanus* de Gregorio, p. 119.
- 1892 *Vermetus cristatus* f. *minor* Monterosato, p. 43.
- 1995 *Dendropoma* (*Novastao*) *glomeratum* (Bivona, 1832) – Scuderi, p. 2, pl. 1, figs 1-7.
- 1996 *Vermetus* (*Vermetus*) *cristatus* Biondi, 1857 [*sic*] – Giannuzzi-Savelli *et al.*, p. 146, fig. 622.

**Material and dimensions** – Maximum diameter 10.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1361 (1), NHMW 2016/0103/1362 (1), NHMW 2016/0103/1749 (1). **Sceaux d'Anjou**: NHMW 2016/0103/1787 (23), RGM.1347872 (4), RGM.1347875 (5), LC (2).

**Discussion** – Recent phylogenetic analysis using morphological, anatomical and molecular data concluded that the genus *Dendropoma* s.l. was not monophyletic and that the Mediterranean species all belong to the genus *Dendropoma* s.s. (Golding *et al.*, 2014). For the Mediterranean, Calvo *et al.* (2009) demonstrated the presence of a species complex consisting of four species. Templado *et al.* (2016) assigned the names *D. lebeche* Templado, Richter & Calvo, 2016 and *D. anguliferum* (Monterosato, 1878) to two species within this complex, and recognised an unnamed third. For the fourth, *D. petraeum sensu stricto* they accepted a senior synonym, *D. cristatum* (Biondi, 1859), as had been proposed previously by Scuderi (1995). Unfortunately, these species cannot be separated based on their teleoconchs and we can only say that the species complex is represented in the Assemblage I fauna by a species with a shell similar to that of *D. cristatum*. We have also been unable to find any European Neogene fossil record for the genus.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Little can be said about the specific stratigraphic distribution within this genus that cannot be separated on shell characters.



**Plate 75.** *Dendropoma cristatum* s. l. (Biondi, 1859); 1. NHMW 2016/0103/1361, diameter 10.9 mm; 2. NHMW 2016/0103/1749, diameter 6.8 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



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

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

1826 *Alvania* Risso, p. 140.

For generic synonymy see Van Dingenen *et al.* (2016, p. 135).

***Alvania acuticarinata* nov. nom.**

Plate 76, figs 1-4

1854 *Delphinula Carinata* Millet, 1854, p. 158 (*non* Woodward, 1833).

1964 *Pyrgula (Trachypyrgula) carinata* Millet, 1854 – Brébion, p. 145, pl. 4, fig. 7.

*Type material* – Syntypes: Sceaux-d’Anjou, lost (*vide* Brébion, 1964, p. 145).

*Material and dimensions* – Maximum height 2.5 mm, width 1.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0355-0356 (2), NHMW 2016/0103/0357 (50+), NHMW 2016/01031696-1697 (2), RGM.1347940 (1), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0359 (3), RGM.1309585 (2), RGM.1347986 (1). **Re-nauleau:** NHMW 2016/0103/0358 (3).

*Etymology* – Name honouring Millet’s intention to highlight the prominent carina, adding the Latin ‘*acutus, acuta*’ adjective, meaning sharp, so sharply carinate. *Alvania* gender feminine.

*Locus typicus* – Sceaux-d’Anjou.

*Stratum typicum* – Tortonian, upper Miocene.

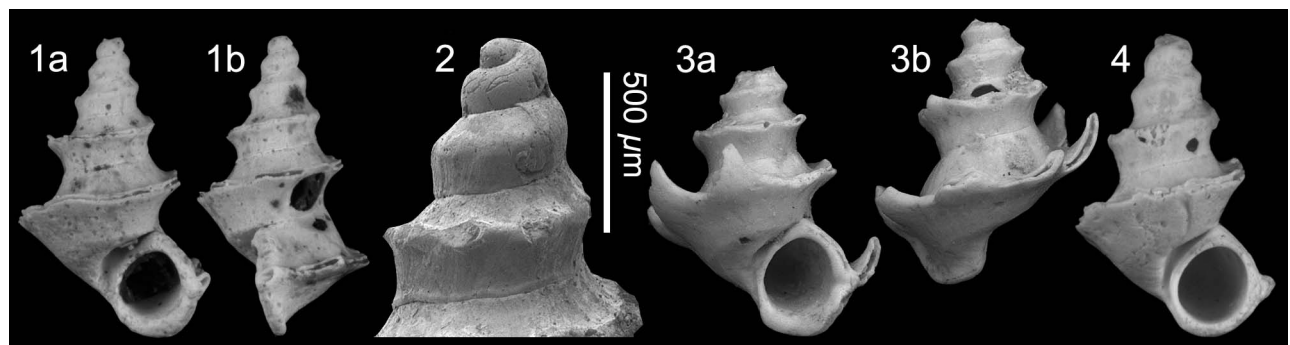
*Original description* – ‘*Carinata, Millet. — Sceaux. —*

*Très rare. — Chaque tour de spire est surmonté d’une carène dentée*’ (Millet, 1854, p. 158).

*Revised description* – Shell small, rissoiform, slender with acutely carinate whorls. Protoconch composed of two elevated smooth whorls, with medium sized nucleus. Transition with teleoconch marked by protoconch lip. Teleoconch consisting of just over three angular whorls. Suture linear, superficial. A single, elevated, spinous spiral cord, placed mid-whorl, runs along shoulder; broad concave subsutural ramp above, straight sided and tapering to suture below. Shoulder cord gains in strength abapically so that last two whorls coronate mid-whorl. Axial sculpture absent. Last whorl with broad straight to concave subsutural ramp, sharply angular at shoulder, shoulder cord strongly elevated, bearing 8-9 short spines. Base weakly convex, devoid of sculpture, with narrow, elongated umbilical chink. Aperture small, circular; outer lip strongly thickened by varix, smooth within. Peristome complete; columellar and parietal callus thickened, sharply delimited, forming very narrow erect callus rim delimiting medial border of umbilical chink.

*Discussion* – There is little with which to compare this remarkable little shell. Brébion (1964, p. 145) placed it in the hydrobiid subgenus *Pyrgula (Trachypyrgula)* Cossmann, 1921 (type species *Pyrgula pagoda* Neumayr in Herbich & Neumayr, 1875, by original designation; *non Trachypyrgula* Radoman, 1955: not available; no type species designated. Junior homonym of *Trachypyrgula* Cossmann, 1921). The type species is a fossil fresh-water taxon from Romania and not upper Miocene Sarmatian as stated by Cossmann. *Pyrgula pagoda* was extensively illustrated by Jekelius (1932, pl.10, figs 1-32) and although the whorls are strongly carinate, as in the French species, the apertural characters are quite different. More interesting is the species described as *A. alboranensis* Peñas & Rolán, 2006, possibly subfossil, from the Alboran Sea. The shape, sculpture and apertural characters are highly reminiscent of the French species. It differs most obviously in having a prominent basal carina that is missing in the French species.

Millet (1954, p. 158) erected the name *Delphinula carina-*



**Plate 76.** *Alvania acuticarinata* nov. nom; 1. NHMW 2016/0103/0355, height 2.5 mm, width 1.7 mm; 2. NHMW 2016/0103/0356 (juvenile), detail of protoconch (SEM image); 3. NHMW 2016/0103/1696, height 3.0 mm, width 2.6 mm; 4. NHMW 2016/0103/1697, height 2.9 mm, width 2.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*ta* for the French shell. Unfortunately, this name is invalid as it is a primary homonym of *D. carinata* Woodward, 1833, which is itself a junior subjective synonym of *Littorina littorea* (Linnaeus, 1758). Placement of the species in the genus *Alvania* also makes the name a secondary homonym of *A. carinata* (da Costa, 1778). We therefore propose *Alvania acuticarinata* nov. nom. for the French upper Miocene species.

Grateloup (1845, pl. 12, fig. 15) illustrated a similar shell from the Oligocene of France under the name *Delphinula pyramidata* (Grateloup, 1828). As well as having a prominent spinous mid-whorl carina, it differs from *A. acuticarinata* in having the whorls covered in spiral cords. If we are correct in ascribing Grateloup's species to *Alvania pyramidata*, unfortunately it becomes a secondary homonym of *A. pyramidata* Risso, 1826, a junior subjective synonym of *Alvania cimex* (Linnaeus, 1758). We have not seen Grateloup's species, which seems to be exceedingly rare. No specimens are present at the MNHN Paris (J.M. Pacaud personal communication with BL, 2016), and we have not been able to find any in private collections. Therefore we do not propose a *nom. nov.* for Grateloup's species.

Millet (1854, p. 158) recorded *A. acuticarinata* from the Assemblage I locality of Sceaux-d'Anjou, Brébion (1964, p. 146) added St-Clément-de-la-Place, to which we add Renauleau.

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

***Alvania armata* nov. sp.**

Plate 77, figs 1-2

*Type material* – Holotype MNHN.F.A66707, height 2.6 mm, width 1.6 mm; paratype 1 MNHN.F.A66708, height 2.4 mm, width 1.4 mm; paratype 2 NHMW 2016/0103/1586, height 2.8 mm, width 1.6 mm; paratype 3 NHMW 2016/0103/1587, height 2.7 mm, width 1.6 mm; paratype 4 NHMW 2016/0103/1588, height 2.8 mm, width 1.6 mm, **Renauleau**. Paratype 5 RGM.1348731, height 2.9 mm, width 1.6 mm; paratype 6 RGM.1348732, height 2.7 mm, width 1.5 mm, **St-Clément-de-la-Place**.

*Other material* – Maximum height 2.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1778 (8), RGM.1348733 (17), RGM.1348955 (6). **Renauleau**: NHMW 2016/0103/1589 (50+), RGM.1349013 (20), LC (50+), FVD (50+). **Beugnon**: RGM.1348503 (3).

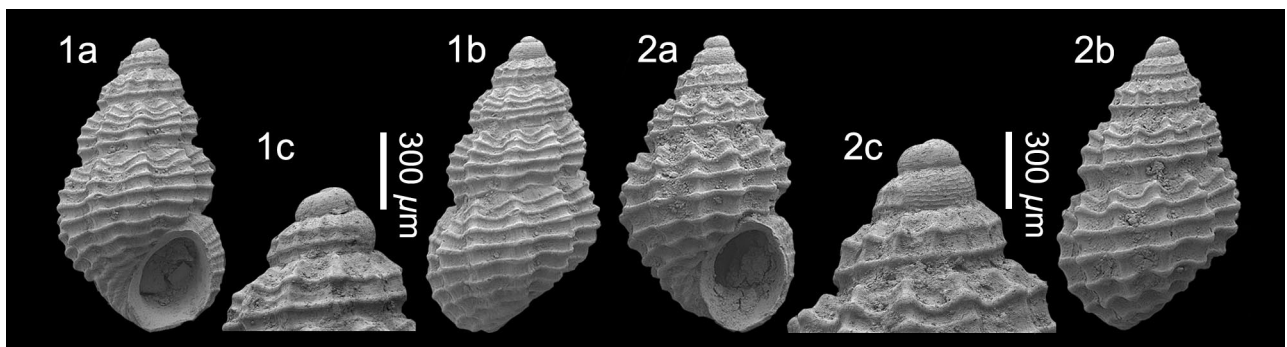
*Etymology* – Latin 'armatus, -a', adjective, meaning armoured or armour-clad, reflecting the solid shell and strong sculpture. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of small size, solid, with protoconch of 1.5 whorls bearing spiral sculpture on protoconch II, teleoconch of four convex whorls separated by impressed suture, penultimate whorl with 10-12 broad ribs and 3 major plus 1-2 minor cords on subsutural ramp that overrun cords without forming tubercles, base not delimited, aperture small, outer lip strongly thickened, not flared, smooth within.

*Description* – Shell small, solid, rissoiform. Protoconch paucispiral, composed of 1.5 convex whorls, with a medium-sized nucleus; Protoconch I surface abraded; protoconch II sculptured by irregular spiral threads (dp = 370  $\mu$ m, hp = 280  $\mu$ m). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of four convex whorls, with periphery just below mid-whorl. Suture weakly undulating, impressed. Axial sculpture of broad orthocline ribs; 10-12 on penultimate whorl, about half width of their interspaces. Spiral sculpture on first teleoconch whorl bearing two narrow cords; on second whorl, secondary cord develops between cords 1 and 2, strengthening abapically, plus 1-2 cords on subsutural ramp; penultimate whorl bearing three primary cords plus 1-2 weaker cords below suture. Spirals overrun cords, without developing tubercles at intersections. Last whorl evenly rounded, bearing 10-12 spiral cords; base not delimited, imperforate. Aperture small, ovate, outer lip rounded, not flared abapically, thickened by varix, smooth within. Columella broadly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.



**Plate 77.** *Alvania armata* nov. sp.; 1. **Holotype** MNHN.F.A66707, height 2.6 mm, width 1.6 mm, 1c, detail of protoconch; 2. **Paratype 1** MNHN.F.A66708, height 2.4 mm, width 1.4 mm, 1c, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – *Alvania armata* nov. sp. is a very characteristic species with its small solid shell, strong sculpture of broad ribs and narrow elevated cords, and small thickened aperture. There is some variability in the number of cords, as illustrated in the series figured (Pl. 77, figs 1-2). In the Assemblage I fauna it could only be confused with *A. robusta* Calas, 1949, but that species is larger, and has a more conical spire with a canaliculated suture, more numerous and narrower ribs, and a wider aperture with a denticulate outer lip. In the extant faunas two eastern Mediterranean species have similar sculpture; *A. aspera* (Philippi, 1844) has a subangular last whorl on which the axial ribs disappear on the base and *A. colossophilus* Oberling, 1970 has a subangular last whorl on which the axial ribs persist on the base, but has a more pointed spire. In the Italian lower Pliocene *A. caporlii* Chirli, 2006 is also small and solid shelled, with a spirally-striate paucispiral protoconch, a teleoconch with broad ribs over-run by narrow elevated cords and a small aperture, but it is squatter than *A. armata*, the teleoconch whorls are subangular, the ribs weaken and disappear mid-base, and the outer lip is denticulate within. Also from the Mediterranean Pliocene, *A. monterosatoi* (Fischer, 1877), is small and robust, with similar teleoconch sculptural elements (slightly fewer ribs and more cords), but differs in having a micropustular paucispiral protoconch.

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

***Alvania couffoni* nov. sp.**

Plate 78, figs 1-2

*Type material* – Holotype MNHN.F.A57714, height 4.0 mm, width 2.3 mm; paratype 1 MNHN.F.A57715, height 3.9 mm, width 2.3 mm; paratype 2 NHMW 2016/0103/0344, height 4.2 mm, width 2.4 mm; paratype 3 NHMW 2016/0103/0345, height 4.1 mm, width 2.2 mm; paratype 4 RGM.1348567, height 4.4 mm, width 2.1 mm; paratype 5 RGM.1348568, height 4.5 mm, width 2.2 mm.

*Other material* – Maximum height 4.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0346 (50+), RGM.1348569 (5), LC (50+), FVD (50+).

*Etymology* – Named in honour of Olivier Couffon (1882-1937), director of the Muséum d'histoire naturelle d'Angers (1929-1937), in recognition of his work on the NW French upper Miocene assemblages. *Alvania* gender feminine.

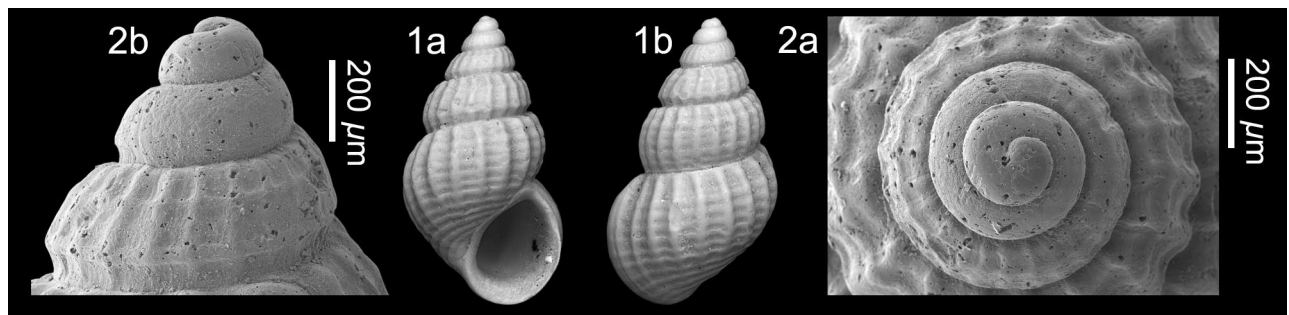
*Locus typicus* – Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of average size, protoconch of 2.2 smooth whorls, teleoconch of four convex whorls separated by canaliculated suture, with predominantly axial sculpture of narrow rounded ribs, 19-20 on penultimate whorl, obsolete over base, and flattened cords in interspaces, 6-7 on penultimate whorl.

*Description* – Shell average size for genus, rissoiform. Protoconch dome-shaped, composed of 2.2 smooth whorls (dp = 460 µm, hp = 430 µm, dn = 120 µm, dp1 = 245 µm). Transition with teleoconch abrupt marked by beginning of teleoconch sculpture. Teleoconch consisting of four whorls, Spire whorls weakly convex to abapical cord placed a short distance above suture forming periphery, angled and tapered inwards below to suture. Suture deeply impressed, canaliculate. Axial sculpture consisting of narrow, initially opisthoclinal, later orthoclinal, elevated, rounded ribs, roughly one-third width of their interspaces, 19-20 on penultimate whorl. Spiral sculpture subordinate, visible only in interspaces between ribs; on first teleoconch whorl one cord placed abapically just above suture appears first. Further flattened cords of subequal strength develop abapically, slightly wider than their interspaces, 6-7 on penultimate whorl. Last whorl globose, evenly rounded, bearing 17-19 axial ribs, obsolete over base and 13-15 spiral cords; base imperforate. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by varix, smooth within. Columella short, weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – The most distinctive characters of *Alvania couffoni* nov. sp. are the protoconch composed of 2.2 smooth whorls, the deep canaliculated suture formed by tapering inwards of the preceding whorl at the abapical



**Plate 78.** *Alvania couffoni* nov. sp.; 1. **Holotype** MNHN.F.A57714, height 4.0 mm, width 2.3 mm; 2. **Paratype 1** MNHN.F.A57715, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



spiral cord, and the narrow predominant axial ribs with flattened cords present in the interspaces. *Alvania mariae* (d'Orbigny, 1852) from the lower Miocene Aquitaine Basin of France also has a canalculated suture formed in the same manner, but differs in having fewer axial ribs and cords and the cords overrun the axial ribs (Lozouet *et al.*, 2001, pl. 13, fig. 4), whereas in *A. couffoni* they are seen only in the interspaces between the ribs. *Alvania spiralis* Glibert, 1949 from the middle Miocene of the Atlantic Loire Basin of France has similar sculpture, but lacks the canalculated suture and has a small umbilical chink absent in *A. couffoni*. *Alvania cioppii* Chirli, 2006 from the Italian Pliocene again shows the same sort of canalculated suture and predominant axial sculpture, but differs in having a protoconch with spiral microsculpture and fewer axial ribs on the teleoconch whorls. In the present-day European fauna several species with a similarly canalculated suture occur; *A. schwartziana* Brusina, 1866, *A. discors* (Allan, 1818) *A. dorbignyi* (Audouin, 1826) and *A. lineata* Risso 1826 (Giannuzzi Savelli *et al.*, 1996, figs 373-380), but they all differ in having far broader axial ribs.

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

***Alvania fezata* nov. sp.**

Plate 79, figs 1-2

*Type material* – Holotype MNHN.F.A66720, height 3.1 mm, width 2.0 mm; paratype 1 MNHN.F.A66721, height 3.0 mm, width 1.8 mm; paratype 2 NHMW

2016/0103/1751, height 3.1 mm, width 2.1 mm; paratype 3 NHMW 2016/0103/1752, height 3.0 mm, width 2.0 mm; paratype 4 NHMW 2016/0103/1753, height 2.9 mm, width 1.9 mm; paratype 5 RGM.1348541, height 4.5 mm, width 2.4 mm; paratype 6 RGM.1348542, height 3.5 mm, width 2.4 mm.

*Other material* – Maximum height 3.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1754 (31), RGM.1348543 (6), RGM.1348724 (2), RGM.1348956 (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1705 (8), RGM.1348615 (1). **Renauleau**: NHMW 2016/0103/1750 (10), RGM.1349017 (14).

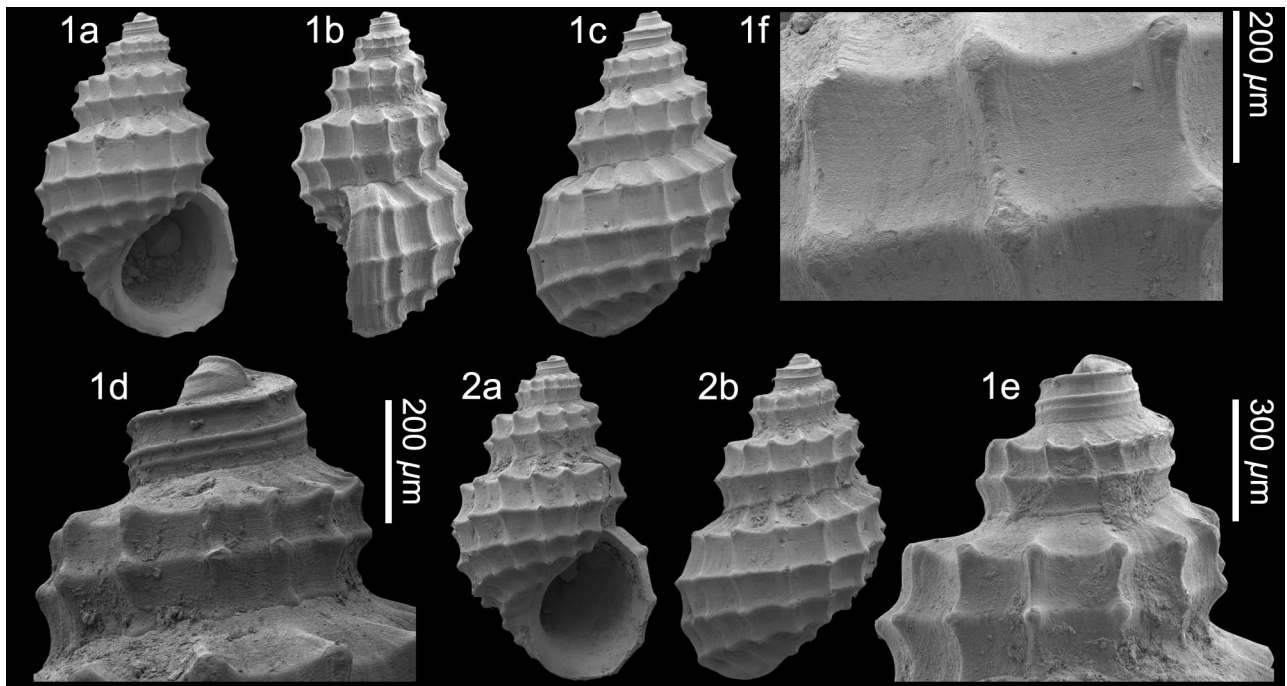
*Etymology* – Named after the cylindrical fez hat from Morocco, reflecting the shape of the protoconch, which gives the shell the appearance of wearing a fez. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of small size, solid, with protoconch of two angular whorls bearing three strong spiral cords, teleoconch of 3.5 whorls with open reticulated sculpture formed by narrow spirals and axials of equal strength, pointed tubercles at intersections, aperture rounded, outer lip smooth within.

*Description* – Shell small, solid, rissoiform. Protoconch I and II not delimited, composed of 2 whorls with flat, almost horizontal subsutural platform, straight-sided be-



**Plate 79.** *Alvania fezata* nov. sp.; 1. **Holotype** MNHN.F.A66720, height 3.1 mm, width 2.0 mm, 1d, e, detail of protoconch, 1f, detail of teleoconch microsculpture; 2. **Paratype 1** MNHN.F.A66721, height 3.0 mm, width 1.8 mm (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

low, bearing three strong rounded spiral cords; adapical cord delimits subsutural platform, second cord placed mid-whorl, third, slightly weaker, runs between mid-whorl and suture. Junction with teleoconch marked by beginning of adult sculpture. Teleoconch of 3.5 angular whorls, bearing two elevated narrow spiral cords per spire whorl, 13-14 narrow elevated axial ribs; axial and spiral elements of roughly equal strength forming open reticulated pattern; small pointed tubercles developed at intersections. Interspaces concave, surface bearing fine micropustular sculpture. Suture impressed, weakly undulating. Last whorl evenly rounded, bearing 5 spiral cords, 15-16 ribs; base not delimited, imperforate. Aperture moderately large, ovate, outer lip rounded, slightly flared abapically, thickened by varix, smooth within. Columella leaning adaxially. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – *Alvania fezata* nov. sp. is immediately separated from all its Assemblage I congeners in the character of its strongly carinate paucispiral protoconch. The teleoconch sculpture is similar to that of *Alvania milletii* nov. nom., but the cords and ribs are sharper and the aperture is wider with a more expanded outer lip. Several European *Alvania* species with spirally striate paucispiral protoconchs and cancellate teleoconchs have been described. The most similar is *Alvania nestaresi* Oliverio & Amati, 1990 from the Mediterranean coast of southern Spain, but that species differs in having more numerous spiral cords on the protoconch (5 vs. 3), which is less angular than in *A. fezata*. The cancellate teleoconch sculpture in *A. nestaresi* is denser and the aperture is less expanded. *Alvania aartseni* Verduin, 1986 from the present-day coast of Algeria has a shouldered protoconch rather sharply angled as in *A. fezata* and the nucleus is convex, the shoulder only starting after the first half whorl, whereas in *A. fezata* the nucleus already bears the three carinae. *Alvania amantii* Oliverio, 1986 from the eastern Mediterranean has cords on the protoconch, but they are more numerous and the protoconch is less angular at the shoulder, the cancellate teleoconch sculpture is again denser and the aperture less expanded than in *A. fezata*.

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

***Alvania globosa* nov. sp.**

Plate 80, fig. 1

2016 *Alvania* sp. – Van Dingenen *et al.*, p. 140, pl. 9, fig. 7, pl. 10, fig. 1 (*cum syn.*).

*Type material* – Holotype MNHN.F.A57704, height 2.7 mm, width 1.7 mm; paratype 1 MNHN.F.A57705, height 2.8 mm, width 1.7 mm; paratype 2 NHMW 2016/0103/0289, height 2.8 mm, width 1.7 mm; paratype 3 NHMW 2016/0103/0290, height 2.7 mm, width 1.6 mm; paratype 4 RGM.1348261, height 2.7 mm; paratype 5 RGM.1348563, height 2.6 mm, **St-Clément-de-la-Place**. Paratype 8 RGM.1348612, height 2.7 mm, **Sceaux-d’Anjou**.

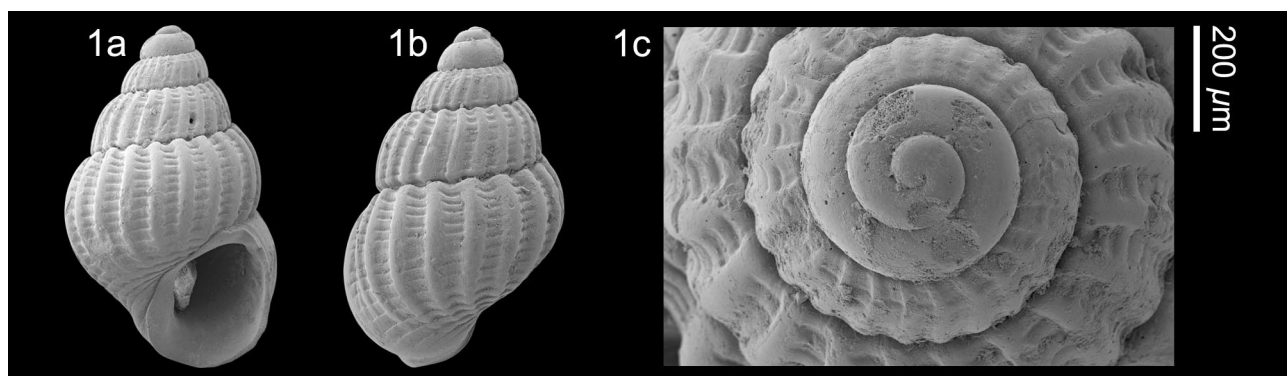
*Other material* – Maximum height 2.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0291 (50+), RGM.1348739 (25), RGM.1348957 (2), LC (50+), FVD (50+). **Sceaux-d’Anjou**: NHMW 2016/0103/0342 (32), RGM.1348592 (1), RGM.1348690 (7), RGM.1348758 (3), RGM.1348791 (3), RGM.1348820 (17), RGM.1348941 (1), RGM.1348971 (8). Maximum height 2.4 mm. **Le Pigeon Blanc**, Le Landreau, Nantes area, Loire-Atlantique department, NW France: NHMW 2015/0133/0289-0290 (1), NHMW 2015/0133/0291 (11), LC (5), FVD (1).

*Etymology* – Latin ‘*globosus*, –a, –um’, adjective meaning round, spherical. *Alvania* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with a small, globose shell, multispiral protoconch of 2.5 smooth whorls, teleoconch of three strongly convex whorls with predominantly axial sculpture of close-set rounded ribs, roughly equal in width to their interspaces, weak spiral cords only visible



**Plate 80.** *Alvania globosa* nov. sp.; 1. **Holotype** MNHN.F.A57704, height 2.7 mm, width 1.7 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

in interspaces, and strongly oblique and thickened outer lip, weakly denticulate within.

*Description* – Shell small, rissoiform, globular. Protoconch multispiral, dome-shaped, composed of 2.5 smooth whorls (dp = 500  $\mu$ m, dn = 70  $\mu$ m, dpl = 155  $\mu$ m). Transition with teleoconch not sharply delimited. Teleoconch consisting of three convex whorls, with periphery at abapical suture. Suture undulating, deeply impressed. Axial sculpture consisting of close-set, opisthoclinal, elevated, rounded ribs, roughly equal in width to their interspaces, 18–20 on penultimate whorl. Spiral sculpture weak, visible only in interspaces between axial ribs, consisting of low cords separated by narrow grooves, eight on penultimate whorl. Last whorl globose, evenly rounded; base not delimited, imperforate. Aperture ovate, outer lip strongly prosocline in profile, strongly thickened by varix, somewhat flared abapically, weakly denticulate/lirate within. Columella excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

*Discussion* – This small, globose *Alvania* species is quite distinctive, characterised by its squat shell, broad axial ribs, weak spiral sculpture, strong labial varix and strongly prosocline outer lip margin when viewed laterally. It was first recorded from the lower Pliocene Assemblage III locality of Le Pigeon Blanc as *Alvania* sp. by Van Dingenen *et al.* (2016, p. 140, pl. 9, fig. 7, pl. 10, fig. 1), who suggested to wait until this paper in order to formally describe the species based on the better preserved material from St-Clément-de-la-Place. The only species with which *Alvania globosa* nov. sp. can be confused is *Alvania lachesis* (de Basterot, 1825) (see below), but this species is larger, taller-spired, the teleoconch consists of a greater number of whorls, the axial sculpture is less crowded and the outer lip is less prosocline in profile.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

***Alvania insulsa* nov. sp.**

Plate 81, fig. 1

*Type material* – Holotype MNHN.F.A57708, height 2.1 mm, width 1.4 mm; paratype 1 MNHN.F.A57709, height 2.1 mm, width 1.4 mm; paratype 2 NHMW 2016/0103/0295, height 2.3 mm, width 1.5 mm; paratype 3 NHMW 2016/0103/0296, height 2.2 mm, width 1.4 mm; paratype 4 RGM.1348597, height 2.1 mm; paratype 5 RGM.1348598, height 2.2 mm.

*Other material* – Maximum height 2.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0297 (50+), RGM.1348599 (5), RGM.1348734 (50+), RGM.1348958 (9), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1797 (6). **Renauleau**: NHMW 2016/0103/1402 (50+), LC (50+), FVD (50+).

*Etymology* – Latin ‘*insulsus*, –a, –um’, adjective meaning boring, stupid, referring to the rather drab sculpture of this species. *Alvania* gender feminine.

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

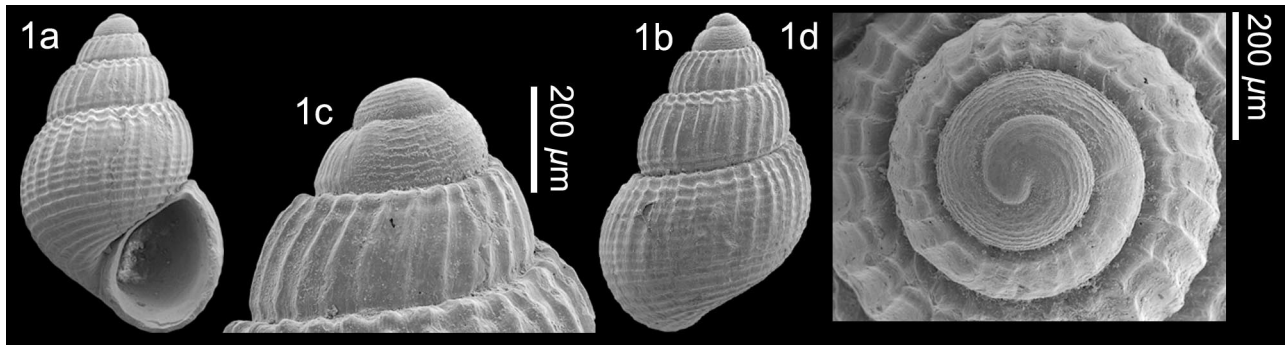
*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with small, globose shell, protoconch of two whorls, Protoconch II sculptured by irregular interrupted cordlets, teleoconch of three convex whorls with predominantly axial sculpture of close-set narrow rounded ribs and weak spiral cords, on spire whorls developed only adjacent to suture, globose last whorl, with axial sculpture weakening over base and spiral sculpture developed along entire whorl, overrunning axial ribs.

*Description* – Shell small, rissoiform. Protoconch dome-shaped, composed of two whorls; Protoconch I smooth, Protoconch II sculptured by irregular, interrupted spiral cordlets (dp = 360  $\mu$ m, hp = 250  $\mu$ m, dn = 80  $\mu$ m, dpl = 190  $\mu$ m). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of three whorls, with periphery just above abapical suture, spire whorls weakly convex. Suture weakly undulating, impressed. Axial sculpture consisting of narrow, opisthoclinal, elevated, rounded ribs, roughly one-third width of their interspaces, 23–25 on penultimate whorl. Spiral sculpture subordinate; on first teleoconch two narrow cords just below and above suture, penultimate whorl with two cords below and above suture, spiral sculpture absent mid-whorl. Last whorl globose, evenly rounded, bearing evenly spaced spiral cords along entire width, most strongly developed below suture, axials weaken over base; base not delimited, small umbilical chink. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by varix, smooth within. Columella short, excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

*Discussion* – This small, globose *Alvania* species is characterised by its sculpture of irregular, interrupted spiral cords on Protoconch I and sculpture of close-set axial ribs and cords on the last whorl. The spire whorls are only weakly convex with spiral cords only developed adjacent to the suture. *Alvania dautzenbergi* Glibert, 1949 from the middle Miocene of the Loire Basin of France is larger, with more numerous spire whorls, which are more strongly convex and bear reticulated sculpture covering the entire whorl surface on the spire whorls. According to the original description the protoconch is composed of two smooth whorls. The Pliocene to present-day European *A. punctura* (Montagu, 1803) differs again in having more convex spire whorls, more regularly reticulated sculpture and has a protoconch of 2.75–3.0 whorls sculptured by micropustules (Fretter & Graham, 1978, fig. 159). *Alvania parvula* (Jeffreys, 1884) from the present-day western Mediterranean has a similar protoconch, although the spiral cords are more regular on Protoconch





**Plate 81.** *Alvania insulsa* nov. sp.; 1. **Holotype** MNHN.F.A57708, height 2.1 mm, width 1.4 mm; 1c-d, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

II (Giannuzzi-Savelli *et al.*, 1996, fig. 432), but like the preceding species the teleoconch differs in having more rounded whorls entirely covered in reticulated sculpture.

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

***Alvania josephineae* nov. sp.**

Plate 82, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1719, height 3.2 mm, width 1.9 mm; paratype 1 NHMW 2016/0103/1720, height 2.9 mm, width 1.7 mm; paratype 2 RGM.1349018, height 3.2 mm, width 1.8 mm; paratype 3 RGM.1349019, height 3.0 mm, width 1.7 mm.

*Other material* – Maximum height 3.2 mm. **Renauleau:** NHMW 2016/0103/1721 (50+), RGM.1349020 (40), LC (40), FVD (50+). **Beugnon:** RGM.1348378423 (1).

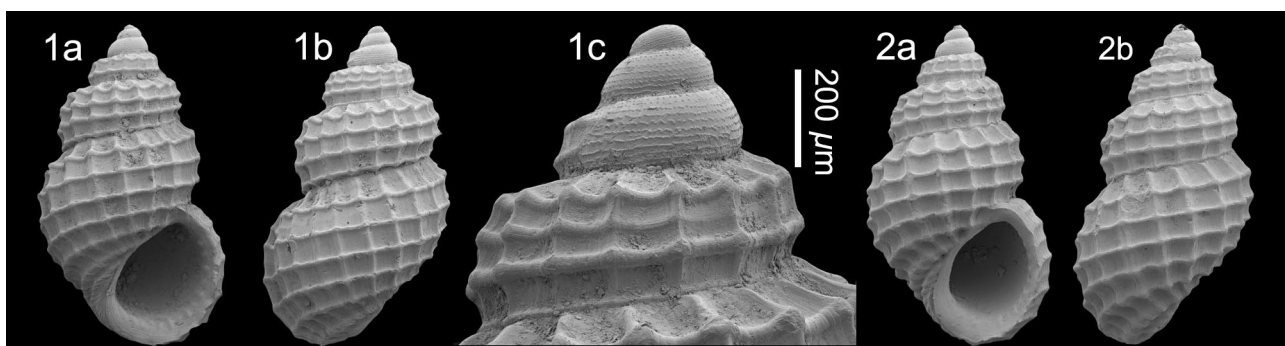
*Etymology* – Named after Joséphine de Beauharnais (1763-1814), first wife of Napoleon I. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of small size, solid, with multispiral protoconch of three convex whorls bearing irregular spiral threads and micropustules, teleoconch of three whorls with reticulated sculpture formed by narrow spirals; two on first whorl, four on second, seven on last whorl and 18-20 axials, spirals slightly predominant, tubercles at intersections, aperture rounded, outer lip weakly denticulate within.

*Description* – Shell small, solid, rissoiform. Protoconch multispiral, composed of three convex whorls. Protoconch I sculptured by irregular spiral threads with micropustules scattered in the interspaces; Protoconch II bearing rows of micropustules, ten on last whorl, composed of sparse pustules adapically, denser and coalescing into irregular spiral threads abapically. Junction with teleoconch sharply delimited. Teleoconch of three convex whorls separated by impressed suture. Axial sculpture of narrow prosocline ribs, 16 on penultimate whorl, overrun by slightly stronger narrow cords; two on first teleoconch whorl, four on second whorl, forming reticulated sculpture with small tubercles developed at intersections. Last whorl evenly rounded, bearing seven spiral cords, 18-20 ribs; base not delimited, imperforate. Aperture moderately large, ovate, outer lip rounded, hardly flared abapically, thickened by varix, weakly denticulate within. Columella leaning adaxially, hardly excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.



**Plate 82.** *Alvania josephineae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1719, height 3.2 mm, width 1.9 mm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1720, height 2.9 mm, width 1.7 mm (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – *Alvania josephineae* nov. sp. is characterised by its multispiral protoconch bearing spiral rows of micropustules and its sharp cancellate teleoconch sculpture. Compared to other Assemblage I congeners; *Alvania susieae* nov. sp. and *A. parasusieae* nov. sp., have similar sculptural elements, but both have a protoconch with only two whorls with a medium-sized nucleus suggestive of lecithotrophic larval development, whereas the protoconch of *A. josephineae* is multispiral typical of planktotrophic development. The cancellate teleoconch sculpture is sharper and the spaces slightly wider and smooth in *A. josephineae*, whereas *A. susieae* and *A. parasusieae* have prominent secondary spiral threads in the interspaces. As the name suggests, *A. robusta* Calas, 1949 is more solid-shelled, the sculpture is heavier and the protoconch of just over two whorls with a medium-sized nucleus and subobsolete spiral sculpture is again suggestive of lecithotrophic development. *Alvania subtiliangulosa* nov. sp. also has a protoconch of just over two whorls with a medium-sized nucleus with weaker spirals than *A. josephineae* and much finer cancellate teleoconch sculpture. *Alvania tutaudierei* nov. sp. is smaller, the protoconch sculpture is weaker, the cancellate sculpture finer and the outer lip has an adapical sinus absent in *A. josephineae*.

The Pliocene to present-day eastern Atlantic and Mediterranean species *A. cimicoides* (Forbes, 1844) is closely similar in sculpture to *A. josephineae*, the protoconch is also multispiral, but bears cruciform granules rather than interrupted or pustular spirals seen in *A. josephineae*. The last whorl in *A. cimicoides* is comparatively squatter and broader and the axials tend to weaken and disappear over the base, which is not so in *A. josephineae*.

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

#### *Alvania lachesis* (de Basterot, 1825)

Plate 83, figs 1-2

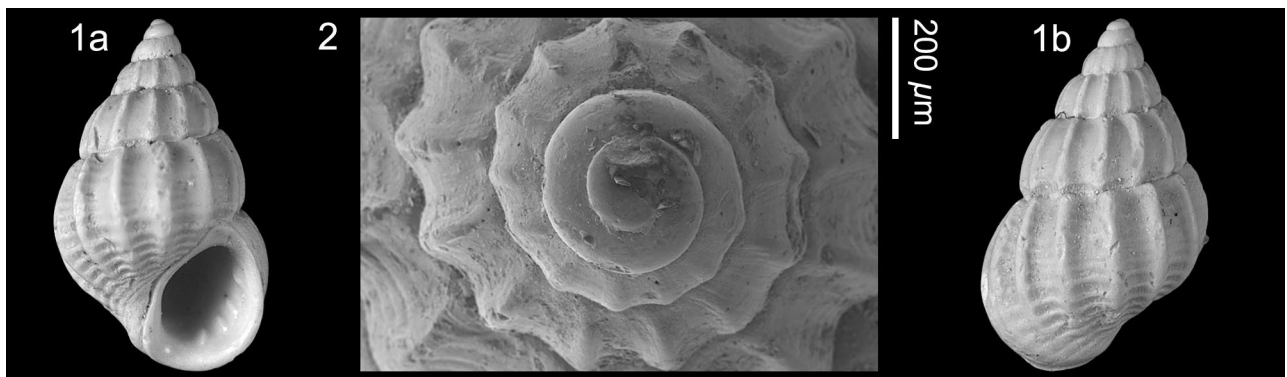
- \*1825 *Turbo Lachesis* de Basterot, p. 27, pl. 1, fig. 4.  
1854 *Rissoa Ovata* Millet, p. 154 (*nomen nudum*).

- 1865 *Rissoa ovata* Millet, p. 580.  
1949 *Alvania (Alvania) curta* Dujardin – Calas, p. 165.  
1964 *Alvania curta* Dujardin, 1837 – Brébion, p. 151.  
?1964 *Rissoa segregata* Cossmann et Peyrot – Brébion, p. 181, pl. 4, fig. 36 (*non* Cossmann & Peyrot, 1919).  
2013 *Alvania lachesis* (de Basterot, 1825) – Landau *et al.*, 2013, p. 70, pl. 6, fig. 4, pl. 57, fig. 5 (*cum syn.*).  
2016 *Alvania lachesis* (de Basterot, 1825) – Van Dingenen *et al.*, 2016, p. 137, pl. 8, fig. 3, pl. 9, figs 1, 2 (*cum syn.*).

*Material and dimensions* – Maximum height 5.1 mm, width 3.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0308-0309 (2), NHMW 2016/0103/0310 (50+), RGM.1349351 (50+), RGM.1348620 (11), RGM.1348874 (50+), RGM.1348949 (50+), LC (50+), FVD (50+). **Sceaux-d’Anjou**: NHMW 2016/0103/0312 (50+), RGM.1348065 (21), RGM.1348084 (50+), RGM.1348354 (50+), RGM.1348587 (22), RGM.1348698 (50+), RGM.1348786 (50+), RGM.1348816 (50+), RGM.1348939 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0311 (30), RGM.1348982 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1348450 (6).

*Discussion* – *Alvania lachesis* (de Basterot, 1825) was discussed by Kowalke & Harzhauser (2004, p. 118) under the name *Alvania (Alvania) curta* (Dujardin, 1837). The two taxa were synonymised by Lozouet *et al.* (2001) and further discussed by Landau *et al.* (2013, p. 71) and Van Dingenen *et al.* (2016, p. 137). In the Assemblage I deposits this species is variable in size and shape. Some smaller forms are more slender and probably represent the form identified by Brébion (1964, p. 181, pl. 4, fig. 36) as *Rissoa segregata* Cossmann et Peyrot, 1919. This was proposed by those authors as a replacement name for *Rissoa lachesis* Basterot in Hörnes (1856, pl. 48, fig. 16) from the middle Miocene of the Paratethys.

*Distribution* – Lower Miocene: Atlantic (Aquitanian-Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1919; Lozouet *et al.*, 2001); Proto-Mediterranean



**Plate 83.** *Alvania lachesis* (de Basterot, 1825); 1. NHMW 2016/0103/0308, height 5.0 mm, width 2.9 mm; 2. NHMW 2016/0103/0309, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

***Alvania lachrimula* nov. sp.**

Plate 84, fig. 1

*Type material* – Holotype NHMW 2016/0103/1565, height 2.8 mm, width 1.6 mm; paratype 1 NHMW 2016/0103/1775, height 2.7 mm, width 1.6 mm; paratype 2 NHMW 2016/0103/1780, height 2.8 mm, width 1.6 mm.

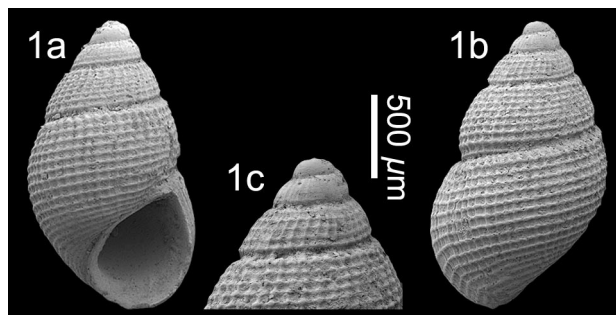
*Other material* – **St-Clément-de-la-Place**: NHMW 2016/0103/1781 (8).

*Etymology* – Latin ‘*lachrima*, -ae’, noun, meaning tear drop, in diminutive form. *Alvania* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of small size, solid, tear drop-shaped, protoconch of two whorls, teleoconch of 3.5 convex whorls separated by canaliculated suture,



**Plate 84.** *Alvania lachrimula* nov. sp.; 1. **Holotype** NHMW 2016/0103/1565, height 2.8 mm, width 1.6 mm, 1c, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

with fine mesh-like sculpture, 34 ribs and eight cords on penultimate whorl, base not sharply delimited, outer lip not thickened by varix, lirate within.

*Description* – Shell small, solid, tear-shaped. Protoconch low dome-shaped, composed of about two whorls, surface abraded (dp = 420 μm, hp = 260 μm). Transition with teleoconch abrupt marked by beginning of axial sculpture. Teleoconch consisting of three convex whorls, with periphery at abapical suture. Suture deeply impressed, narrowly canaliculate. Axial sculpture consisting of narrow, initially opisthocline, later orthocline ribs, roughly one-third width of their interspaces, 34 on penultimate whorl. Spiral sculpture slightly stronger, overrunning axial ribs, eight cords on penultimate whorl, with small tubercles at intersections, forming fine reticulated surface pattern. Last whorl regularly convex, bearing 41 axial ribs, obsolete over base and 20 spiral cords; base imperforate. Aperture moderate size, ovate, outer lip hardly flared abapically, thick, but lacking varix, lirate within. Columella short, weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – Although represented by a single specimen, formal description of this species is important as it is the only Assemblage I specimen representing a group of European fossil to present-day *Alvania* species with solid, tear drop-shaped shells, and fine mesh-like sculpture. *Alvania beanii* (Hanley in Thorpe, 1844) from the Pliocene to present-day European Atlantic frontage and Mediterranean is typical of this group. It differs from *Alvania lachrimula* nov. sp. in being larger, in having a multispiral protoconch and having teleoconch sculpture with a wider mesh (*i.e.*, fewer ribs and cords). *Alvania aglaja* (De Stefani & Pantanelli, 1878) from the Italian Pliocene is also larger and has a multispiral protoconch, but differs from *A. beanii* in having an even wider mesh. Both *A. beanii* and *A. aglaja* have a more strongly lirate or denticulate outer lip than than *A. lachrimula*. *Alvania florentina* Chirli, 2006 from the lower Pliocene of Italy is another member of this group with a paucispiral protoconch and a lirate lip, but has a wider mesh than *A. lachrimula*. This group has been present in the Atlantic at least since the upper Oligocene, represented by *A. sancitipaulensis* Lozouet, 1998, which also has a paucispiral protoconch, but differs in having fewer and broader ribs and cords and therefore the tubercles formed at the intersections are larger. *Alvania lachrimula* is therefore the smallest and finest-sculptured member of the group.

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

***Alvania milleti* nov. nom.**

Plate 85, figs 1-2

1854 *Rissoa Suturalis* Millet, p. 154 (*nomen nudum*).

1865 *Rissoa suturalis* Millet, p. 580 (*non* Philippi, 1844).



1964 *Alvania suturalis* Millet, 1854 [sic] – Brébion, p. 157, pl. 4, figs 16, 17 (*non Rissoa suturalis* Philippi, 1844).

*Type material* – Syntypes: Thorigné, Sceaux-d'Anjou, St-Clément-de-la-Place and Renauleau, Musée d'Angers, France (*fide* Brébion, 1964, p. 158).

*Material and dimensions* – Maximum height 4.0 mm, width 2.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0299-0300 (2), NHMW 2016/0103/0301 (50+), RGM.1348545 (50+), RGM.1348638 (8), RGM.1348723 (50+), RGM.134880073 (44), RGM.1348951 (41), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0302 (50+), RGM.1348614 (32), RGM.1348691 (11), RGM.1348787 (50+), RGM.1348934 (50+), LC (12), FVD (7). **Renauleau**: NHMW 2016/0103/1401 (6), RGM.1349021 (5). **Beugnon**: NHMW 2016/0103/0303 (4).

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

*Locus typicus* – Given as Sceaux-d'Anjou, Thorigné, Renauleau and St-Clément-de-la-Place.

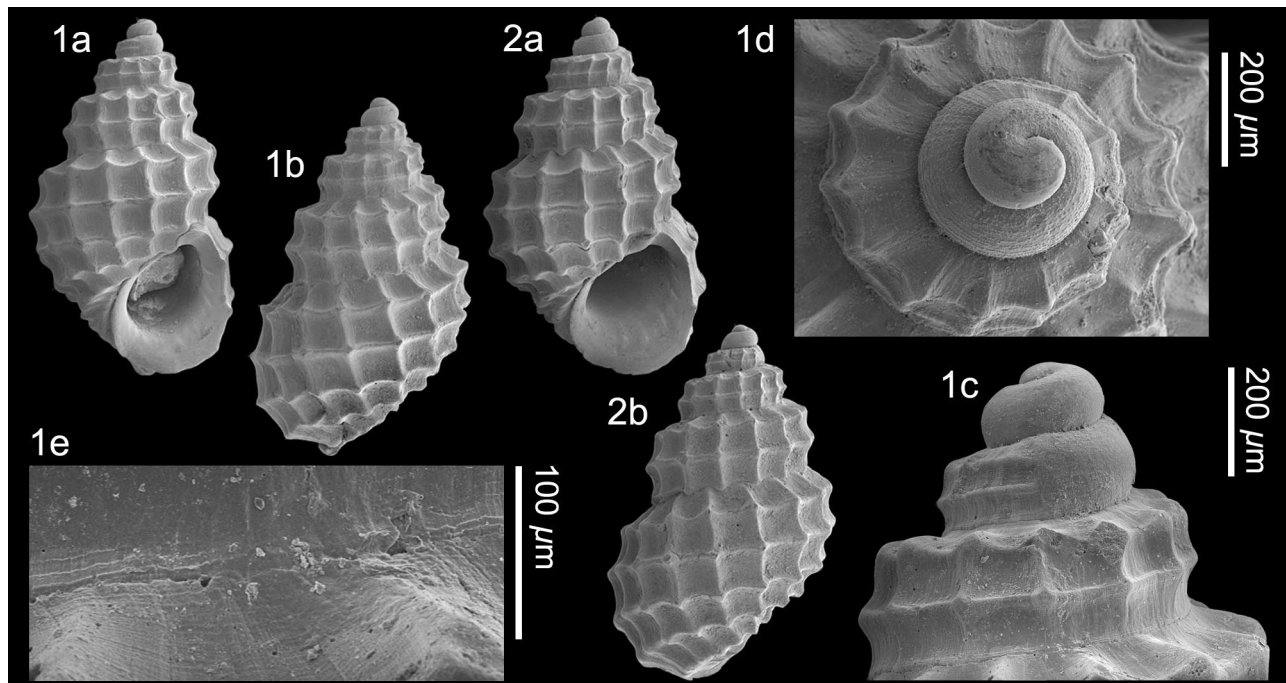
*Stratum typicum* – Tortonian, upper Miocene.

*Original description* – ‘*Rissoa suturalis*, Millet. Coq. ovoïde, obtuse au sommet; formée de 5-6 tours de spire anguleux, séparés les uns des autres par une large dé-

pression qui s'étend sur la suture; chaque tour est comme gaufré par le croisement des côtes avec les fortes stries transversales dont il est orné. Longueur: 4 millimètres; diamètre: 2 millimètres. Sc, Th., Ren., Saint-Clément' (Millet, 1865, p. 580).

*Revised description* – Shell average for genus, rissoiform. Protoconch dome-shaped, composed of two strongly convex whorls, with a medium-sized nucleus; Protoconch I and II sculptured by close-set spiral rows of micropustules (dp = 390  $\mu$ m, hp = 370  $\mu$ m, dn = 125  $\mu$ m, dp1 = 230  $\mu$ m). Transition with teleoconch abrupt, marked by end of protoconch sculpture. Teleoconch consisting of three angular whorls separated by impressed undulating suture. First teleoconch whorl bearing two narrow cords, adapical forming shoulder delimiting shallow sub-sutural ramp, abapical mid-whorl delimiting periphery. Orthocone axial ribs, equal in strength to cords, 13-14 on penultimate whorl, form open reticulated sculpture with small tubercles developed at intersections, interspaces concave. Last whorl evenly rounded, bearing five tubercular spiral cords, plus one weaker periumbilical cord; base not delimited, small umbilical chink. Aperture moderate size, ovate, outer lip somewhat flared abapically, strongly thickened by varix, lirate within. Columella short. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

*Discussion* – With this species we offer a revised description to supplement the short original one given by Millet (1865, p. 580). Unfortunately, *Rissoa suturalis* Millet, 1865 is a junior homonym of *R. suturalis* Philippi, 1844 and therefore invalid. We offer the replacement name *Al-*



**Plate 85.** *Alvania milleti* nov. nom.: 1. NHMW 2016/0103/0299, height 3.5 mm, width 2.2 mm; 1c-d, detail of protoconch; 1e detail of microsculpture on teleoconch (SEM image); 2. NHMW 2016/0103/0300, height 3.3 mm, width 2.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*vania milleti* nov. nom.

*Alvania milleti* is closely similar to the present-day Mediterranean species *A. clathrella* L. Seguenza, 1903. They both have a teleoconch with an open reticulate pattern with axial and spiral elements of roughly equal strength, and the same number of ribs and cords. They also both have a protoconch of about two whorls and of roughly equal diameter (*A. clathrella* 375  $\mu\text{m}$ , Micali *et al.*, 2004, fig. 1l), but the whorls are lower and the micropustules are coarser and not arranged in spiral rows. Moreover, the microsculpture seen in *A. clathrella* of incised spiral lines (Micali *et al.*, 2004, fig. 1g) is not seen in *A. milleti* (Pl. 85, fig. 1e), which has a microsculpture of relatively wider spaced spiral threads. *Alvania villarii* Micali, Tisselli and Giunchi, 2004, another present-day Mediterranean species with an open reticulated sculpture, has the same number of spiral cords, but more numerous axial ribs ( $\approx 20$  on the penultimate whorl). The protoconch, also of two whorls, has a microsculpture of spiral threads with numerous irregularly scattered tubercles in the interspaces. The teleoconch microsculpture is also pustular (Micali *et al.*, 2004, fig. 1c, f). *Alvania dictyophora* (Philippi, 1844) and *A. bicingulata* (G. Seguenza, 1876), two further present-day Mediterranean species with the same teleoconch sculpture, have protoconch microsculpture of coarser, irregularly scattered tubercles (Palazzi & Villari, 2001, pl. 6).

Brébion (1964, p. 158) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Renauleau, Thorigné, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches), Assemblage II (Apigné), Assemblage III (Palluau) and Assemblage IV (Gourbesville). Van Dingenen *et al.* (2016) did not find it in the Assemblage III locality of Le Pigeon Blanc and Brébion's Assemblage III and IV records are excluded from the distribution pending review.

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

***Alvania cf. milleti* nov. nom.**

Plate 86, fig. 1

**Material and dimensions** – Height 3.0 mm, width 1.5 mm.

**St-Clément-de-la-Place:** RGM.1348725 (28), LC (12). **Sceaux-d'Anjou:** RGM.1348588 (30), RGM.1348609 (50+), RGM.1348675 (41), RGM.1348785 (50+), RGM.1348817 (50+), RGM.1348935 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1718 (1), RGM.1349005 (18), LC (50+), FVD (31).

**Discussion** – We are unsure whether this form is conspecific with *Alvania milleti* nov. nom. The protoconch is slightly larger, of 2.5 rather than two whorls, and the rows of micropustules are more widely spaced. The teleoconch is more elongate than that typical for the species, but the sculpture and denticulation within the outer lip is identical in the two. Both forms occur sympatrically in most Assemblage I localities and in some cases it is not easy to ascribe specimens to one or other form.

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

***Alvania milletispinosa* nov. sp.**

Plate 87, figs 1-3

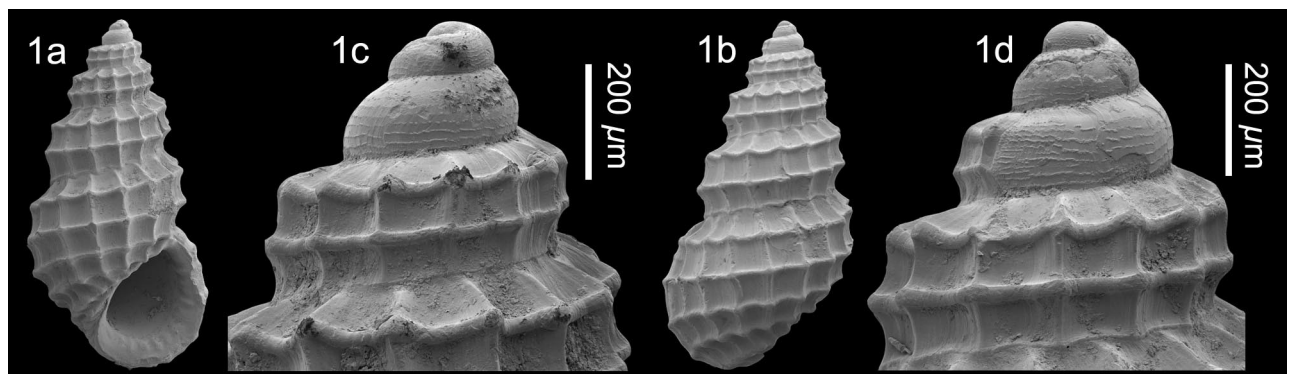
**Type material** – Holotype NHMW 2016/0103/1331, height 5.1 mm, width 3.1 mm; paratype 1 NHMW 2016/0103/1332, height 5.0 mm, width 3.3 mm, width 1.8 mm; paratype 2 NHMW 2016/0103/1333 (juvenile).

**Other material** – Maximum height 5.1 mm, width 3.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1334 (4 incomplete adults), RGM.1348847 (1 incomplete). **Sceaux-d'Anjou:** RGM.1348819 (2 incomplete).

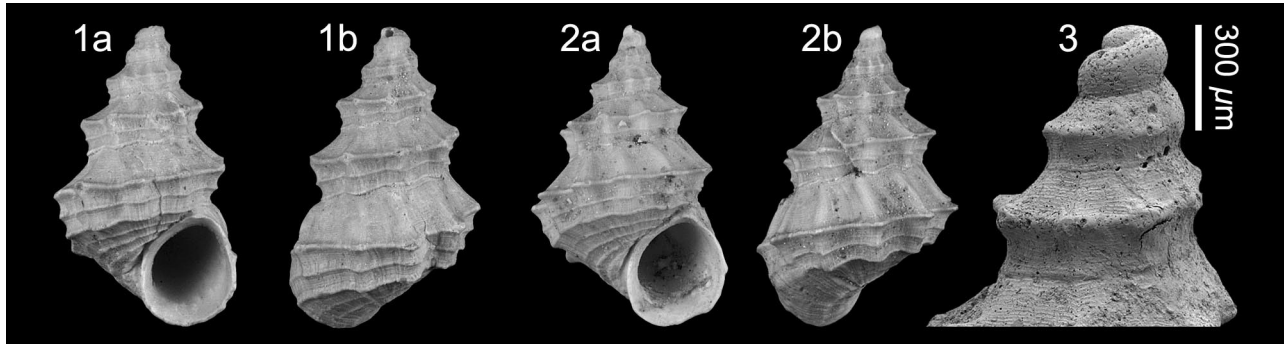
**Etymology** – Named honouring Pierre-Aimé Millet de la Turtaudière (1783-1873), pioneer in the palaeontology of Maine-et-Loire and reflecting the close resemblance to the present-day species *Alvania spinosa*. *Alvania* gender feminine.

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

**Stratum typicum** – Tortonian, upper Miocene.



**Plate 86.** *Alvania cf. milleti* nov. nom.; 1. NHMW 2016/0103/1718, height 3.0 mm, width 1.5 mm; 1c-d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 87.** *Alvania milletispinosa* nov. sp.; 1. **Holotype** NHMW 2016/0103/1331, height 5.1 mm, width 3.1 mm; 2. **Paratype 1** NHMW 2016/0103/1332, height 5.0 mm, width 3.3 mm; 3. **Paratype 2** NHMW 2016/0103/1333 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Diagnosis** – *Alvania* species of relatively large size, protoconch of two raised whorls with spiral microsculpture, teleoconch of 4.5 strongly angular whorls, with steep, wide, concave subsutural ramp, strong shoulder cord, two weaker cords below, axial sculpture of eight broad ribs forming spines at shoulder, surface covered in spiral microsculpture, biangular last whorl, with strong shoulder and basal cord, with one intermediate cord, base with four or five cords, aperture ovate, outer lip not thickened by varix, smooth within.

**Description** – Shell relatively large for genus, rissoiform. Protoconch tall, consisting of two convex whorls, with medium-sized nucleus, sculptured by spiral cords (dp = 330  $\mu$ m, hp = 390  $\mu$ m). Teleoconch consisting of 4.5 strongly angular whorls, with periphery mid-whorl, separated by weakly impressed linear suture. First teleoconch whorl bearing single strong elevated cord mid-whorl, whorl profile concave either side to suture. On second whorl, second weaker spiral develops between shoulder cord and base. Axial sculpture of eight broad, poorly delimited ribs, forming strong pointed tubercles at shoulder cord. Surface covered in fine dense spiral microsculpture. Last whorl biangular; steep, broad subsutural ramp to shoulder cord, one weaker cord between shoulder and basal cord, base weakly convex, bearing four or five further cords, small umbilical chink. Aperture mid-size, ovate, peristome complete, outer lip not thickened by varix, hardly flared abapically, smooth within. Columella evenly thickened, parietal callus thin, forming narrow callus rim.

**Discussion** – *Alvania milletispinosa* nov. sp. belongs to a small group of eastern Atlantic and Mediterranean Neogene to present-day species with whorls made strongly angular by a prominent shoulder cord, above which the subsutural ramp is broad and often concave. The last whorl is often angulated both at the shoulder and base and the sculpture is predominantly spiral, with the ribs only prominent at the shoulder cord where they each produce a sharp tubercle. *Alvania spinosa* (Monterosato, 1890) is the most extreme member of the group, with the longest spines developed at the shoulder. Apart from the stronger

spines, it differs from *A. milletispinosa* in lacking the intermediate primary cord between the shoulder and basal cords seen in that species. *Alvania pagodula* (Bucquoy, Dollfus & Dautzenberg, 1884) has a more slender shell with two equally spinous cords at the periphery. *Alvania maurizioi* Chirli, 2006 from the Italian lower Pliocene has more numerous spirals. It seems that all these species have a similar protoconch composed of two whorls with spiral sculpture (Van Aartsen *et al.*, 1984, p. 113, figs 110, 110a; Chirli, 2006, pl. 13, figs 4-6). In the Assemblage I fauna the only species with which this new species can be compared is *Alvania redoniana* nov. sp., but the latter is smaller, the protoconch is dome-shaped and smooth, and the whorls less angular, without tubercles developed at the shoulder.

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

***Alvania miocalasi* nov. sp.**

Plate 88, figs 1-2

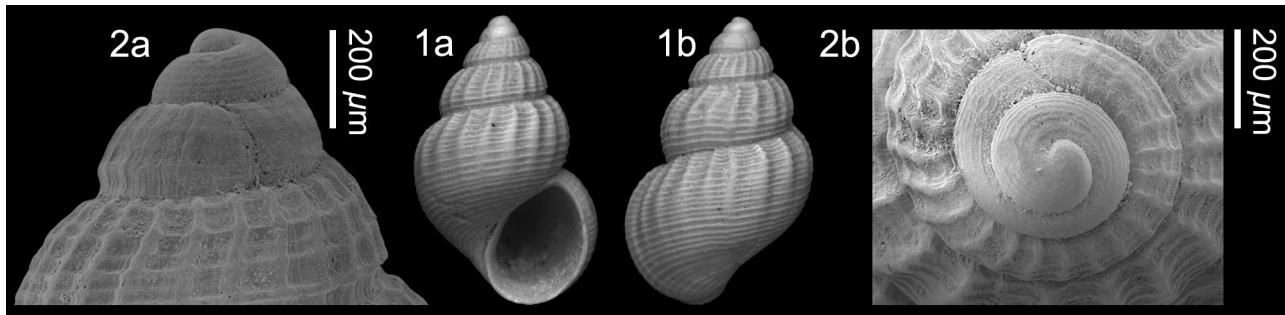
?1949 *Alvania* sp. Calas, p. 167.

?1964 *Alvania* (*Massotia*) *apiniacensis* Calas mss, 1954 – Brébion, p. 163, pl. 4, figs 20, 21 (*nomen nudum*).

**Type material** – Holotype MNHN.F.A57710, height 3.3 mm, width 1.9 mm; paratype 1 MNHN.F.A57711, height 3.2 mm, width 1.8 mm; paratype 2 NHMW 2016/0103/0304, height 3.4 mm, width 2.2 mm; paratype 3 NHMW 2016/0103/0305, height 3.5 mm, width 2.0 mm; paratype 4 RGM.1348308, height 3.0 mm; paratype 5 RGM.1348309, height 2.8 mm.

**Other material** – Maximum height 3.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0306 (50+), RGM.1348310 (3), RGM.1348564 (2), RGM.1348740 (19), RGM.1348967 (6), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0307 (18), RGM.1348252 (1), RGM.1348759 (2), RGM.1348789 (1), RGM.1348821 (6). **Renauleau:** LC (5?).





**Plate 88.** *Alvania miocalasi* nov. sp.; 1. **Holotype** MNHN.F.A57710, height 3.3 mm, width 1.9 mm; 2. **Paratype 1** MNHN.F.A57711, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Etymology* – Compound name from Miocene, the time in which this species is found and named after Pierre Calas, in recognition of his work on the Redonian rissoid gastropods. *Alvania* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with small globose shell, protoconch of just over two whorls, sculptured by eight cords, teleoconch of 3.5 convex whorls with predominantly axial sculpture of narrow, sinuous ribs that do not extend onto base and narrow crowded spiral cords, large aperture, dilated outer lip edged by varix, smooth within.

*Description* – Shell small, rissoiform, globose. Protoconch dome-shaped, multispiral, consisting of 2.2 whorls, with medium-sized nucleus, sculptured by eight spiral cords ( $dp = 445 \mu\text{m}$ ,  $hp = 390 \mu\text{m}$ ,  $dn = 90 \mu\text{m}$ ,  $dp1 = 240 \mu\text{m}$ ). Teleoconch consisting of 3.5 whorls, with periphery just above abapical suture, Suture linear, deeply impressed, shallowly canaliculate on first teleoconch whorl. First teleoconch whorl bearing two narrow spiral cords, profile convex to abapical cord, concave below, accentuating suture. Axial sculpture of narrow, sinuous opisthocline ribs. Penultimate whorl regularly convex, with eight narrow subequal cords and 15-16 sinuous axial ribs that weaken towards abapical suture. Last whorl globose, strongly convex in profile, base not delimited, bearing about 18 sinuous axial ribs, obsolete over base, and 23-24 narrow spiral cords. Aperture wide, ovate, peristome complete, outer lip thickened by varix, flared abapically, smooth within. Columella short, thickened abapically, parietal callus thin, forming narrow callus rim.

*Discussion* – Although Brébion's (1964, pl. 4, figs 20, 21) figures are poor, this is probably the species referred to by him as *Alvania (Massotia) apiniacensis* Calas mss, 1954 (*nomen nudum*). The description given, which is copied from another unpublished thesis by Calas that we have not been able to see, describes the protoconch and axial sculpture: 'Protoconque obtuse, de deux tours envi-

rons, à sculpture spirale très atténués, formée d'environ 8 cordons très plats, répartis sur toute la hauteur du tour, souvent effacés par l'usure. L'ornementation définitive début par des côtes flexueuses, serrées...' (Brébion, 1964, p. 163).

*Alvania miocalasi* nov. sp. is most similar to *Alvania calasi* Van Dingenen, Ceulemans & Landau, 2016 from the Assemblage III locality of Le Pigeon Blanc, but *A. calasi* differs in having 1) a more globose shell, 2) a lower dome-shaped protoconch of 1.75 whorls, with a sculpture of micropustules instead of spiral cords 3) more numerous axial ribs, and 4) in having a well-developed anal sinus forming a distinctive notch adapically on the outer lip.

Brébion (1964, p. 164) recorded this species only from the Assemblage II locality of Apigné. We here add Assemblage I (St-Clément-de-la-Place and Sceaux-d'Anjou).

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

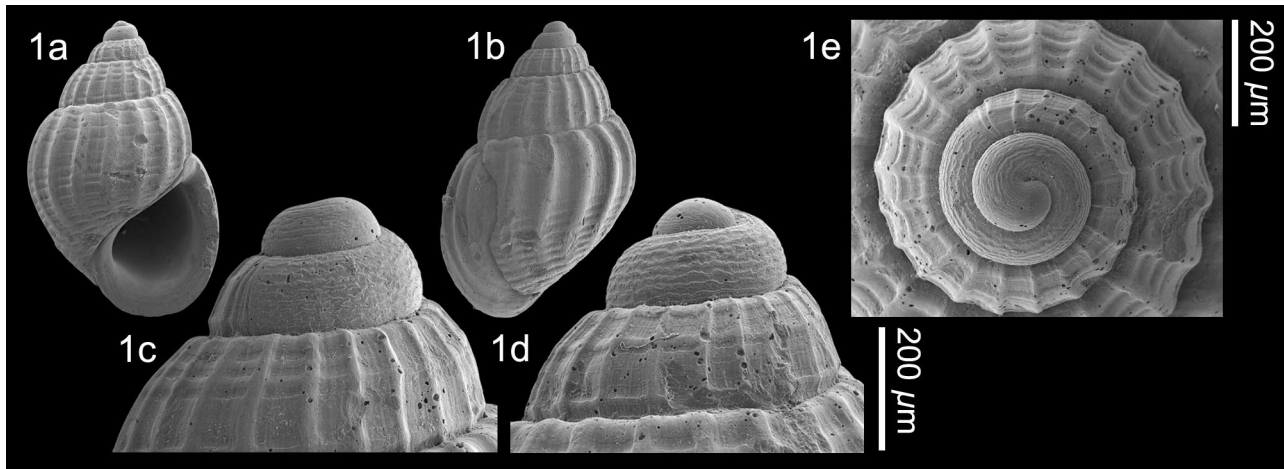
#### *Alvania miolactea* nov. sp.

Plate 89, fig. 1

*Type material* – Holotype MNHN.F.A57706, height 2.6 mm, width 1.7 mm; paratype 1 MNHN.F.A57707, height 2.7 mm, width 1.7 mm; paratype 2 NHMW 2016/0103/0292, height 2.7 mm, width 1.7 mm; paratype 3 NHMW 2016/0103/0293, height 2.7 mm, width 1.7 mm; paratype 4 RGM.1348260, height 2.6 mm; paratype 5 RGM.1348741, height 2.7 mm, width 1.7 mm; paratype 6 RGM.1348742, height 2.6 mm, width 1.6 mm.

*Other material* – Maximum height 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0294 (50+), RGM.1348743 (13), RGM.1348953 (2), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0343 (1), RGM.1348972 (1).

*Etymology* – Compound name from Miocene, the time in which this species is found and reflecting the close affinity to *Alvania lactea* (Michaud, 1830). *Alvania* gender feminine.



**Plate 89.** *Alvania miolactea* nov. sp.; 1. **Holotype** MNHN.F.A57706, height 2.6 mm, width 1.7 mm; 1c-e, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with small globose shell, protoconch of just under two whorls, Protoconch II sculptured by irregular interrupted cords, teleoconch of three convex whorls with predominantly axial sculpture of narrow rounded ribs and weak spiral cords only visible in interspaces, large aperture, dilated outer lip edged by thick varix, smooth within.

*Description* – Shell small, rissoiform, globular, with large aperture. Protoconch dome-shaped, composed of 1.9 whorls, with a medium-sized nucleus; Protoconch I smooth, Protoconch II sculptured by irregular, interrupted spiral cords (dp = 380 µm, hp = 250 µm, dn = 100 µm, dp1 = 210 µm). Transition with teleoconch abrupt, marked by beginning of adult sculpture. Teleoconch consisting of three convex whorls, with periphery at abapical suture. Suture weakly undulating, deeply impressed. Axial sculpture consisting of narrow, weakly opisthocline, elevated, rounded ribs, roughly half to one-third width of their interspaces, 18-19 on penultimate whorl. Spiral sculpture subordinate, visible only in interspaces between ribs; on first teleoconch whorl three narrow cords, abapically cords broaden, flatten, separated by narrow grooves, seven on penultimate whorl. Last whorl globose, evenly rounded; base not delimited, imperforate. Aperture large, ovate, outer lip strongly flared abapically, strongly thickened by varix, smooth within. Columella short, excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – The teleoconch of *Alvania miolactea* nov. sp. is closely similar to that of the Pliocene to present-day European species *A. lactea* (Michaud, 1830), especially forms in which the axial sculpture is predominant such

as the shell from Jersey illustrated by Fretter & Graham (1978, fig. 160). However, the protoconch of the present-day species is composed of just 1.5 whorls (dp = 380 µm; Fretter & Graham, 1978, p. 187) as opposed to 1.9 whorls (dp = 380 µm). This alone seems a small difference, however, the protoconch was illustrated by Ponder (1985a, fig. 90f) and shows quite different sculpture composed of narrow spiral threads with numerous micropustules in the interspaces as opposed to the relatively broad, irregular, interrupted cords seen in *A. miolactea* (Pl. 89, fig. 1d, e). Apart from the protoconch differences, *A. miolactea* is about half the size of *A. lactea* (average height 2.6 mm vs. 5-6 mm; Fretter & Graham, 1978; Giannuzzi-Savelli *et al.*, 1996). There is hardly any variability in shape or sculpture in the French Miocene shells, whereas the relative strength and number of axial and spiral elements is highly variable in present-day *A. lactea* (Giannuzzi-Savelli *et al.*, 1996, figs 494-498). The Italian fossil shells illustrated by Chirli (2006) as *A. lactea* have a protoconch of 2.2 whorls, sculptured by spiral rows of micropustules, similar, but not identical to the protoconch illustrated by Ponder (1985a). The teleoconch sculpture is finely and evenly reticulated, which is also seen in some present-day forms. They probably fit within the variability of *A. lactea*.

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

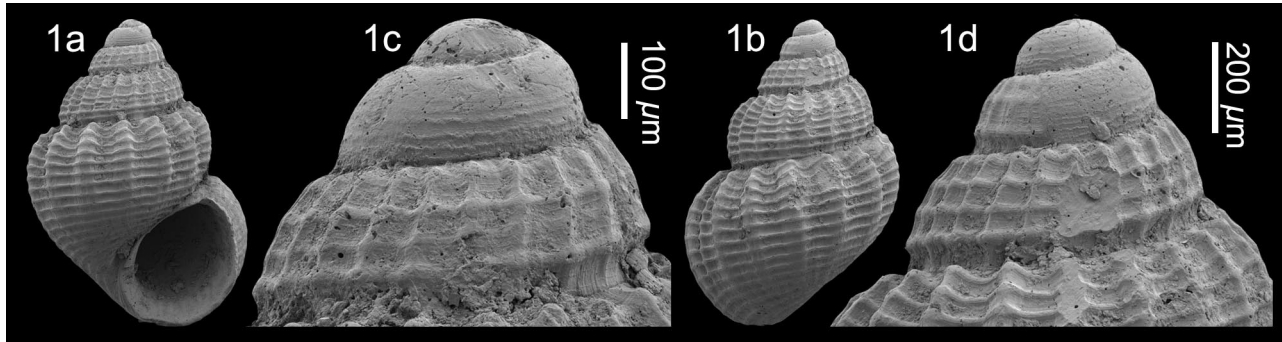
***Alvania napoleoni* nov. sp.**

Plate 90, fig. 1

*Type material* – Holotype NHMW 2016/0103/1717, height 2.4 mm, width 1.6 mm.

*Other material* – Known only from holotype.

*Etymology* – Named after the Napoléon Bonaparte (1769-1821), Emperor of France (1804-1814), one of the most



**Plate 90.** *Alvania napoleoni* nov. sp.; 1. **Holotype** NHMW 2016/0103/1717, height 2.4 mm, width 1.6 mm, 1c, d, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

important figures in European history. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species of small size, solid, squat, with paucispiral protoconch bearing spiral threads, low convex teleoconch whorls, slightly constricted at suture, narrow axial sculpture predominant, 17 on penultimate whorl, overrun by eight narrow spiral cords, last whorl inflated, depressed, 14 ribs, 19 cords, aperture weakly denticulate within.

*Description* – Shell small, squat, solid, rissoiform. Protoconch paucispiral, low dome-shaped composed of 1.75 convex whorls, Protoconch I and II not sharply delimited, bearing irregular spiral threads. Junction with teleoconch marked by beginning of adult sculpture. Teleoconch of 3.25 convex whorls, with periphery just above suture, slightly constricted below at deeply impressed suture. Axial sculpture predominant, composed of narrow orthocline rounded ribs, 17 on penultimate whorl, overrun by narrow spiral cords, eight on penultimate whorl, without forming spines or tubercles at intersections. Entire surface covered in fine irregular spiral threads, similar to those present on protoconch. Last whorl rounded, markedly inflated, somewhat depressed, 14 somewhat broader axial ribs overrun by 19 narrow spiral cords; base not delimited, small umbilical chink. Aperture moderately large, ovate, outer lip rounded, not flared abapically, thickened by varix, weakly denticulate within. Columella broadly excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – Although represented by a single specimen it is quite unlike any of its Assemblage I congeners. Indeed, its paucispiral spirally striate protoconch, squat teleoconch shell shape rounded ribs and close-set spirals make it difficult to compare usefully with any other European Neogene *Alvania* species. The present-day West African species *A. gascognei* Rolán, 2001 from São Tomé has similar sculpture, but a far more elongate teleoconch,

weaker axials and a broader labial varix.

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

***Alvania parasusieae* nov. sp.**

Plate 91, figs 1-3

*Type material* – Holotype MNHN.F.A66703, height 2.7 mm, width 1.5 mm; paratype 1 MNHN.F.A66704, height 2.9 mm, width 1.6 mm; paratype 2 NHMW 2016/0103/1558, height 2.8 mm, width 1.6 mm; paratype 3 NHMW 2016/0103/1559, height 2.5 mm, width 1.7 mm; paratype 4 NHMW 2016/0103/1560, height 2.7 mm, width 1.5 mm; paratype 5 RGM.1348560, height 2.5 mm; paratype 6 RGM.1348561, height 2.6 mm.

*Other material* – Maximum height 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1561 (40), RGM.1348562 (2), RGM.1348666 (5), RGM.1348735 (50+), RGM.1348959 (6). **Sceaux-d'Anjou**: 2016/0103/1566 (11).

*Etymology* – Compound name using the Greek prefix ‘para-’, meaning beside, or side by side and the trivial name ‘susieae’, reflecting the close similarity to that species; Susie Fenollera Ruiz, sister of the first author [BL]. *Alvania* gender feminine.

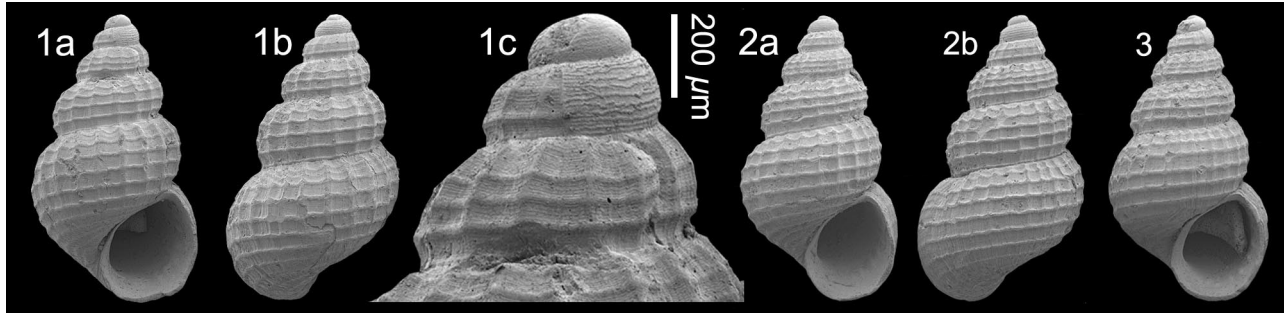
*Locus typicus* – Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with protoconch of two whorls bearing rows of irregular spiral cordlets, teleoconch of four convex whorls separated by impressed suture, penultimate whorl with 14-16 narrow ribs and 5 narrow cords forming reticulated sculpture, fine spiral microsculpture covering entire whorl surface, base not delimited; axial sculpture weakening over base, aperture ovate, lip weakly flared abapically, smooth within.

*Description* – Shell small, rissoiform. Protoconch com-





**Plate 91.** *Alvania parasusieae* nov. sp.; 1. **Holotype** MNHN.F.A66703, height 2.7 mm, width 1.5 mm; 1c, detail of protoconch (SEM image); 2. **Paratype 1** MNHN.F.A66704, height 2.9 mm, width 1.6 mm; 3. **Paratype 2** NHMW 2016/0103/1558, height 2.8 mm, width 1.6 mm (all SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

posed of two convex whorls, with medium sized nucleus; Protoconch I and II sculptured by close-set irregular spiral cordlets ( $dp = 370 \mu\text{m}$ ,  $hp = 280 \mu\text{m}$ ). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of four convex whorls, separated by linear, impressed suture. Axial sculpture of narrow orthocone to weakly opisthocline ribs; 14-16 on penultimate whorl. Spiral sculpture at teleoconch junction of two narrow cords, third cord develops below suture; second whorl with 3-4 cords, narrow subsutural ramp; third whorl with five cords, sutural ramp not delimited; spirals overrun cords without forming tubercles, forming horizontally elongated reticulated sculpture. Surface covered in spiral microsculpture. Last whorl evenly rounded, bearing 11 equal spiral cords, axials weaken over base; base not delimited, small umbilical chink. Aperture moderate size, ovate, outer lip weakly flared abapically, slightly thickened by narrow varix, smooth within. Columella weakly excavated. Columellar callus thickened, sharply delimited, forming narrow callus rim.

*Discussion* – Although at first glance *Alvania parasusieae* nov. sp. is similar to *Alvania susieae* nov. sp., and both have the same number of whorls and type of sculpture, *A. parasusieae* is smaller, with a smaller protoconch, on the teleoconch the axial ribs are orthocone to weakly opisthocline, whereas in *A. susieae* they are sinuous, and there are more numerous spirals on the last whorl (11 vs. 8), which results in a slightly denser reticulated sculpture in *A. parasusieae*. In the European Pliocene to extant faunas *A. parvula* (Jeffreys, 1884) has similar protoconch sculpture, but denser reticulate sculpture on the teleoconch (Gofas & Warén, 1982, pl. 3, fig. 21, pl. 4, figs 25-28). *Alvania spiralis* Glibert, 1949 from the Atlantic middle Miocene Loire Basin of France is similar in shape, but has thicker ribs and cords and has predominantly axial sculpture, whereas in *A. parasusieae* neither sculptural element is predominant. For comparison with *A. turtaudierei* nov. sp. and *A. subtiliangulosa* nov. sp., with which it co-occurs, see under *A. subtiliangulosa*.

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

***Alvania redoniana* nov. sp.**

Plate 92, figs 1-2

*Type material* – Holotype MNHN.F.A57712, height 3.2 mm, width 1.9 mm; paratype 1 MNHN.F.A57713, height 2.9 mm, width 1.7 mm; paratype 2 NHMW 2016/0103/0317, height 4.8 mm, width 3.0 mm; paratype 3 NHMW 2016/0103/0318, height 4.5 mm, width 2.7 mm; paratype 4 RGM.1348314, height 2.5 mm; paratype 5 RGM.1348315, height 2.5 mm.

*Other material* – Maximum height 4.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0319 (50+), RGM.1348316 (50+), RGM.1348673 (50+), RGM.1348747 (40), RGM.1348849 (1), RGM.1348960 (5), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0320 (14), RGM.1348591 (5), RGM.1348613 (3), RGM.1348640 (4), RGM.1348790 (12), RGM.1348822 (15), RGM.1348938 (11). **Renauleau:** NHMW 2016/0103/1398 (3).

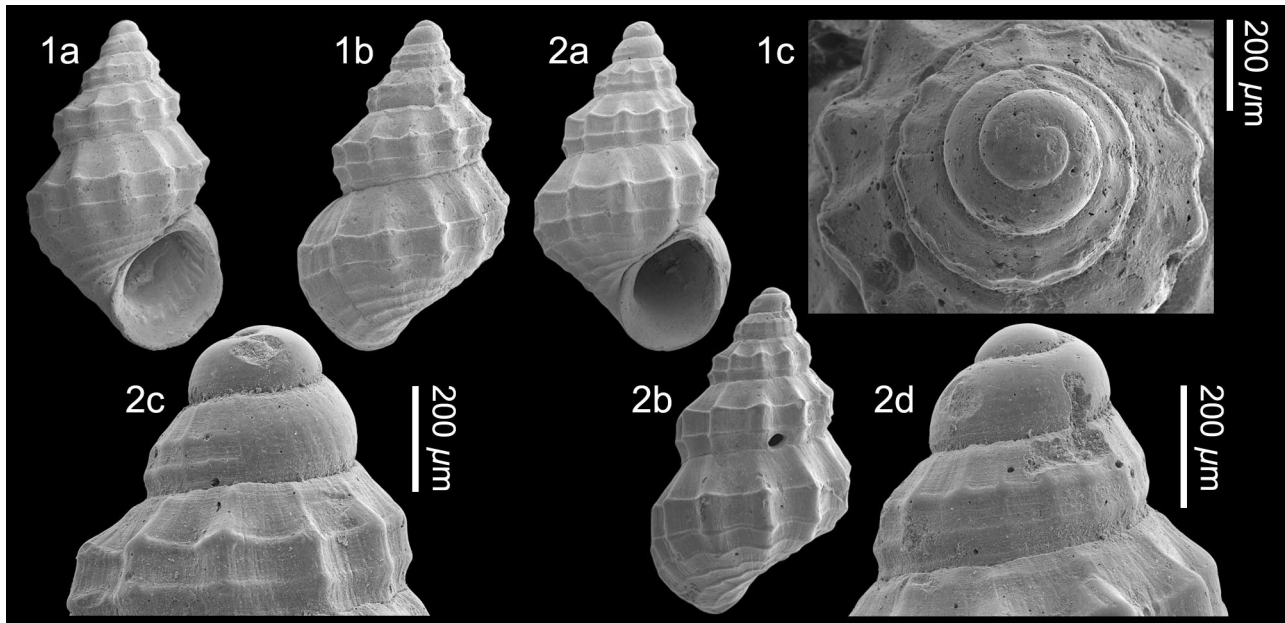
*Etymology* – Named after the 'Redonian' stage, the name used until recently for these NW French post-middle Miocene assemblages. *Alvania* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with a small angular shell, protoconch of two smooth whorls, teleoconch with sharply shouldered spire whorls, sculptured by 10-11 broad ribs crossed by two narrow spiral cords, further spiral cords develop mid-whorl on last whorl, four further cords on base, surface covered in fine spiral microsculpture, thickened outer lip, lirate within.

*Description* – Shell small, angular, rissoiform. Protoconch dome-shaped, composed of two smooth whorls, with a large nucleus ( $dp = 395 \mu\text{m}$ ,  $hp = 350 \mu\text{m}$ ,  $dn = 140 \mu\text{m}$ ,  $dp1 = 250 \mu\text{m}$ ). Transition with teleoconch abrupt, marked by beginning of spiral sculpture. Teleoconch consisting of 3.5 whorls, with periphery mid-whorl, sepa-



**Plate 92.** *Alvania redoniana* nov. sp.; 1. **Holotype** MNHN.F.A57712, height 3.2 mm, width 1.9 mm; 1c, detail of protoconch (SEM image); 2. **Paratype 1** MNHN.F.A57713, height 2.9 mm, width 1.7 mm; 2c-d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

rated by impressed linear suture. Spiral sculpture of two narrow cords, adapical placed just above mid-whorl more strongly developed forms shoulder, delimiting broad flat subsutural ramp; abapical cord placed midway between shoulder and suture. Axial sculpture consisting of broad rounded ribs, 10-11 on penultimate whorl. Spiral cords slightly swollen where they cross axial ribs, a third primary cord develops just above suture on penultimate whorl. Surface covered in fine spiral microsculpture. Last whorl with broad, flat, steeply-sloping subsutural ramp, sharply angled at shoulder, convex below, with three primary spiral cords mid-whorl. Base not delimited, bearing four further cords. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by varix, lirata within. Columella short, weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

**Discussion** – *Alvania redoniana* nov. sp. is characterised by its smooth dome-shaped protoconch composed of two whorls, its rather angular teleoconch whorls, with a broad, steeply-sloping subsutural ramp and sculpture of broad axial ribs crossed by two narrow cords on spire whorls and three mid-whorl on the last whorl. There is some variability in the height/width ratio, some specimens being rather slender, but the sculpture is relatively constant, although in the larger specimens it tends to be worn. There is little with which to compare this species. *Alvania* (*Alvinia*) *dictyophora* var. *carinata* Sacco, 1895, from the Pliocene of Italy, is probably the most similar taxon. It also seems to have a smooth protoconch of about two whorls. The carina is a little sharper than in the French Miocene shells and there are only two spiral cords on the base. The Italian shell seems to not to have

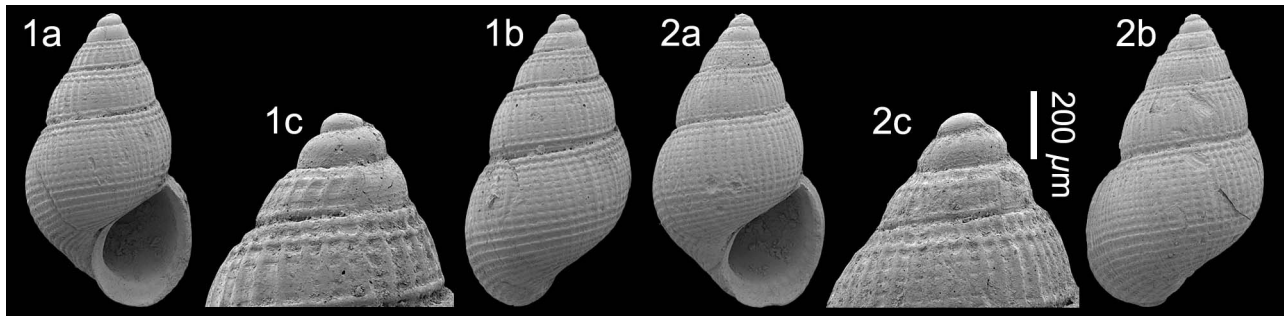
lirae within the outer lip (Ferrero Mortara *et al.*, 1984, pl. 39, figs 4, 5). It is possible that they are conspecific, but we do not include it in the synonymy as we have not seen this species. In any case, Sacco's name is a secondary homonym of *Alvania carinata* (Da Costa, 1778), and therefore invalid. Chirli (2006, pl. 5, figs 4-11) figured a similar species from the Italian Pliocene under the name *A. brevis* (Allan?), a name on a label accompanying the specimens in the collection of Geology & Palaeontology in the Museo di Storia Naturale dell'Università di Firenze. It differs in having more numerous axial ribs (15-16 vs. 11-12 on last whorl), a spiral cord on the subsutural ramp and micropustules on the protoconch. Both *A. maurizioi* Chirli, 2006 and *A. leopardiana* Brunetti & Vecchi, 2012, also from the Italian Plio-Pleistocene, differ in having a protoconch with a sculpture of spiral cords or rows of micropustules (respectively) and more numerous spiral cords. In the Assemblage I fauna the only species with which this new species can be compared is *Alvania milletispinosa* nov. sp., but the latter is larger, the protoconch is taller, covered in spiral microsculpture, and the whorls are more angular, especially at the shoulder, where sharp tubercles develop at the sculptural intersections.

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

***Alvania renauleauensis* nov. sp.**

Plate 93, figs 1-2

**Type material** – Holotype MNHN.F.A66697, height 2.5 mm, width 1.4 mm; paratype 1 MNHN.F.A66698, height 2.8 mm, width 1.6 mm; paratype 2 NHMW



**Plate 93.** *Alvania renauleauensis* nov. sp.; 1. **Holotype** MNHN.F.A66697, height 2.5 mm, width 1.4 mm; 2. **Paratype 1** MNHN.F.A66698, height 2.8 mm, width 1.6 mm; 1c, 2c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

2016/0103/1335, height 2.7 mm, width 1.5 mm; paratype 3 NHMW 2016/0103/1336, height 2.6 mm, width 1.5 mm; paratype 4 NHMW 2016/0103/1337, height 2.7 mm, width 1.6 mm; paratype 5 RGM.1349022, height 2.4 mm; paratype 6 RGM.1349023, height 2.3 mm.

*Other material* – Maximum height 2.7 mm. **Sceaux-d'Anjou:** NHMW 2016/0103/0339 (7), LC (1). **Renauleau:** NHMW 2016/0103/0338 (50+), RGM.1349024 (10), LC (50+), FVD (50+).

*Etymology* – Named after the type locality of Renauleau. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with small globose shell, protoconch of 2.5 whorls bearing rows of micropustules, teleoconch of 3.5 convex whorls separated by narrowly canaliculated suture, penultimate whorl with about 40 ribs and 9-10 cords forming fine reticulated sculpture; two most adapical and abapical cords slightly stronger, base not delimited; axial sculpture weakening over base, aperture ovate, lip somewhat flared abapically, smooth within.

*Description* – Shell small, rissoiform. Protoconch dome-shaped, composed of 2.5 whorls; Protoconch I and II sculptured by spiral rows of micropustules ( $dp = 370 \mu\text{m}$ ,  $hp = 290 \mu\text{m}$ ). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of 3.5 regularly convex whorls, with periphery at abapical suture. Suture linear, impressed, narrowly canaliculated. Axial sculpture consisting of narrow, almost orthocline, flattened ribs, roughly equal in width to their interspaces, about 40 on penultimate whorl. Spiral sculpture subordinate; on first teleoconch whorl four flattened cords, penultimate whorl 9-10, separated by narrow grooves visible only in interspaces between ribs; two most adapical and abapical cord slightly stronger. Last whorl globose, evenly rounded, bearing finely reticulated sculpture; abapical ribs weaken, interspaces between cords broaden; base

not delimited, without umbilical chink. Aperture moderate size, ovate, outer lip flared abapically, thickened by varix, smooth within. Columella short, excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

*Discussion* – *Alvania renauleauensis* nov. sp. is similar to *A. lactanea* Glibert, 1949 from the middle Miocene of the Atlantic Loire Basin, but differs in having rows of micropustules on the protoconch [Glibert (1949, p. 108) described the protoconch as smooth, although it is possible that the microsculpture is abraded, which is usual in material from the Loire Basin], in having less numerous ribs and cords (about 80 ribs and 12 cords in *A. lactanea*). Also, the ribs become obsolete on the periphery of the last whorl in *A. lactanea*, below which only spiral sculpture is present, whereas in *A. renauleauensis* they weaken, but persist onto the base. The present-day Atlantic Moroccan species *A. zylensis* Gofas & Warén, 1982 also has finely reticulate surface sculpture on the teleoconch, but differs in having strong zig-zag protoconch sculpture and more strongly convex teleoconch whorls with less flattened cords and ribs and not having the two most adapical cords reinforced.

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

#### *Alvania robusta* Calas, 1949

Plate 94, figs 1-3

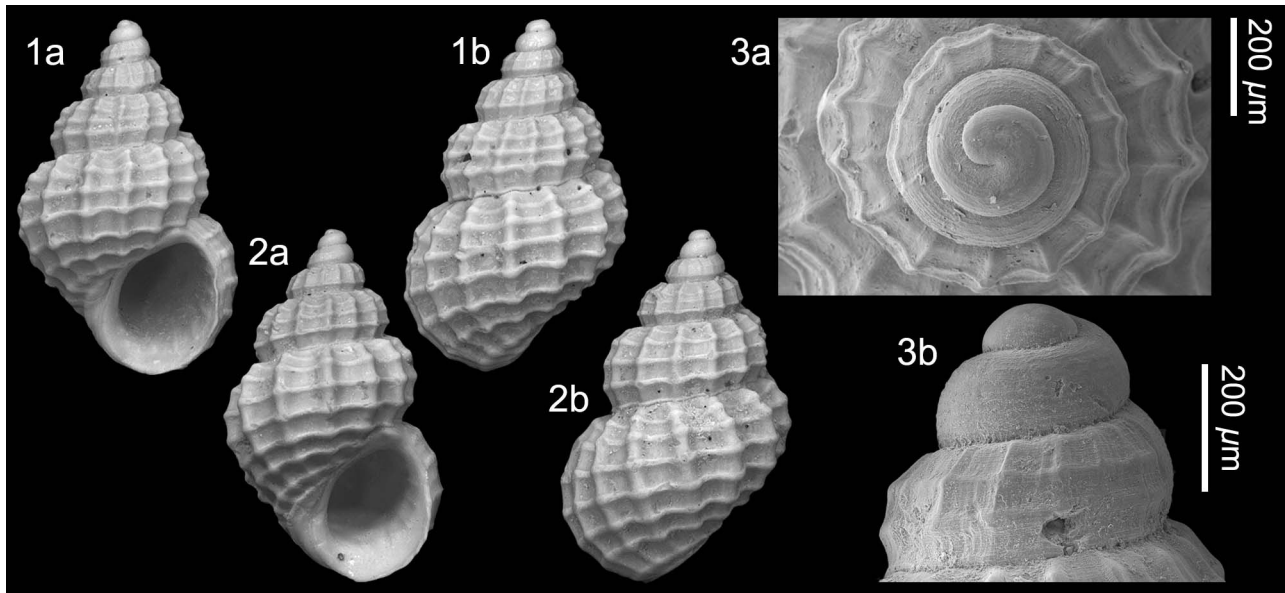
1949 *Alvania (Alvania) venus* var. *robusta* Calas, p. 166.

1964 *Alvania venus* var. *robusta* Calas, 1949 – Brébion, p. 153, pl. 4, fig. 11.

*Type material* – Syntypes: St-Clément-de-la-Place, Musée d'Angers, France (*vide* Brébion, 1964, p. 154).

*Material and dimensions* – Maximum height 4.7 mm, width 2.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0335-0337 (3), NHMW 2016/0103/0338 (50+), RGM.1348546 (1), RGM.1348556 (50+), RGM.1348726 (12),





**Plate 94.** *Alvania robusta* Calas, 1949; 1. NHMW 2016/0103/0335, height 3.8 mm, width 2.3 mm; 2. NHMW 2016/0103/0336, height 4.2 mm, width 2.6 mm; 3. NHMW 2016/0103/0337, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

RGM.1348863 (20), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0339 (50+), RGM.1348590 (21), RGM.1348611 (50+), RGM.1348688 (50+), RGM.1348788 (50+), RGM.1348824 (50+), RGM.1348937 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1652 (27), RGM.1349004 (19), LC (20?).

*Original description* – ‘*Se distingue du type par sa taille plus grande, la présence constante de 4 cordons sur l'avant-dernier tour, les côtes moins nombreuses, très fortes surtout dans leur partie supérieur. Les denticulations du labre, bien marquées, se rapprochent de celles de la forme du Bassin de Vienne*’ (Calas, 1949, p. 166).

*Discussion* – Calas (1949) originally described this species as a subspecies of the French Atlantic lower Miocene species *A. venus* (d'Orbigny, 1852). That species was recently refigured by Lozouet *et al.* (2001, pl. 12, fig. 6, pl. 13, fig. 5). It differs from *A. robusta* in having just a couple of very fine rows of spiral micropustules just above the suture on the protoconch as opposed to spiral sculpture covering the entirety of Protoconch II, as seen in *A. robusta*. The teleoconch sculpture in both is reticulate, although *A. robusta* has two more spiral cords on the last whorl resulting in horizontally elongate axial sculpture rather than the regular square reticulation seen in *A. venus*. *Alvania robusta* is the largest *Alvania* species occurring in the Assemblage I fauna and has a very solid shell. *Alvania zbyzewska* Van Dingenen, Ceulemans & Landau, 2016 from the lower Pliocene Assemblage I is similar in sculpture, but is smaller (maximum height 4.7 mm for *A. robusta* vs. 3.5 mm for *A. zbyzewska*; Van Dingenen *et al.*, 2016, p. 139) with a smaller protoconch (*A. robusta*; dp = 495  $\mu$ m, hp = 500  $\mu$ m, dn = 140  $\mu$ m, dp1 = 270  $\mu$ m; Pl. 94, fig 3; *A. zbyzewska*; dp = 405  $\mu$ m,

hp = 580  $\mu$ m, dn = 130  $\mu$ m, dp1 = 240  $\mu$ m; Van Dingenen *et al.*, 2016, pl. 9, fig. 6). Furthermore, *A. zbyzewska* has a less solid shell, the spire is taller and the suture less canalculated.

Calas (1949, p. 167) reported this species from Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Thorigné. Brébion (1964, p. 154) added St-Michel and we add Renauleau and Beugnon. Both Calas and Brébion reported the species from the Assemblage III locality of Le Pigeon Blanc, but it we suspect these Assemblage III records refer to *A. zbyzewska*.

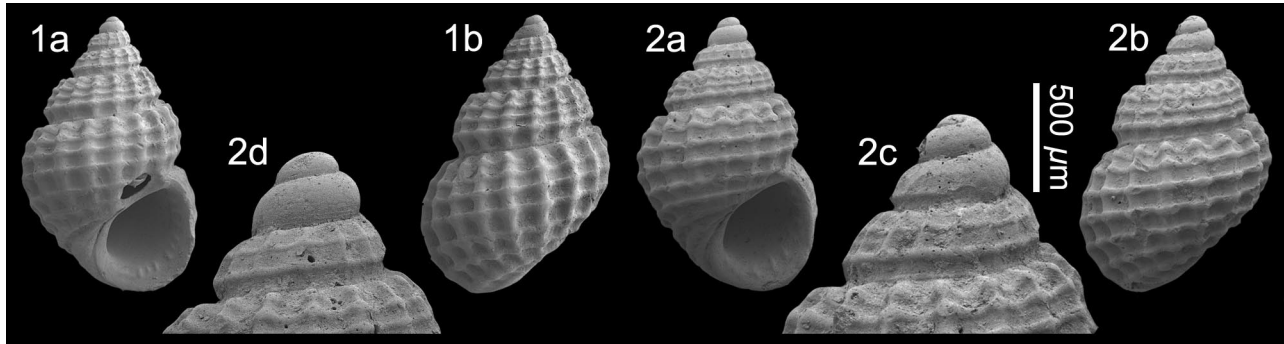
*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Calas, 1949; Brébion, 1964).

#### *Alvania cf. robusta* Calas, 1949

Plate 95, figs 1-2

*Material and dimensions* – Maximum height 4.2 mm, width 2.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0347-0348 (2), NHMW 2016/0103/0349 (32), RGM.1348565 (20). **Renauleau:** NHMW 2016/0103/0340 (50+), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0341 (4).

*Discussion* – Some specimens in each of the Assemblage I localities are rather smaller and squatter than typical *Alvania robusta* Calas, 1949 (see above), with a more accentuated sutural gutter. The number of sculptural elements is similar in both species, but the squatter form and smaller size make the reticulation finer. The figured specimens (compare Pl. 94, figs 1-2 with Pl. 95, figs 1-2) at first glance suggest separate species, but some specimens in all localities are difficult to assign to one or other



**Plate 95.** *Alvania* cf. *robusta* Calas, 1949; 1. NHMW 2016/0103/0347, height 4.0 mm, width 2.5 mm; 2. NHMW 2016/0103/0348, height 3.1 mm, width 2.0 mm, 2c, d, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

form. The protoconch is similar in both forms although worn spiral sculpture can also be seen in *A. cf. robusta* (Pl. 95, fig. 2d). We illustrate both forms, but suspect they represent extremes of a single species.

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

***Alvania subtiliangulosa* nov. sp.**

Plate 96, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1562, height 3.0 mm, width 1.7 mm; paratype 1 NHMW 2016/0103/1563, height 2.8 mm, width 1.6 mm; paratype 2 NHMW 2016/0103/1564, height 2.6 mm, width 1.4 mm.

*Other material* – Maximum height 3.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1783 (5). **Reneauleau:** NHMW 2016/0103/1622 (29).

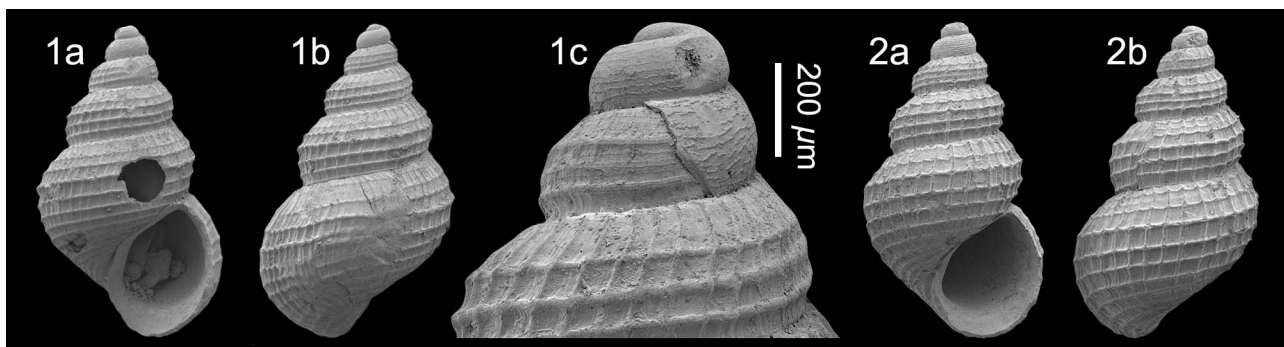
*Etymology* – Latin ‘*subtilis*, -e’ adjective, meaning finely or subtly, and ‘*angulosus*, -a, -um’, adjective meaning angled. *Alvania* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with protoconch of two whorls bearing rows of irregular spiral threads, teleoconch of 3.5 weakly angular whorls separated by impressed suture, penultimate whorl with 25-28 narrow ribs and 5-6 narrow cords forming reticulated sculpture, fine spiral microsculpture, base not delimited, axial sculpture weakening over base, aperture relatively large, ovate, lip flared abapically, smooth within.

*Description* – Shell small, rissoiform. Protoconch composed of two strongly convex whorls, with medium-sized nucleus; Protoconch I and II sculptured by irregular spiral threads (dp = 410 µm, hp = 380 µm). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of 3.5 slightly angular whorls, separated by linear impressed suture. Axial sculpture of narrow opisthocline sinuous ribs; 25-28 on penultimate whorl. Spiral sculpture of three whorls at teleoconch junction, further cords appearing adapically, 5-6 on penultimate whorl; spirals overrun cords, without forming tubercles, resulting in relatively dense square reticulated sculpture. Fine spiral microsculpture on teleoconch. Last whorl bearing 12-14 spiral cords, weakly angled at third shoulder cord; base not delimited, no umbilical chink. Aperture relatively large, ovate, outer lip flared abapi-



**Plate 96.** *Alvania subtiliangulosa* nov. sp.; 1. **Holotype** NHMW 2016/0103/1562, height 3.0 mm, width 1.7 mm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1563, height 2.8 mm, width 1.6 mm (all SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cally, thickened by narrow varix, smooth within. Columella weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

**Discussion** – A number of *Alvania* species found in the Assemblage I fauna share the character of a protoconch of about two convex whorls with irregular spiral sculpture. They can be separated by the fineness of the reticulate surface pattern on the teleoconch. *Alvania subtiliangulosa* nov. sp. has the finest reticulate surface (30-35 axials; 12-14 spirals on the last whorl) and is the only species within the group with subtly angled whorls. *Alvania susieae* nov. sp. is similar in size, but has more open reticulation (18 axials; 8 spirals on the last whorl). *Alvania parasusieae* nov. sp. is smaller with denser reticulation than *A. susieae* but less so than in *A. subtiliangulosa* (20 axials; 11 spirals on the last whorl). *Alvania turtaudierei* nov. sp. differs in being smaller, in having irregular rows of micropustules on the protoconch rather than spirals and in having less dense sculpture on the teleoconch (17 axials; 9-10 spirals on the last whorl).

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

***Alvania susieae* nov. sp.**

Plate 97, figs 1-2

**Type material** – Holotype MNHN.F.A66699, height 4.7 mm, width 2.6 mm; paratype 1 MNHN.F.A66700, height 4.7 mm, width 2.6 mm; paratype 2 NHMW 2016/0103/1550, height 4.3 mm, width 2.2 mm; paratype 3 NHMW 2016/0103/1551, height 4.4 mm, width 2.4 mm; paratype 4 NHMW 2016/0103/1552, height 4.5 mm, width 2.4 mm; paratype 5 RGM.1348727, height 4.2 mm, width 2.2 mm; paratype 6 RGM.1348728, height 4.4 mm, width 2.3 mm.

**Other material** – Maximum height 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1553 (25), RGM.1348729 (38), RGM.1348861 (21).

**Etymology** – Named after Susie Fenollera Ruiz, sister of

the first author [BL]. *Alvania* gender feminine.

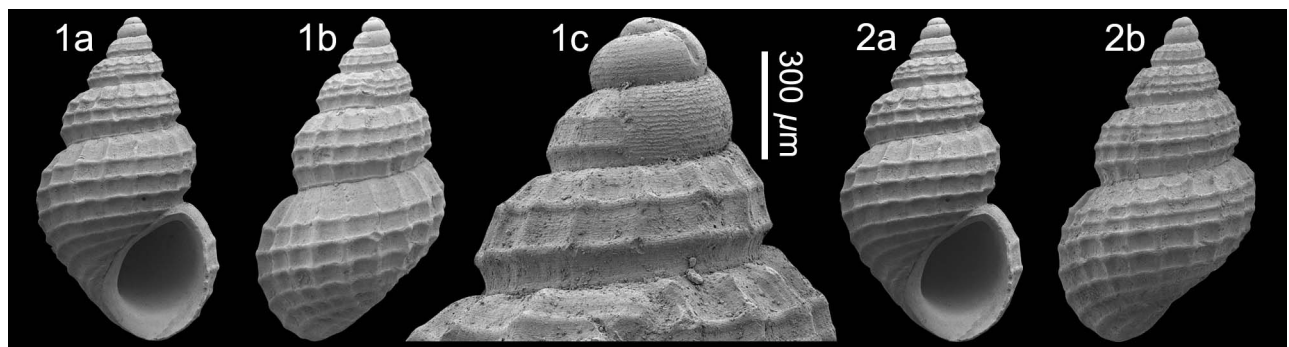
***Locus typicus*** – Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

***Stratum typicum*** – Tortonian, upper Miocene.

**Diagnosis** – *Alvania* species with protoconch of two whorls bearing dense rows of irregular spiral threads, teleoconch of four convex whorls separated by impressed suture, penultimate whorl with 15 narrow ribs and 5 narrow cords forming open reticulated sculpture, fine spiral microsculpture covering entire whorl surface, base not delimited; axial sculpture weakening over base, aperture ovate, lip somewhat flared abapically and smooth within.

**Description** – Shell average size for genus, rissoiform. Protoconch composed of just over two strongly convex whorls, with medium-sized nucleus; Protoconch I and II sculptured by close-set irregular spiral threads (dp = 460  $\mu$ m, hp = 410  $\mu$ m). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of four convex whorls. Suture linear, impressed. Axial sculpture of narrow opisthocline sinuous ribs; 15 on penultimate whorl. Spiral sculpture on first teleoconch whorl bearing two narrow cords; third cord develops between these cords on second whorl, fourth weaker subsutural cord and fifth just exposed at lower suture appear shortly after; spirals overrun cords, slightly thickened, but without forming tubercles, forming open, horizontally elongated reticulated sculpture. Surface covered in fine spiral microsculpture. Last whorl evenly rounded, bearing eight equal spiral cords, plus one weaker subsutural cord, axials weaken over base; base not delimited, no umbilical chink. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by narrow varix, smooth within. Columella weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

**Discussion** – Numerous *Alvania* species have similar sculpture. Two species from the Atlantic lower and middle Miocene of France are similar to *A. susieae* n. sp.; *Alvania mariae* (d'Orbigny, 1852) has thicker ribs and more



**Plate 97.** *Alvania susieae* nov. sp.; 1. **Holotype** MNHN.F.A66699, height 4.7 mm, width 2.6 mm; 1c, detail of protoconch (SEM image); 2. **Paratype 1** MNHN.F.A66700, height 4.7 mm, width 2.6 mm (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



numerous spirals on the last whorl; *A. venus* (d'Orbigny, 1852) has stronger axials and spirals forming a regularly reticulate pattern with tubercles at the intersections. Neither of these two has spirals on Protoconch II. The Pliocene to present-day Atlantic and Mediterranean species *A. cimicoides* (Forbes, 1844) is probably the most similar. The protoconch in *A. cimicoides* bears rows of cruciform pustules, giving it a finely and irregularly reticulated surface and its sculpture has a similar number of elements, but these are thicker and more elevated. The Pliocene to present-day species *A. hispidula* (Monterosato, 1884) also has spirals on the protoconch, but these are less crowded and the teleoconch sculpture is far stronger, varicose on the last whorl and the outer lip is lirate within. For comparison with *A. parasusiae* nov. sp., *Alvania turtaudierei* nov. sp. and *A. subtiliangulosa* nov. sp. with which it co-occurs, see under *A. subtiliangulosa*.

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

***Alvania tenuisculpturata* nov. sp.**

Plate 98, fig. 1

*Type material* – Holotype MNHN.F.A66711, height 2.2 mm, width 1.3 mm; paratype 1 MNHN.F.A66712, height 2.3 mm, width 1.3 mm; paratype 2 NHMW 2016/0103/1598, height 2.5 mm, width 1.5 mm; paratype 3 NHMW 2016/0103/1623, height 2.4 mm, width 1.4 mm; paratype 4 NHMW 2016/0103/1624, height 2.6 mm, width 1.4 mm, **Renauleau**. Paratype 5 RGM.1348695, height 2.5 mm, **Sceaux-d'Anjou**. Paratype 6 RGM.1348736, height 2.8 mm; paratype 7 RGM.1348737, height 2.9 mm, **St-Clément-de-la-Place**.

*Other material* – Maximum height 2.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1779 (50+), RGM.1348738 (5), RGM.1348961 (2), LC (50+), FVD (50+). **Sceaux-d'Anjou**: RGM.1348942 (1). **Renauleau**: NHMW 2016/0103/1625 (41), RGM.1349025 (8).

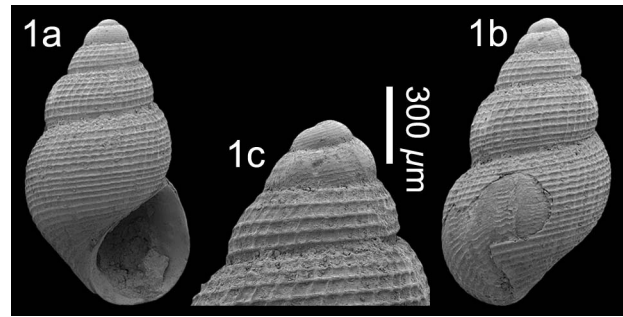
*Etymology* – Latin ‘*tenuis*, -ue, -ior’, adjective, meaning delicate, thin or fine, referring to the sculpture. *Alvania* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Alvania* species with protoconch of two whorls bearing rows of micropustules, teleoconch of three convex whorls separated by impressed suture, with fine-mesh sculpture composed of close-set sinuous axials and spirals of roughly equal strength; 38 axials and eight spirals on penultimate whorl, base not delimited; axial sculpture weakening over base, aperture of moderate size, lip hardly flared abapically, smooth within.

*Description* – Shell small, rissoiform. Protoconch dome-



**Plate 98.** *Alvania tenuisculpturata* nov. sp.; 1. **Holotype** MNHN.F.A66711, height 2.2 mm, width 1.3 mm; 1c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

shaped, slightly inclined with respect to central axis of teleoconch, composed of two whorls, sculptured by spiral rows of micropustules ( $dp = 410 \mu\text{m}$ ,  $hp = 265 \mu\text{m}$ ). Transition with teleoconch abrupt marked by end of protoconch sculpture. Teleoconch consisting of just over three convex whorls, with periphery just above abapical suture. Suture linear, impressed. Axial sculpture consisting of narrow, opisthocline, close-set, sinuous ribs, roughly one-quarter width of their interspaces, 38 on penultimate whorl. Spiral sculpture of roughly equal strength; five cords on first teleoconch whorl, eight on penultimate whorl; spirals overrun axials, slightly reinforced at intersections, forming fine-mesh surface sculpture. Last whorl globose, evenly rounded, bearing roughly evenly spaced spiral cords along entire width, axials weaken over base; base not delimited, imperforate. Aperture moderate size, ovate, outer lip hardly flared abapically, not thickened by varix, smooth within. Columella short, excavated. Columellar and parietal callus thickened, sharply delimited, forming very narrow callus rim.

*Discussion* – In the Assemblage I deposits *Alvania tenuisculpturata* nov. sp. is somewhat similar to *Alvania insulsa* nov. sp.; both have spirally sculptured protoconchs and teleoconchs with fine-mesh sculpture, but in *A. insulsa* the axials are dominant and the spirals below the suture are reinforced. *Alvania lachrimula* nov. sp. is also finely sculptured, but the teleoconch is far thicker-shelled and tear drop-shaped and the whorls less convex. *Alvania renauleauensis* nov. sp. has even finer sculpture, with thicker axials and spirals, so that the interspaces resemble small pits. The Italian Pliocene species *A. magistra* Chirli 2006 has somewhat similar teleoconch sculpture, but a more inflated last whorl and a much larger aperture and expanded outer lip, with a marked labial varix and anal notch adapically. *Alvania magistra* is unusual in having honey-comb surface microsculpture on the first protoconch whorl (Chirli, 2006, pl. 11, fig. 16). The Pliocene to present-day European species *A. punctura* (Montagu, 1803) also has rows of micropustules on the protoconch, but the protoconch has almost three whorls and the teleoconch sculpture has a wider mesh. The Mediterranean species *A. parvula* (Jeffreys, 1884) also has a

spirally sculptured protoconch of about two whorls, but more widely spaced teleoconch sculpture. We have used the trivial name '*tenuisculpturata*' to avoid possible homonymy with *Rissoa tenuisculpta* Boettger, 1869, which is a *taxon inquirendum* (Faber, 2016; WoRMS).

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

### *Alvania tiberiana* (Coppi, 1876)

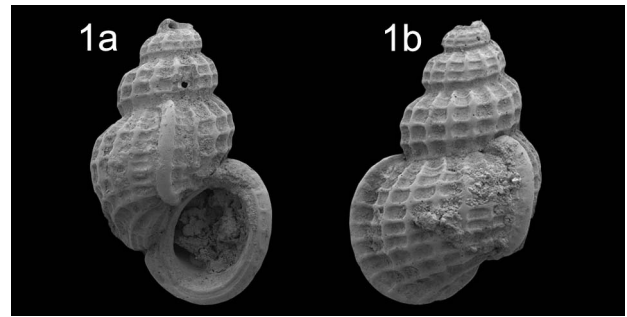
Plate 99, fig. 1

- 1862 *Rissoa tuba* Doderlein, p. 17 (*nomen nudum*).  
 \*1876 *Rissoa Tiberiana* Coppi, p. 201.  
 1895b *Galeodinopsis tiberiana* (Coppi, 1876) – Sacco, p. 28, pl. 1, fig. 67.  
 1895b *Galeodinopsis tiberiana* var. *percrassicosta* Sacco, p. 28, pl. 1, fig. 68.  
 1921 *Galeodinopsis Tiberiana* (Coppi, 1876) – Cossmann, p. 23, pl. 1, figs 55, 56.  
 1938 *Galeodinopsis tiberiana* (Coppi, 1876) – Wenz, p., fig. 1715.  
 1990a *Manzonia fariai* Rolán & Fernandes, p. 64, pl. 1, figs 4-6.  
 1994 *Alvania (Alvania) tiberiana* (Coppi, 1876) – Bernasconi & Robba, p. 77, pl. 4, figs 1, 2.  
 1999 *Alvania fariai* (Rolán & Fernandes) – Gofas, p. 88, figs 39-42.  
 2004a *Alvania fariai* (Rolán & Fernandes) – Landau *et al.*, p. 41, pl. 7, figs 3, 4.  
 2006 *Alvania tiberiana* (Coppi, 1876) – Chirli, p. 37, pl. 18, figs 10-12.  
 2008 *Galeodinopsis tiberiana* (Coppi, 1876) – Garilli, p. 43, figs 81-99.  
 2010 *Galeodinopsis tiberiana* (Coppi, 1876) – Sosso & Dell'Angelo, p. 21, p. 32 mid-row centre unnumbered fig.

*Material and dimensions* – Maximum height 2.8 mm, width 1.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1776 (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1686 (1), NHMW 2016/0103/1724 (2)

*Discussion* – Although missing its protoconch, this species can confidently be identified as *Alvania tiberiana* (Coppi, 1876), which is characterised by its strongly convex whorls, inflated last whorl, open cancellate sculpture, strong varix often present on the last whorl and double-rimmed outer lip. Landau *et al.* (2004a, p. 41) identified specimens from the lower Upper Pliocene of the Estepona Basin, southern Spain as *Alvania fariai* (Rolán & Fernandes, 1990), which was synonymised with *A. tiberiana* by Garilli (2008).

Garilli (2008) used the genus *Galeodinopsis* Sacco, 1895 for this species. Although we do not believe *Alvania* to be monophyletic, we await molecular genetic data before assigning genera. This and the record of Doderlein's material given by Garilli (2008) are the only Miocene records we can find. This species is uncommon in the Assemblage I



**Plate 99.** *Alvania tiberiana* (Coppi, 1876); 1. NHMW 2016/0103/1686 height 2.8 mm, width 1.8 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

deposits and has so far been found only at St-Clément-de-la-Place and Sceaux-d'Anjou. *Alvania tiberiana* is found today in the tropical eastern Atlantic and illustrates the gradual southwards range contraction of thermophilic species resulting from cooling sea since Miocene times.

*Distribution* – Miocene (indeterminate): central Proto-Mediterranean, Italy (Garilli, 2008). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: western Mediterranean, northeastern Spain (NHMW coll.); central Mediterranean, Italy (Sacco, 1895b; Bernasconi & Robba, 1994; Chirli, 2006; Garilli, 2008; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, southern Spain (Landau *et al.*, 2004a), central Mediterranean, Italy (Garilli, 2008). Present-day: Atlantic: Senegal-northern Angola (Rolán & Fernandes 1990a; Gofas, 1999).

### *Alvania turtaudierei* nov. sp.

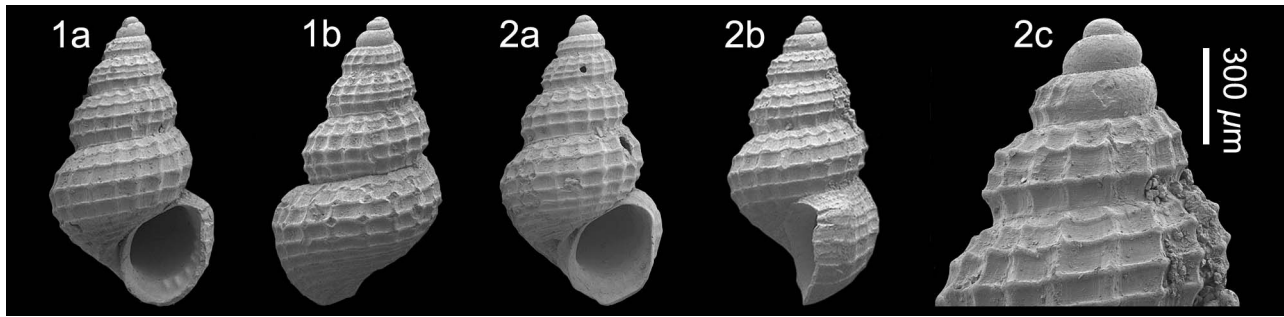
Plate 100, figs 1-2

*Type material* – Holotype MNHN.F.A66701, height 2.7 mm, width 1.5 mm; paratype 1 MNHN.F.A66702, height 2.7 mm, width 1.5 mm; paratype 2 NHMW 2016/0103/1554, height 2.6 mm, width 1.4 mm; paratype 3 NHMW 2016/0103/1555, height 2.7 mm, width 1.4 mm; paratype 4 NHMW 2016/0103/1556, height 2.6 mm, width 1.4 mm; paratype 5 RGM.1348557, height 3.3 mm; paratype 6 RGM.1348558, height 3.2 mm.

*Other material* – Maximum height 2.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1557 (50+), RGM.1348559 (2), RGM.1348962 (8), LC (50+), FVD (50+).

*Etymology* – Named after Pierre-Aimé Millet de la Turtaudière (1783-1873), French naturalist and Secrétaire Général de la Société d'Agriculture d'Angers in recognition of his pioneering work on the upper Miocene assemblages of northwestern France. *Alvania* gender feminine.

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



**Plate 100.** *Alvania turtaudierei* nov. sp.; 1. **Holotype** MNHN.F.A66701, height 2.7 mm, width 1.5 mm; 2. **Paratype 1** MNHN.F.A66702, height 2.7 mm, width 1.5 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Alvania* species with protoconch of 2.5 whorls bearing irregular rows of micropustules, teleoconch of four convex whorls separated by impressed suture, penultimate whorl with 17 narrow ribs and 5 narrow cords forming reticulated sculpture with small tubercles at intersections, fine spiral microsculpture covering entire whorl surface, base not delimited; axial sculpture weakening over base, aperture ovate, anal notch conspicuous, lip somewhat flared abapically and denticulate to smooth within.

**Description** – Shell small, rissoiform, relatively slender. Protoconch composed of 2.5 strongly convex whorls, with a medium-sized nucleus; Protoconch I and II sculptured by irregular rows of micropustules (dp = 340 µm, hp = 340 µm). Transition with teleoconch abrupt, marked by end of protoconch sculpture. Teleoconch consisting of four convex whorls, with periphery just below mid-whorl. Suture linear, impressed. Axial sculpture of narrow orthocline ribs; 17 on penultimate whorl. Spiral sculpture on first teleoconch whorl bearing two narrow cords; on second whorl, third cord develops below suture, fourth between cords 1 and 2 shortly after, and 5<sup>th</sup> cord just exposed at lower suture; spirals overrun cords, developing small tubercles at intersections, resulting in horizontally elongated reticulated sculpture. Surface covered in fine spiral microsculpture. Last whorl evenly rounded, bearing 9-10 equal spiral cords, axials weaken over base; base not delimited, small umbilical chink. Aperture moderate size, ovate, outer lip bearing conspicuous anal notch distorting labial margin, somewhat flared abapically, thickened by varix, smooth or denticulate within. Columella excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

**Discussion** – The teleoconch sculpture in *Alvania turtaudierei* nov. sp. and *Alvania susieae* nov. sp. is similar; both have about the same number of weak axials and spirals, which appear in similar order. However, they differ in protoconch sculpture; the spirals in *A. susieae* are closer-spaced and more solid. The teleoconch in *A. turtaudierei* nov. sp. is more slender and the axials are

less sinuous. An unusual character of this new species is the strong anal notch that distorts the outer lip abapically. This is not present in *A. susieae*. *Alvania punctura* (Montagu, 1803), widespread in the Pliocene to present-day European Atlantic and Mediterranean faunas, has similar sculpture, although the reticulate surface sculpture is denser, but it is immediately separated by its protoconch sculpture composed of larger micropustules and it lacks an anal sinus. Other European and West African species with relatively slender teleoconchs and reticulate sculpture composed of narrow ribs, such as *A. jeffreysi* (Waller, 1864) and *A. imperspicua* (Pallary, 1920), can also be separated by their protoconch sculpture and the absence of an anal sinus. In spite of the genus *Alvania* being extremely speciose in the Neogene to present-day eastern Atlantic frontage and Mediterranean, we can find no other species with such a marked sinus except *A. magistra* Chirli, 2006 from the Italian lower Pliocene, but that species is more inflated, with finer mesh sculpture. For comparison with *A. parasusieae* nov. sp. and *A. subtiliangulosa* nov. sp. with which it co-occurs, see under *A. subtiliangulosa*.

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

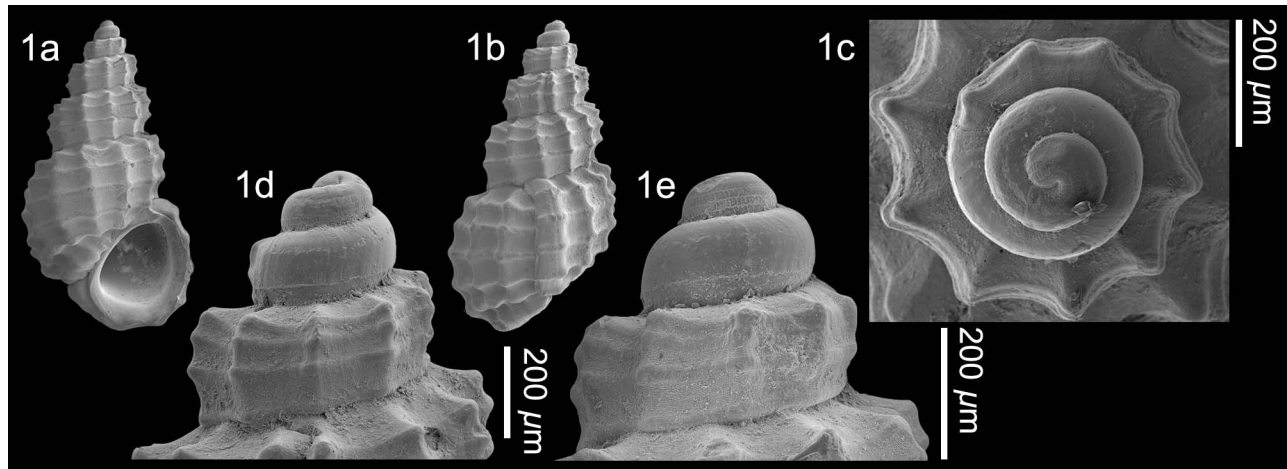
#### *Alvania zetlandica* (Montagu, 1815)

Plate 101, fig. 1

- \*1815 *Turbo Zetlandicus* Montagu, p. 194, pl. 13, fig. 3.
- 1949 *Alvania (Taramellia) zetlandica* Montagu, 1914 [sic] – Calas, p. 167.
- 1964 *Alvania (Taramellia) zetlandica* Montagu, 1811 [sic] – Brébion, p. 167, pl. 4, figs 24, 25.
- 2016 *Alvania zetlandica* (Montagu, 1815) – Van Dingenen *et al.*, p. 138, pl. 8, fig. 6, pl. 9, fig. 4 (*cum syn.*).

**Material and dimensions** – Maximum height 4.3 mm, width 2.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0286 (1), NHMW 2016/0103/0286 (50+), RGM.1348544 (16), RGM.1348566 (1), RGM.1348730 (17), RGM.1348862 (2), RGM.1348952 (4), LC (50+), FVD (50+). **Sceaux-**





**Plate 101.** *Alvania zetlandica* (Montagu, 1815); 1. NHMW 2016/0103/0286, height 3.7 mm, width 2.0 mm; 1c-e, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**d'Anjou:** NHMW 2016/0103/0287 (43), RGM.1348589 (4), RGM.1348610 (8), RGM.1348784 (50+), RGM.1348818 (8), RGM.1348936 (10). **Renauleau:** NHMW 2016/0103/0298 (50+), RGM.1349003 (13), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0288 (7), RGM.1348502 (1).

**Discussion** – *Alvania zetlandica* (Montagu, 1815) is a very characteristic species with coarse sculpture, in which axial and spiral sculptural elements are almost equal in strength, and with a double-rimmed outer lip. The protoconch is perfectly preserved in the material from St-Clément-de-la-Place and multispiral with netted microsculpture on Protoconch I and an abapical spiral thread and a few micropustules on Protoconch II ( $n = 2.5-2.7$ ,  $dp = 420 \mu\text{m}$ ,  $hp = 340 \mu\text{m}$ ,  $dn = 65 \mu\text{m}$ ,  $dp1 = 160 \mu\text{m}$ ). The protoconch figured (Pl. 101, fig. 1c-e) has a slightly larger diameter than that of the present-day British shells ( $n = 2.5$ ,  $dp = 285 \mu\text{m}$ ; Fretter & Graham, 1978, p. 181) and the upper Pliocene specimens from the western Mediterranean Estepona Basin ( $n = 2.25$ ,  $dp = 284 \mu\text{m}$ ,  $dn = 104 \mu\text{m}$ ,  $dp1 = 169 \mu\text{m}$ ; Landau *et al.*, 2004a, p. 45). The protoconch illustrated by Giannuzzi-Savelli (1996, fig. 480d) has a similar microsculpture, except that protoconch 2 has a further thread running along the shoulder and spirally elongate tubercles between the shoulder and the abapical thread, missing in the protoconch illustrated from St-Clément-de-la-Place. We consider these differences to be subspecific.

Brébion (1964, p. 169) recorded this species from Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place, Chalonnes), Assemblage III (Palluau), to which Van Dingenen *et al.* (2016) added Le Pigeon Blanc, and Assemblage IV (Gourbesville).

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Calas, 1949; Brébion, 1964; Van Dingenen *et al.*, 2016); NSB, Coralline Crag, England (Wood, 1848; Harmer, 1920), Luchtbal Formation, Belgium (Marquet & Landau, 2006); central Mediterranean, Italy (Chirli,

2006). Upper Pliocene: NSB, Red Crag, England (Harmer, 1920); western Mediterranean, Estepona (Landau *et al.*, 2004a); central Mediterranean, Italy (Anfossi *et al.*, 1983; Tabanelli *et al.*, 2011). Pliocene (indeterminate): The Netherlands (Beets, 1946; Van Regteren Altena *et al.*, 1954; Raad *et al.*, 2013). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: Atlantic, British Isles (Harmer, 1920); central Mediterranean, Italy (Cerulli-Irelli, 1914; Di Geronimo & La Perna, 1997). Present-day: Atlantic, Norway, southwards to Morocco, Mediterranean (Poppe & Goto, 1991).

#### *Alvania ziziphina* Calas, 1949

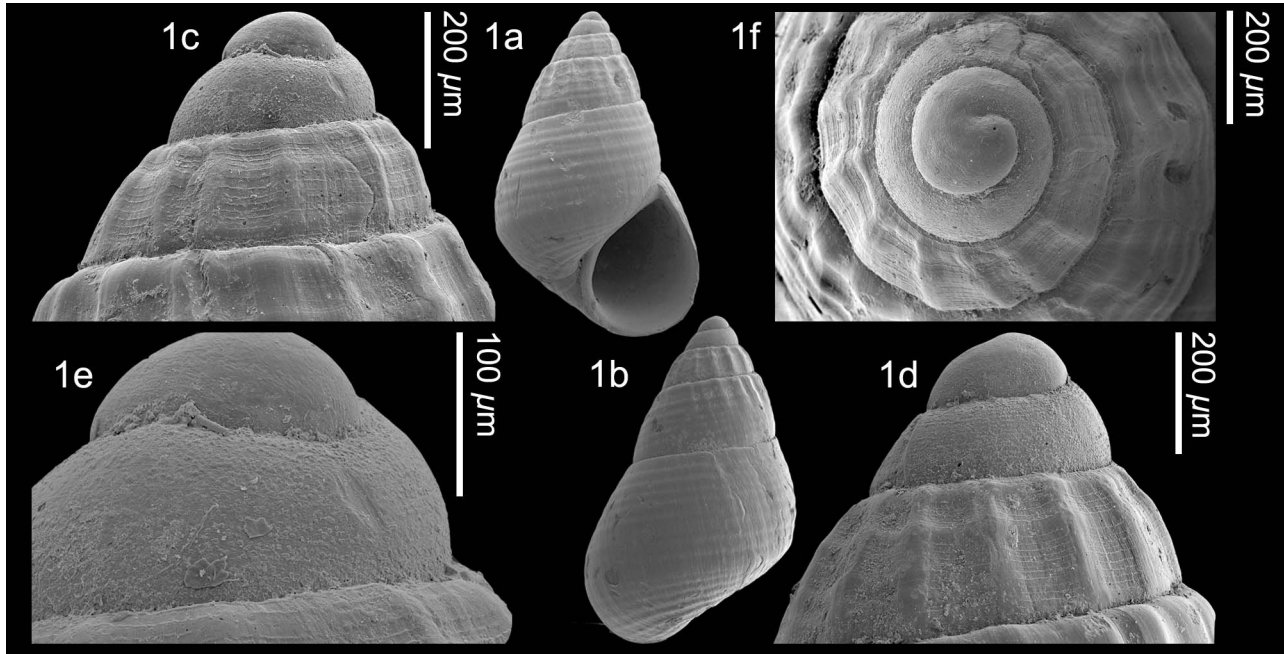
Plate 102, fig. 1

- \*1949 *Alvania* (*Massotia*) *ziziphina* Dollfus in Calas, p. 165.
- 1964 *Alvania* (*Massotia*) *ziziphina* Dollfus in Calas, 1949 – Brébion, p. 165, pl. 4, figs 22, 23.
- 2016 *Alvania ziziphina* Calas, 1949 – Van Dingenen *et al.*, p. 138, pl. 8, figs 7, 8, pl. 9, fig. 5 (*cum syn.*).

**Type material** – Syntypes: Apigné, MNHN Paris, France (*vide* Brébion, 1964, p. 166).

**Material and dimensions** – Maximum height 3.4 mm, width 2.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0281 (1), NHMW 2016/0103/0282 (50+), RGM.1347938 (3), RGM.1348667 (50+), RGM.1348963 (5), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0284 (3), RGM.1347972 (1). **Renauleau:** NHMW 2016/0103/0283 (50+), RGM.1349014 (3), LC (35), FVD (20).

**Discussion** – The exquisitely preserved material from St-Clément-de-la-Place allows us to add a few details to the revised description given by Van Dingenen *et al.* (2016, p. 139). The protoconch is not smooth as previously described; Protoconch I is sculptured with crowded fine micropustules (Pl. 102, fig. 1e), and Protoconch II



**Plate 102.** *Alvania ziziphina* Calas, 1949; 1. NHMW 2016/0103/0281, height 2.7 mm, width 1.8 mm; 1c, detail of teleoconch micro-sculpture; 1d-f, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

bears close-set spiral threads (Pl. 102, fig 1d, f). Fine spiral threads are also present on the first teleoconch whorl (Pl. 102, fig 1c, d). As noted by Calas (1949) and Van Dingenen *et al.* (2016, p. 138), specimens from the lower Pliocene Assemblage III locality of Le Pigeon Blanc are about half as large again as the Assemblage I specimens (average height 4.5 mm vs. 2.9 mm). The protoconch is also smaller in the Assemblage I population ( $n = 2$ ,  $dp = 470 \mu\text{m}$ ,  $hp = 295 \mu\text{m}$ ,  $dn = 140 \mu\text{m}$ ,  $dp1 = 250 \mu\text{m}$ ; St-Clément-de-la-Place, Pl. 102, fig. 1f:  $n = 2-2.5$ ,  $dp = 560 \mu\text{m}$ ,  $hp = 450 \mu\text{m}$ ; Le Pigeon Blanc; Van Dingenen *et al.*, 2016). The smaller size of conspecific specimens from Assemblage I compared to those from Assemblage III is a theme we will visit repeatedly during this series. For comparison with similar species see Van Dingenen *et al.* (2016, p. 139).

*Alvania ziziphina* was recorded by Calas (1949) and Brébion (1964, p. 167) from Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place); we can add Renauleau, Assemblage II localities (Apigné) and Assemblage III (Le Pigeon Blanc).

**Distribution** – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Calas, 1949; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Calas, 1949; Brébion, 1964; Van Dingenen *et al.*, 2016).

Genus *Manzonia* Brusina, 1870

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

1870 *Manzonia* Brusina, p. 37.

### ***Manzonia crassa* (Kanmacher, 1798)**

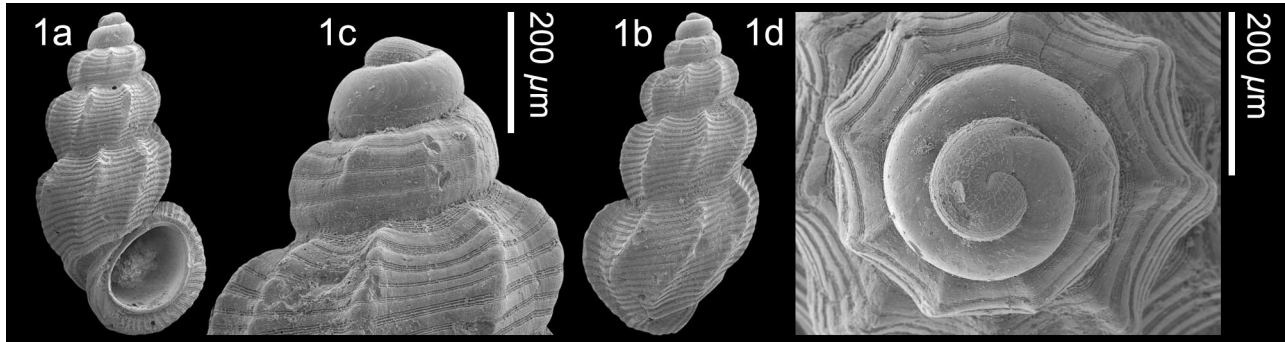
Plate 103, fig. 1

- \*1798 *Turbo crassus* Kanmacher, p. 638, fig. 20.
- 2016 *Manzonia crassa* (Kanmacher, 1798) – Van Dingenen *et al.*, p. 140, pl. 10, fig. 2.

**Material and dimensions** – Maximum height 2.4 mm, width 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0277 (1), NHMW 2016/0103/0278 (50+), RGM.1348255 (50+), RGM.1348307 (21), RGM.1348954 (2), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0280 (22), RGM.1349015 (2). **Beugnon:** NHMW 2016/0103/0279 (9).

**Discussion** – The beautifully preserved material from St-Clément-de-la-Place allow us to confirm the position taken by Van Dingenen *et al.* (2016, p. 140) in considering the Atlantic middle and upper Miocene specimens from France described as *Manzonia costata falunica* (de Morgan, 1915) to be conspecific with *Manzonia crassa* (Kanmacher, 1798). The teleoconch of the middle Miocene (maximum height 2.7 mm; average 2.4 mm; Ferrière-Larçon, NHMW coll.) and upper Miocene French specimens (maximum height 2.2 mm; average 2.0 mm; St-Clément-de-la-Place) is indeed smaller than usual for the Pliocene (height 2.9-3.4 mm, Italy; Chirli, 2006, pl. 20) and present-day European specimens (height 3-3.5 mm; Fretter & Graham, 1978, p. 172). The teleoconch shape and sculpture are indistinguishable.

The protoconch of the specimens from St-Clément-de-la-Place have 2.25-2.5 whorls ( $dp = 345 \mu\text{m}$ ,  $dn = 50 \mu\text{m}$ ,  $dp1 = 130 \mu\text{m}$ ; Pl. 103, fig 1d). This is half a whorl larger



**Plate 103.** *Manzonia crassa* (Kanmacher, 1798); 1. NHMW 2016/0103/0277, height 2.4 mm, width 1.2 mm. Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

than described for present-day British specimens ( $n = 2$ ,  $dp \approx 200 \mu\text{m}$ ; Fretter & Graham, 1978, p. 171). We note that Chirli (2006, p. 42) described the Italian Pliocene specimens as having a protoconch of 2.25 whorls. The netted microsculpture seen on Protoconch I is similar to that seen in present-day specimens (Ponder, 1985a, fig. 99b). We therefore consider 2-2.5 whorls within intraspecific variability for *M. crassa*. For further discussion see Van Dingenen *et al.* (2016, p. 140).

Brébion (1964, p. 150) recorded this species from the Assemblage I locality of Beaulieu, to which we add St-Clément-de-la-Place, Renauleau and Beugnon, and the assemblage II locality of Apigné. Van Dingenen *et al.* (2016, p. 141) added the Assemblage III locality of Le Pigeon Blanc.

**Distribution** – Middle Miocene: Atlantic, Loire Basin (de Morgan, 1915; Cossmann, 1918; Glibert, 1949); Paratethys (Langhian-Serravallian), Vienna Basin, Austria (Kowalke & Harzhauser, 2004), Hungary (Strausz, 1966), Poland (Friedberg, 1923; Bałuk, 1975), Romania (Kowalke & Harzhauser, 2004); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Calas, 1949; Brébion, 1964); Proto-Mediterranean Sea (Tortonian and Messinian), Po Basin, Italy (Sacco, 1895b; Venzo & Pelosio, 1963). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); central Mediterranean, Italy (Chirli, 2006); Tunisia (Fekih, 1975). Upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a); central Mediterranean, Italy (Sacco, 1895b; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010; Tabanelli *et al.*, 2011). Lower upper Pleistocene: North Sea Basin, British Isles (Harmer, 1918); western Mediterranean, France (Glibert, 1962); central Mediterranean, Italy (Cerulli-Irelli, 1914; Bucchieri, 1970). Upper Pleistocene: The Netherlands (Van Regteren Altena *et al.*, 1954; Raad *et al.*, 2013). Present-day: northeastern Atlantic, Norway, southwards to Morocco, Mediterranean, from extreme low tide line to 50 m depth, often on sandy bottoms, but also under stones and in weeds (Poppe & Goto, 1991).

Genus *Pseudosetia* Monterosato, 1884

*Type species* (by subsequent designation, Crosse, 1885) – *Rissoa turgida* Jeffreys, 1870, present-day, Norway.

1884a *Pseudosetia* Monterosato, p. 281.

**Note** – Based on shell characters, Bouchet & Warén (1993) expanded Ponder's (1985a) concept of the genus *Pseudosetia* Monterosato, 1884 and included further European species having in common a paucispiral protoconch without distinction between Protoconch I and Protoconch II and a protoconch sculpture of micro-tubercles and/or interrupted spiral lines. The teleoconch was described by the authors as thin-shelled, rather cylindrical due to the large larval shell, with indistinct reticulate sculpture and a bulging last whorl concealing the parietal wall (Bouchet & Warén, 1993, p. 685).

We have included in this genus four species from the Assemblage I deposits. All four are small, smaller than usual for the genus *Alvania*, and have a paucispiral protoconch in which Protoconch I and II are not delimited. None of the protoconchs have micro-tubercles or interrupted spiral lines, although *P. wareni* nov. sp. and *P. sergegofasi* nov. sp. have spiral ribs. *Pseudosetia ivolasi* nov. sp. and *P. peyroti* nov. sp. have smooth protoconchs. The teleoconch characters also stray from the generic description above; *P. ivolasi* is rather elongate for the genus and *P. peyroti* solid-shelled. Therefore, if the generic position of these new taxa is accepted, they widen considerably the range of generic shell morphology. All four species are easily separated from each other and from all extant *Pseudosetia* species, therefore the species discussions have been kept short.

***Pseudosetia wareni* nov. sp.**

Plate 104, fig. 1

**Type material** – Holotype MNHN.F. A57903, height 1.7 mm, width 1.2 mm; paratype 1 MNHN.F. A57904, height 1.8 mm, width 1.2 mm; paratype 2 NHMW 2016/0103/0571, height 1.8 mm, width 1.3 mm; paratype 3 NHMW 2016/0103/0572, height 1.8 mm, width 1.2 mm;

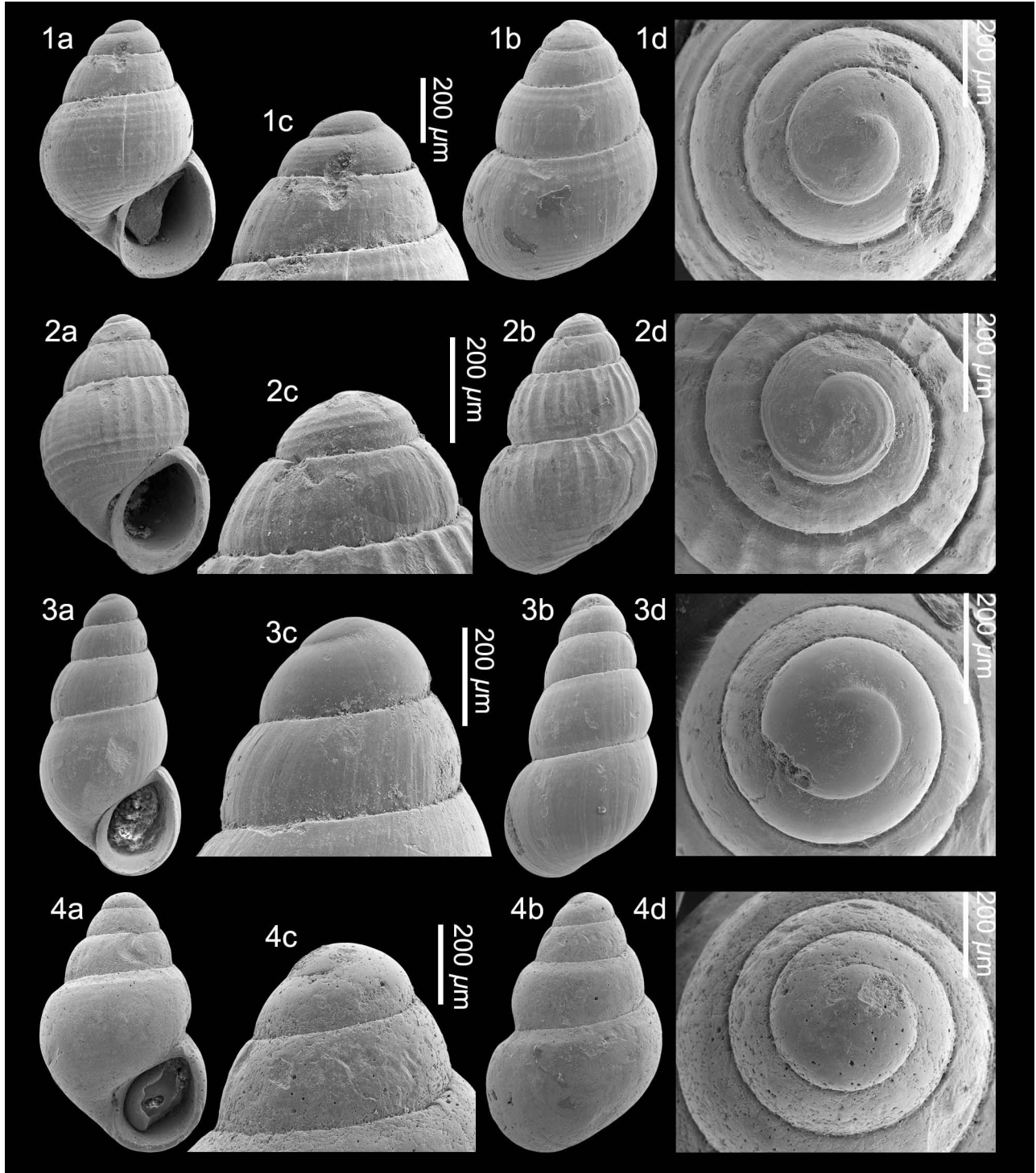


paratype 4 RGM.1348603, height 1.5 mm; paratype 5 RGM.1348604, height 1.5 mm.

0103/1354 (1). **Renauleau**: NHMW 2016/0103/1353 (14), LC (3).

*Other material* – Maximum height 1.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0573 (50+), RGM.1348605 (6), RGM.1348672 (3), RGM.1348748 (50+), LC (50+), FVD (50+). **Sceaux-d’Anjou**: NHMW 2016/

*Etymology* – Named in honour of Anders Warén of the Naturhistoriska Riksmuseet, Stockholm (Sweden), in recognition of his enormous contribution to malacology. *Pseudosetia* gender feminine.



**Plate 104.** 1 *Pseudosetia wareni* nov. sp., **holotype** MNHN.F.A57903, height 1.7 mm, width 1.2 mm; 2. *Pseudosetia sergegofasi* nov. sp., **holotype** MNHN.F. A57902, height 1.6 mm, width 1.0 mm; 3. *Pseudosetia peyroti* nov. sp., **holotype** MNHN.F. A57905, height 2.1 mm, width 1.1 mm; 4. *Pseudosetia ivolasi* nov. sp., **holotype** MNHN.F. A57907, height 2.0 mm, width 1.3 mm (all SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Pseudosetia* species of small size, with paucispiral protoconch bearing spiral cords on last half whorl, squat cylindrical teleoconch with weak spiral sculpture developed only on adapical half of whorls and base, globose last whorl obscuring parietal callus, moderately wide umbilical chink.

**Description** – Shell small, rissoiform, squat cylindrical with blunt apex. Protoconch paucispiral, low dome-shaped, composed of 1.9 whorls, with large nucleus, bearing fine spiral cords on last half whorl; Protoconch I and II not delimited (dp = 540  $\mu$ m, hp = 380  $\mu$ m, dn = 190  $\mu$ m, dp1 = 330  $\mu$ m). Teleoconch of 2.5 convex whorls with periphery at abapical suture. Suture linear, impressed. Sculpture of subobsolete spiral cords, developed only on adapical half of whorls and base. Last whorl globose, evenly convex, base not delimited, bearing moderately broad, round edged umbilical chink. Aperture ovate, outer lip weakly varicose, sharp edged, somewhat expanded abapically. Columella erect, narrow, forming medial border of umbilical chink, parietal callus poorly developed, concealed on ventral view by bulging last whorl.

**Discussion** – Of the four species described here under the genus *Pseudosetia* Monterosato, 1884, *P. wareni* nov. sp. fits most closely within the generic description given by Bouchet & Warén (1993). It differs from all the extant European species discussed by these authors in having a protoconch with well-developed spiral cords on the last half-whorl rather than fine threads seen in the extant species (see Bouchet & Warén, 1993, figs 1603, 1606, 1608, 1610, 1612, 1614). Like the present-day European species the teleoconch has weak but predominant spiral sculpture, but the base is not delimited as it is in the type species *P. turgida* (Jeffreys, 1870) and *P. amydralox* Bouchet & Warén, 1993. *Pseudosetia azorica* Bouchet & Warén, 1993 has similar teleoconch sculpture, but is less squat, taller-spined and has a wider umbilicus.

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

***Pseudosetia sergegofasi* nov. sp.**

Plate 104, fig. 2

**Type material** – Holotype MNHN.F. A57902, height 1.6 mm, width 1.0 mm; paratype 1 MNHN.F. A57914, height 1.5 mm, width 900  $\mu$ m; paratype 2 NHMW 2016/0103/0574, height 1.5 mm, width 950  $\mu$ m; paratype 3 NHMW 2016/0103/0576, height 1.4 mm, width 850  $\mu$ m; paratype 4 RGM.1348256; paratype 5 RGM.1348257, height 1.3 mm; paratype 6 RGM.1348744, height 1.5 mm; paratype 7 RGM.1348745, height 1.4 mm.

**Other material** – Maximum height 1.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0576 (50+), RGM.1348258 (9), RGM.1348746 (50+), RGM.1348964 (1), LC (20), FVD (10). **Renaleau**: NHMW 2016/0103/1615 (3).

**Etymology** – Named in honour of Serge Gofas of the University of Malaga (Spain), in recognition of his enormous contribution to malacology. *Pseudosetia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Pseudosetia* species of small size, with paucispiral protoconch bearing coarse spiral cords, squat cylindrical teleoconch with axial ribs that do not cover base of last whorl, weak spiral sculpture clearly developed only on base, moderately globose last whorl that does not obscure parietal callus, narrow umbilical chink.

**Description** – Shell small, rissoiform, squat cylindrical with blunt apex. Protoconch paucispiral, low dome-shaped, composed of 1.6 whorls, with large nucleus, bearing coarse spiral cords; Protoconch I and II not delimited (dp = 440  $\mu$ m, hp = 315  $\mu$ m, dn = 180  $\mu$ m, dp1 = 310  $\mu$ m). Teleoconch of 2.5 convex whorls, periphery at abapical suture on first whorl, just above on penultimate whorl, whorl slightly constricted above suture. Suture linear, impressed. Sculpture of close-set, narrow orthocline ribs, about 20 on penultimate whorl and subobsolete spiral cords, only clearly developed over base. Last whorl moderately globose, evenly convex, axial ribs well developed adapically, weaken mid-whorl, not continuing onto base. Base not delimited, bearing narrow, round edged umbilical chink. Aperture ovate, outer lip moderately varicose, sharp edged, somewhat expanded abapically. Columella everted, forming medial border of umbilical chink, parietal callus well developed, narrow not concealed on ventral view.

**Discussion** – We place this species in the genus *Pseudosetia* based on its small size, squat cylindrical shell shape and paucispiral protoconch bearing spiral sculpture. However, it fits uncomfortably in this genus, as it would be the only known species with axial sculpture and the last whorl is less globose than usual for the genus and does not obscure the parietal callus, which is strongly developed for *Pseudosetia*. It could also be considered a small *Alvania* species. We therefore name this species *Pseudosetia sergegofasi* nov. sp. in order to avoid possible future problems of homonymy with the extant West African species *Alvania gofasi* (Rolán & Fernandes, 1990), should this species be transferred to that genus.

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

***Pseudosetia peyroti* nov. sp.**

Plate 104, fig. 3

*Type material* – Holotype MNHN.F. A57905, height 2.1 mm, width 1.1 mm; paratype 1 MNHN.F. A57906, height 2.1 mm, width 1.0 mm; paratype 2 NHMW 2016/0103/0577, height 2.1 mm, width 1.0 mm; paratype 3 NHMW 2016/0103/0579, height 2.0 mm, width 1.0 mm; paratype 4 RGM.1348635, height 2.0 mm; paratype 5 RGM.1348636, height 2.1 mm.

*Other material* – Maximum height 2.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0579 (34), RGM.1348637 (1), RGM.1348669 (8), RGM.1348674 (1), RGM.1348749 (27), RGM.1348965 (1). **Renauleau:** NHMW 2016/0103/1616 (14), LC (3).

*Etymology* – Named in honour of Albert Peyrot (1860-1939), French malacologist, in recognition of his enormous contribution to French fossil malacology. *Pseudosetia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Pseudosetia* species of small size, with relatively slender, elongate cylindrical shell, smooth paucispiral protoconch, convex teleoconch whorls devoid of sculpture, except for faint growth lines, moderately tall, globose last whorl that just obscures parietal callus, narrow umbilical chink.

*Description* – Shell small, rissoiform, tall cylindrical with blunt apex. Protoconch paucispiral, dome-shaped, composed of 1.75 smooth whorls, with large nucleus; Protoconch I and II not delimited ( $dp = 455 \mu\text{m}$ ,  $hp = 300 \mu\text{m}$ ,  $dn = 190 \mu\text{m}$ ,  $dp1 = 195 \mu\text{m}$ ). Teleoconch of 3.5 smooth convex whorls, periphery just above abapical suture on first whorl, just below mid-whorl on penultimate whorl. Suture linear, impressed. Sculpture restricted to inconspicuous axial growth lines. Last whorl moderately globose and elongate, evenly convex, base not delimited, umbilical chink almost closed. Aperture small, ovate, outer lip moderately varicose, sharp edged, somewhat expanded abapically. Columella everted, forming medial border of umbilical chink, parietal callus narrow, just concealed on ventral view by moderately bulging last whorl.

*Discussion* – *Pseudosetia peyroti* nov. sp. differs from its fossil and extant congeners in having a totally smooth protoconch and lacking any spiral sculpture. It is also more slender and cylindrical than usual for the genus and the last whorl is less globose so that the ventral bulge just obscures the parietal callus rather than overhanging it as in most of its congeners.

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

***Pseudosetia ivolasi* nov. sp.**

Plate 104, fig. 4

*Type material* – Holotype MNHN.F. A57907, height 2.0 mm, width 1.3 mm; paratype 1 MNHN.F. A57908, height 1.9 mm, width 1.2 mm; paratype 2 NHMW 2016/0103/0580, height 2.1 mm, width 1.3 mm; paratype 3 NHMW 2016/0103/0581, height 2.0 mm, width 1.3 mm; paratype 4 RGM.1348751, height 2.0 mm; paratype 5 RGM.1348752, height 2.1 mm.

*Other material* – Maximum height 2.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0582 (50+), RGM.1348753 (9), LC (10), FVD (3). **Renauleau:** NHMW 2016/0103/1403 (10).

*Etymology* – Named in honour of Pierre Louis Jean Ivolas (1842-1908), French Naturalist, in recognition of his contribution to French fossil malacology. *Pseudosetia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Pseudosetia* species of small size, with smooth paucispiral protoconch of one whorl, squat cylindrical teleoconch with smooth spire whorls, strongly globose last whorl, with narrow constricted subsutural collar, smooth below or with weak spiral sculpture on base in some specimens, almost completely closed umbilical chink.

*Description* – Shell small, rissoiform, solid, squat cylindrical with blunt apex. Protoconch paucispiral, low dome-shaped, composed of one smooth whorl, with large nucleus ( $dp = 405 \mu\text{m}$ ,  $hp = 250 \mu\text{m}$ ,  $dn = 310 \mu\text{m}$ ). Teleoconch of just under three convex whorls with periphery at abapical suture. Suture linear, impressed. Spire whorls smooth. Last whorl globose, evenly convex, bearing a narrow, slightly constricted subsutural collar delimited by a weak spiral cord. Base not delimited, smooth in most specimens, bearing weak spiral sculpture in some, umbilical chink almost closed. Aperture ovate, outer lip moderately varicose, hardly expanded abapically. Columella everted, almost completely closing umbilical chink, parietal callus poorly developed, concealed on ventral view by bulging last whorl.

*Discussion* – *Pseudosetia ivolasi* nov. sp. has the typical squat cylindrical shape of the genus, with the last whorl strongly inflated, slightly overhanging and obscuring the parietal callus in ventral view. It deviates from the generic norm by having a smooth protoconch of just one whorl with a relatively huge nucleus and in having a rather solid shelled teleoconch. Apart from these differences, *P. ivolasi* differs from its congeners in having a narrow, slightly constricted subsutural collar on the last whorl, delimited by a weak spiral cord. In some speci-



mens weak spiral sculpture is also present over the base and the umbilical chink is almost completely closed. Of the Assemblage I congeners *P. wareni* nov. sp. is the most similar in shape, but that species is less solid and lacks the subsutural collar.

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

Genus *Onoba* H. & A. Adams, 1852

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

- 1852 *Onoba* H. & A. Adams, p. 358.  
 1915 *Subonoba* Iredale, pp. 450, 453. Type species (by original designation): *Rissoa fumata* Suter, 1898, present-day, New Zealand.  
 1926 *Powellia* Finlay, p. 403. Type species (by original designation): *Powellia lactea* Finlay, 1926, Miocene, New Zealand.  
 1927 *Austronoba* Powell, p. 541. Type species (by original designation): *Rissoa candidissima* Webster, 1904, present-day, New Zealand.  
 1930 *Badenia* Finlay, p. 41. Type species (by typification of replaced name): *Powellia lactea* Finlay, 1926, Miocene, New Zealand. *Nom. nov. pro Powellia* Finlay, 1926, *non* Maskell, 1879 [Hemiptera].  
 1967 *Liroculma* Ponder, p. 201. Type species (by original designation): *Rissoa apicilirata* Tate & May, 1901, present-day, SE Australia.

### *Onoba galaica* Rolán, 2008

Plate 105, fig. 1

\*2008 *Onoba galaica* Rolán, p. 236, figs 13-31, 52.

*Material and dimensions* – Height 2.9 mm. **Renauleau**: NHMW 2016/0103/1582 (1), NHMW 2016/0103/1614 (2).

*Discussion* – The shell illustrated above falls within the range of *Onoba galaica* Rolán, 2008, an extant species

from the Atlantic coast of Galicia, northern Spain. It differs from *Onoba redoniensis* nov. sp. in being more slender and fusiform, with less convex whorls and in having more closely spaced spirals. The protoconch is similar in both species; *Onoba redoniensis* nov. sp. has an extra  $\frac{1}{4}$ - $\frac{1}{2}$  whorl. As pointed out by Rolán (2008, p. 237), *O. galaica* is superficially similar to *Ceratia proxima* (Forbes & Hanley, 1850), but they differ in their protoconch; *C. proxima* is an iravadiid, and has flatter protoconch, with a smaller nucleus followed by a rapidly expanding whorl, typical of the family. The teleoconch differs from that of *C. proxima* in having higher whorls separated by a deeper suture and having more numerous but less prominent spiral threads. For further comparison with other European extant *Onoba* species, see Rolán (2008, p. 241).

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Present-day: Atlantic of Galicia, northern Spain.

### *Onoba redoniensis* nov. sp.

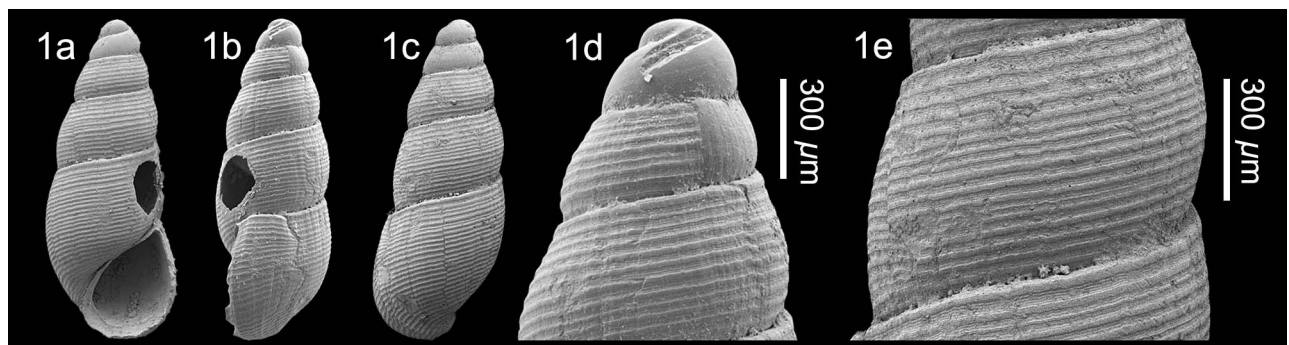
Plate 106, figs 1-2

*Type material* – Holotype MNHN.F.A57899, height 2.1 mm, width 1.0 mm; paratype 1 MNHN.F. 57900, height 2.4 mm, width 1.2 mm; paratype 2 MNHN.F. 57901, height 2.1 mm, width 1.1 mm; paratype 3 NHMW 2016/0103/0583, height 2.1 mm, width 1.0 mm; paratype 4 NHMW 2016/0103/0584, height 2.3 mm, width 1.2 mm; paratype 5 RGM.1348262, height 2.3 mm; paratype 6 RGM.1348263, height 2.3 mm.

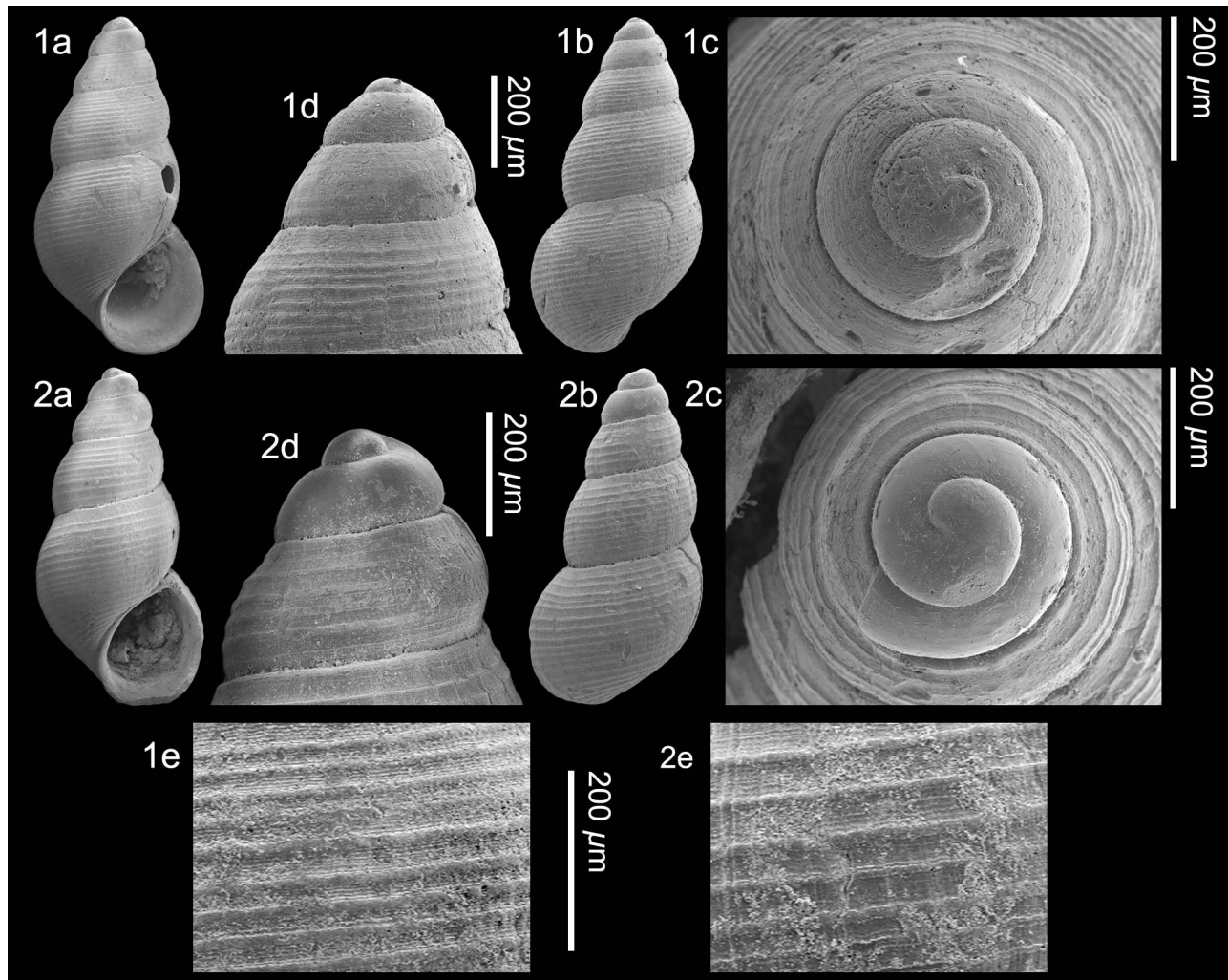
*Other material* – Maximum height 2.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0585 (50+), RGM. 1348671 (15), LC (15), FVD (7). **Renauleau**: NHMW 2016/0103/1467 (13), LC (4).

*Etymology* – Named after the ‘Redonian’ stage, the name used until recently for these NW French post-middle Miocene assemblages. *Onoba* gender feminine.

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



**Plate 105.** *Onoba galaica* Rolán, 2008; 1. NHMW 2016/0103/1582, height 2.9 mm, width 1.0 mm; 1d, detail of protoconch; 1e, detail of teleoconch sculpture (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 106.** *Onoba redoniensis* nov. sp.; 1. **Paratype 1** MNHN.F. 57900, height 2.4 mm, width 1.2 mm; 1c-d, detail of protoconch; 1e, detail of teleoconch microsculpture (SEM image); 2. **Holotype** MNHN.F.A57899, height 2.1 mm, width 1.0 mm; 2c-d, detail of protoconch; 2e, detail of teleoconch microsculpture (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Onoba* species of small size, with protoconch of two smooth whorls, except for some interrupted spiral threads on last quarter whorl, teleoconch sculpture of primary spiral cords with 4-5 threads in interspaces, axial sculpture absent.

**Description** – Shell small, rissoiform, elongate cylindrical. Protoconch dome-shaped, composed of two smooth whorls, with medium-sized nucleus, bearing some interrupted spiral threads on last quarter whorl; Protoconch I and II not delimited ( $dp = 410 \mu\text{m}$ ,  $hp = 350 \mu\text{m}$ ,  $dn = 110 \mu\text{m}$ ,  $dp1 = 240$ ). Teleoconch of three convex whorls with periphery just below mid-whorl. Suture linear, impressed. Sculpture composed of primary spiral cords, 11-12 on penultimate whorl, with 4-5 close-set spiral threads intercalated in interspaces. Last whorl weakly globose, evenly convex, base not delimited, imperforate. Aperture ovate, outer lip not thickened, slightly expanded abapi-

cally. Peristome complete, forming narrow callus rim.

**Discussion** – *Onoba redoniensis* nov. sp. has a dome-shaped protoconch composed of two smooth whorls, with medium-sized nucleus, bearing some interrupted spiral threads on the last quarter-whorl. Protoconch I and II are not delimited. Some European *Onoba* species such as *O. semicostata* (Montagu, 1803), *O. islandica* (Friele, 1886) and *O. obliqua* (Warén, 1974) are immediately separated by having axial sculpture on the teleoconch. *Onoba galatica* (Rolán, 2008) from the present-day northern Atlantic coast of Spain, but also present in the Assemblage I fauna (see above), is most similar in shape and sculpture to *O. redoniensis*, but differs in having a protoconch of similar size but with slightly fewer whorls (1.7-1.75 vs. 2). We note that the protoconch microsculpture, restricted to the last half-whorl, as well as the teleoconch microsculpture, is similar in the two species. The teleoconch whorls in *O. galatica* are less inflated than in *O. redoniensis*, the last whorl is taller and more cylindrical, and the shape of the



aperture is different; in *O. galaica* the columellar callus is straighter and longer, giving the aperture a semicircular rather than ovate outline.

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

***Onoba incisa* nov. sp.**

Plate 107, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1710, height 2.3 mm, width 1.1 mm; paratype 1 NHMW 2016/0103/1711, height 2.3 mm, width 1.1 mm, **Renauleau**. Paratype 2 NHMW 2016/0103/1782, height 2.2 mm, width 1.1 mm, **St-Clément-de-la-Place**.

*Other material* – **Renauleau**: LC (1?).

*Etymology* – Latin ‘*incisus*,-a,-um’, adjective meaning incised describing the sharply incised grooves separating the cords. *Onoba* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

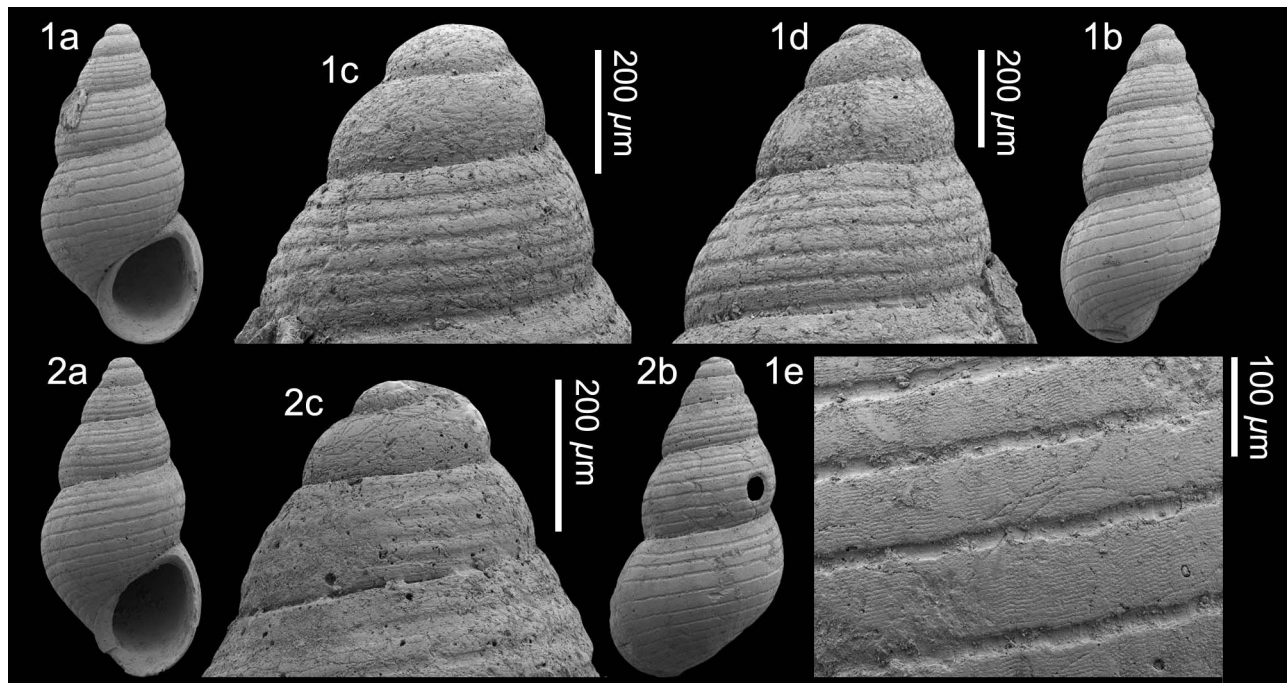
*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Onoba* species of small size, with protoconch of two whorls, probably bearing spiral threads, teleoconch sculpture of flattened cords separated by narrow grooves, 6-7 on penultimate whorl, 12 on last whorl, cords bearing dense spiral microsculpture, axial sculpture and secondary spiral cords absent.

*Description* – Shell small, rissoiform, elongate cylindrical. Protoconch dome-shaped, composed of just over two whorls, with medium-sized nucleus, surface abraded; remnants suggesting fine spiral threads. Teleoconch of three convex whorls with periphery just below mid-whorl. Suture linear, impressed. Sculpture composed of broad subequal flattened cords, 6-7 on penultimate whorl, separated by narrow grooves. Surface of cords bearing microsculpture of dense irregular wavy threads. Last whorl weakly globose, evenly convex, bearing 12 flattened spiral cords; base not delimited, imperforate. Aperture ovate, outer lip not thickened, slightly expanded abapically. Peristome complete, forming narrow callus rim.

*Discussion* – *Onoba incisa* nov. sp. is characterised by its teleoconch sculpture composed of flattened strap-like cords separated by narrowly incised grooves and by the absence of axial sculpture. Compared to congeners also lacking axial sculpture, *Onoba galaica* Rolán, 2008, also present in the Assemblage I deposits, has a more elongate shell shape and the spiral cords are narrower and more numerous. *Onoba redoniensis* nov. sp. is similar in shape, but has narrow cords separated by wider interspaces, as opposed to the broad cords separated by a narrow groove seen in *O. incisa*. In the present-day European faunas both *O. moreleti* Dautzenberg, 1889 from the Azores and *O. josae* Moolenbeek & Hoenselaar, 1987 from the Bay of Algerias have narrower cords than interspaces. All these species have in common the teleoconch microsculpture of dense irregular wavy threads.

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



**Plate 107.** *Onoba incisa* nov. sp.; 1. **Holotype** NHMW 2016/0103/1710, height 2.3 mm, width 1.1 mm; 1c-d, detail of protoconch; 1e, detail of teleoconch microsculpture; 2. **Paratype 1** NHMW 2016/0103/1711, height 2.3 mm, width 1.1 mm; 2c, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



***Onoba fragilis* nov. sp.**

Plate 108, figs 1-2

*Type material* – Holotype NHMW 2016/0103/1712, height 2.2 mm, width 1.1 mm; paratype 1 NHMW 2016/0103/1713, height 2.2 mm, width 1.1 mm.

*Other material* – Renauleau: LC (?).

*Etymology* – Latin ‘*fragilis*, -is, -e’ adjective meaning brittle or fragile, as all known specimens of this thin-shelled species are damaged. *Onoba* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Onoba* species of small size, elongate cylindrical shell shape, with protoconch of two whorls, bearing spiral threads, teleoconch whorls strongly convex, sculpture of fine irregular spiral threads covering entire surface, fine axial ribs developed on subsutural area, aperture expanded abapically.

*Description* – Shell small, rissoiform, elongate cylindrical. Protoconch dome-shaped, composed of two convex whorls, with medium-sized nucleus, surface sculptured by irregular spiral threads. Junction with teleoconch delimited by scar. Teleoconch of 2.5 strongly convex whorls with periphery just below mid-whorl. Suture linear, impressed. Sculpture composed of fine, irregular, somewhat wavy spiral threads. Axial sculpture of fine, close-set sinuous ribs developed only on subsutural part of penultimate and

last whorls. Last whorl weakly globose, evenly convex; base not delimited, imperforate. Aperture ovate, outer lip slightly thickened by weak labial varix, expanded abapically. Peristome complete, forming narrow callus rim.

*Discussion* – *Onoba fragilis* nov. sp. is separated from its Assemblage I congeners in being the only *Onoba* species with axial sculpture, albeit weak and limited to the adapical portion on the last whorl. Several other European *Onoba* species with axials have been described. *Onoba semicos-tata* (Montagu, 1803) is thicker shelled, more cylindrical, and the axials that are restricted to the first two teleoconch whorls are broader than in *O. fragilis*. *Onoba islandica* (Friele, 1886) has inflated, strongly convex whorls separated by a deep suture and has weaker axial sculpture than *O. fragilis*, and *O. obliqua* (Warén, 1974) has coarser spiral sculpture and narrow axials most prominently developed mid-whorl rather than on the adapical portion as in *O. fragilis*.

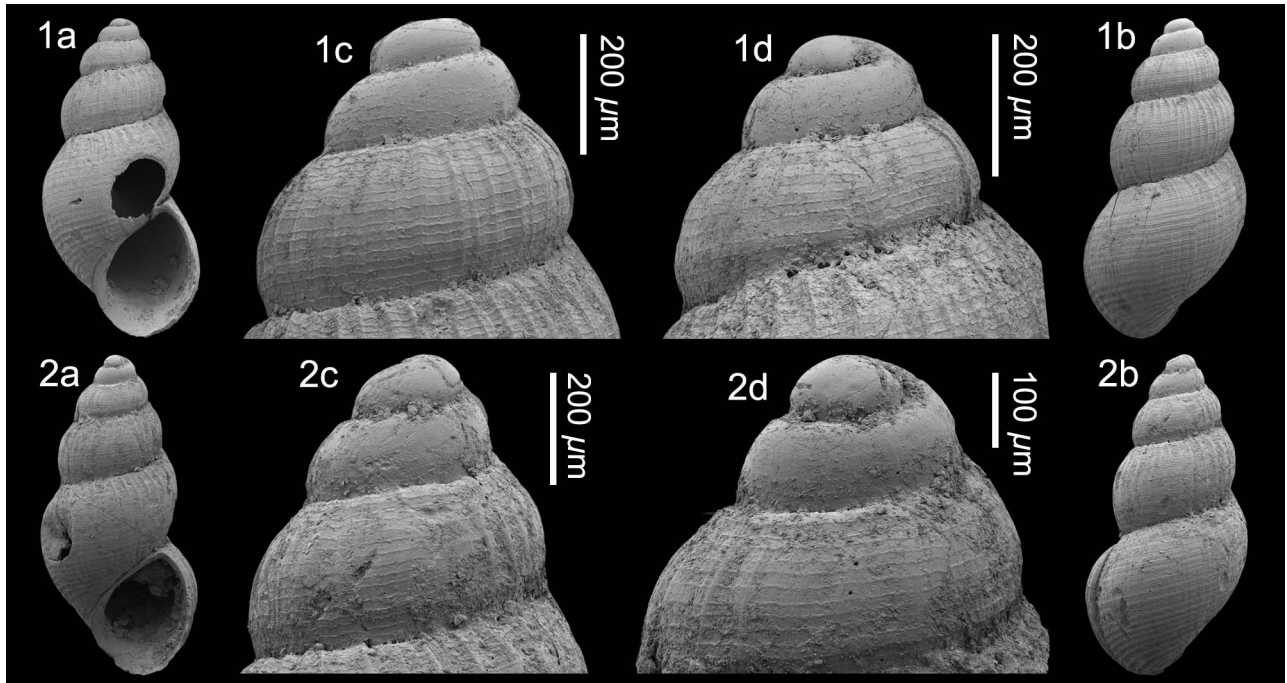
*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper).

Genus *Rissoa* Desmarest, 1814

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

1814 *Rissoa* Desmarest, 1814, p. 7.

For generic synonymy see Van Dingenen *et al.* (2016, p. 141).



**Plate 108.** *Onoba fragilis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1712, height 2.2 mm, width 1.1 mm; 1c-d, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1713, height 2.2 mm, width 1.1 mm; 2c-d, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Rissoa decorticata* nov. sp.**

Plate 109, figs 1-2

*Type material* – Holotype MNHN.F.A66709, height 5.0 mm, width 2.6 mm; paratype 1 MNHN.F.A66710, height 3.1 mm, width 1.8 mm; paratype 2 NHMW 2016/0103/1386, height 4.3 mm, width 2.3 mm; paratype 3 NHMW 2016/0103/11387, height 4.2 mm, width 2.0 mm; paratype 4 NHMW 2016/0103/1596, height 4.7 mm, width 2.1 mm; paratype 5 RGM.1348073, height 4.1 mm, width 2.1 mm; paratype 6 RGM.1348074, height 4.5 mm, width 2.4 mm; paratype 7 RGM.1348699, height 4.5 mm, width 2.3 mm; paratype 8 RGM.1348700, height 4.4 mm, width 2.3 mm.

*Other material* – Maximum height 5.0 mm, width 2.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1388 (50+), RGM.1348075 (25), RGM.1348621 (1), RGM.1348701 (35), RGM.1348968 (1), LC (50+), FVD (50+). **Sceaux-d’Anjou**: RGM.1348376 (1), RGM.1348823 (1), RGM.1348940 (2). **Renauleau**: NHMW 2016/0103/1468 (23), LC (20), FVD (12).

*Etymology* – Latin ‘*decortico*, -are, ‘-avi, atus’, verb meaning stripped away or peeled, and ‘*cortex*’, noun, meaning bark; ‘stripped of its bark’. *Rissoa* gender feminine.

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

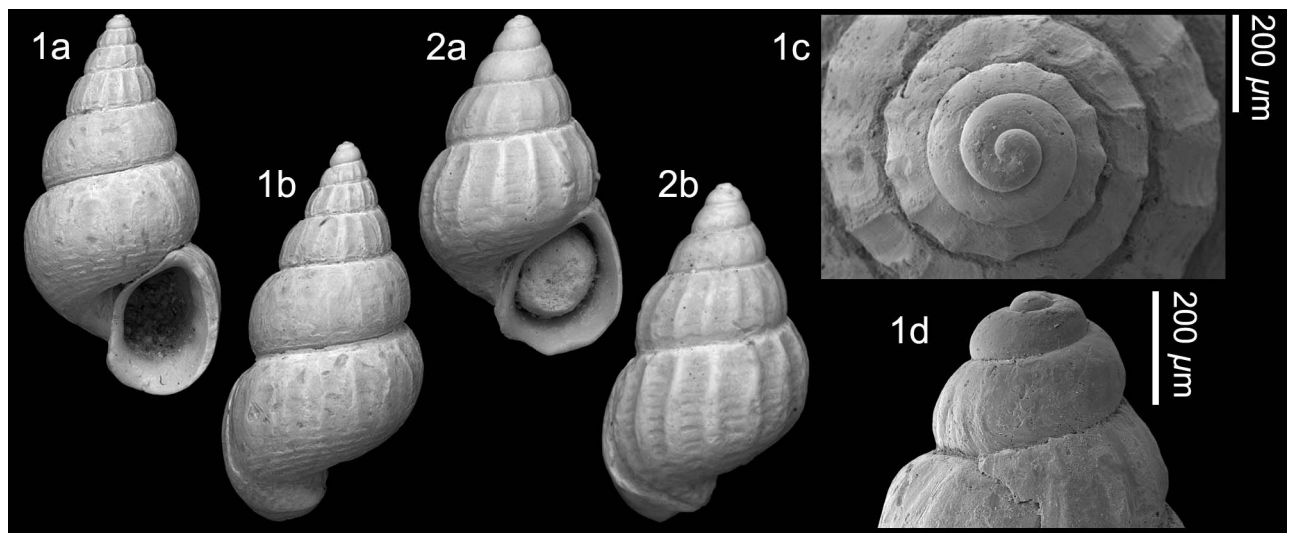
*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Rissoa* species with protoconch of 2.5 smooth whorls, teleoconch of 4-5 convex whorls separated by impressed suture, sculpture of about 14 axial ribs that disappear on third whorl in most specimens, but can persist to last whorl in some, greatly reduced spiral sculpture visible only in some specimens, rounded last whorl with prominent umbilical chink, outer lip strongly flared and everted abapically, obtusely denticulate within.

ture visible only in some specimens, rounded last whorl with prominent umbilical chink, outer lip strongly flared and everted abapically, obtusely denticulate within.

*Description* – Shell small, rissoiform. Protoconch multispiral, composed of 2.5 smooth convex whorls, with small nucleus ( $dp = 320 \mu\text{m}$ ,  $hp = 270 \mu\text{m}$ ,  $dn = 45 \mu\text{m}$ ,  $dp1 = 105 \mu\text{m}$ ). Transition with teleoconch not sharply delimited marked by beginning of axial sculpture. Teleoconch consisting of 4-5 convex whorls, with periphery just above abapical suture. Suture linear, impressed. Axial sculpture of about 14 narrow orthocone to weakly opisthocline ribs that weaken in most specimens, disappearing on third whorl, but persisting onto last whorl in some specimens. Spiral sculpture subobsolete, reduced to weak spiral cords separated by narrow grooves, visible only in interspaces between ribs in some specimens. Last whorl evenly rounded, smooth or axially ribbed; base not delimited, bearing weak spirals, prominent umbilical chink. Aperture moderate size, ovate, outer lip strongly flared and everted abapically, thickened by narrow varix, obtusely to moderately denticulate within. Columella broadly excavated. Columellar callus thickened, sharply delimited, forming narrow callus rim, erect abapically.

*Discussion* – *Rissoa decorticata* nov. sp. is an unusual species in that the surface seems to be decorticate in even the best-preserved specimens from St-Clément-de-la-Place. The effect this gives is to accentuate the suture, making it appear narrowly canaliculated. Similarly, the last portion of the last whorl immediately behind the labial varix is abraded in most specimens, accentuating the varix. The spiral sculpture is greatly attenuated, and either absent or abraded in most specimens. Despite these taphonomic changes, this is a highly variable species; the height of the spire and the extent to which the axial sculpture persists along the teleoconch are variable, as is the strength of the teeth within the outer lip, which in most



**Plate 109.** *Rissoa decorticata* nov. sp.; 1. **Holotype** MNHN.F.A66709, height 5.0 mm, width 2.6 mm; 1c, d, detail of protoconch (SEM image); 2. **Paratype 1** MNHN.F.A66710, height 3.1 mm, width 1.8 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

specimens are rather obtuse or even absent, but in occasional specimens are well-developed.

*Rissoa decorticata* is highly reminiscent of *R. obsoleta* Wood, 1848 (1848, pl. 11, fig. 11) from the Pliocene Coralline and Red Crags of England. In that species the surface is similarly abraded, and Wood (1848) commented on the ‘partial decomposition of the exterior’ (Wood, 1848, p. 105). The English Pliocene species differs in lacking axial sculpture. Marquet (1998, fig. 36) figured a specimen from the Belgian Pliocene with the shell in good condition that does not have the spiral sculpture described by British authors (Harmer, 1925, Wood, 1848). Brébion (1964, p. 175, pl. 4, figs 30-31) figured a similar decorticated rissoid from Gourbesville (Assemblage IV; upper Pliocene-Pleistocene) under the name *Turboella cossmanni* nov. sp. (*nomen nudum*). The shell lacks its spire, but is closely similar to *R. obsoleta* and will be reviewed with the rest of the Assemblage IV fauna. We are not aware of any other *Rissoa* species sharing this tendency to decorticate.

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

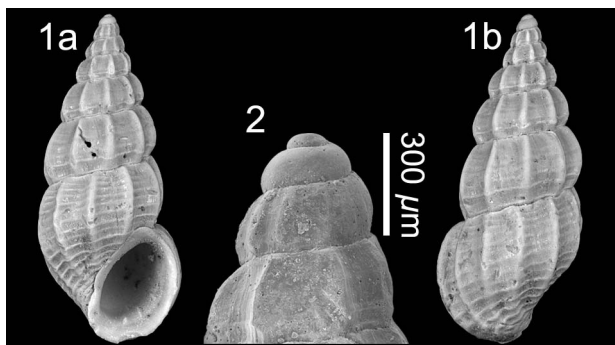
### *Rissoa obeliscoides* nov. nom.

Plate 110, fig. 1

- 1854 *Rissoa Notabilis* Millet, p. 154 (*nomen nudum*).  
 1865 *Rissoa notabilis* Millet, p. 580 (*non* C.B. Adams, 1852).  
 1964 *Rissoa notabilis* Millet, 1854 [*sic*] – Brébion, p. 179, pl. 4, figs 34, 35.

*Type material* – Syntypes: Sceaux-d’Anjou, Thorigné and St-Clément-de-la-Place, lost (*vide* Brébion, 1964, p. 180).

*Material and dimensions* – Maximum height 6.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0383-384 (2), NHMW 2016/0103/0385 (50+), RGM.1348072 (50+), RGM.1348251 (50+), RGM.1348259 (15), RGM.1348328 (50+), RGM.1348830 (50+), RGM.1348950 (13), LC (50+),



**Plate 110.** *Rissoa obeliscoides* nov. nom.; 1. NHMW 2016/0103/0383, height 6.0 mm, width 2.6 mm; 2. NHMW 2016/0103/0384, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0386 (50+), RGM.1347936 (10), RGM.1348355 (4), RGM.1348367 (7), RGM.1348519 (2), RGM.1348897 (20), LC (50+), FVD (50+).

*Etymology* – Latin ‘*obeliscus*, -i’, noun, reflecting the high ornate spire resembling an ancient Egyptian obelisk. *Rissoa* gender feminine.

*Locus typicus* – Sceaux-d’Anjou, Thorigné, St-Clément-de-la-Place.

*Stratum typicum* – Tortonian, upper Miocene.

*Original description* – ‘*Rissoa notabilis*. Millet. *Coq. en ovale allongé, aiguë au sommet; sept à huit tours de spire, marqués de côtes longitudinales, l’intervalle qui les sépare garni de fines stries transversales très-rapprochées. Les deux derniers tours font ensemble plus de la moitié de la longueur totale de la coq. Ouverture en ovale arrondi; bord droit garni de 6 à 8 petites stries très-rapprochées. Longueur: 6-8 millimètres; diamètre: 2-3 millimètres. Sc, Th., Saint-Clément*’ (Millet, 1865, p. 580).

*Discussion* – *Rissoa notabilis* Millet, 1865 is a primary homonym of *R. notabilis* C.B. Adams, 1852 [now accepted as *Ividella notabilis* (C. B. Adams, 1852)]. We propose the replacement name *Rissoa obeliscoides* nov. nom. for Millet’s species.

*Rissoa obeliscoides* is a distinctive species, as Millet’s original epithet ‘*notabilis*’ would suggest. We would add to the original description that the protoconch is multi-spiral, composed of 2.5 smooth, convex whorls, with a small nucleus. The teleoconch sculpture is as stated by Millet, about eight narrow orthocone axial ribs and fine spiral cords; on spire whorls the adapical cords tend to be subobsolete or weak, the abapical primary cord strongest. There is a little variability regarding the height of the spire, the expansion of the outer lip and the strength of the denticles within the outer lip. The sculpture is relatively constant. There are no European fossil or extant congeners that are closely similar. *Rissoa pouwéri* Van Dingenen, Ceulemans & Landau, 2016 from the lower Pliocene Assemblage III locality of Le Pigeon Blanc is superficially similar, but is lower-spined, the last whorl is more globose and the spiral sculpture is closer set, with more numerous subequal spirals, and lacks the more strongly developed abapical spiral cord. Several present-day European congeners: *R. labiosa* (Montagu, 1803), *R. ventricosa* Desmarest, 1814, *R. violacea* Desmarest, 1814, *R. guerini* Récluz, 1843, *R. lia* (Monterosato, 1884) and *R. variabilis* (Megerle von Mühlfeldt, 1824) all have broader axial ribs, more crowded spiral cords and a wider aperture, with an expanded outer lip, without internal denticles.

Brébion (1964, p. 150) recorded this species from the Assemblage I localities (Sceaux-d’Anjou, Thorigné, St-Clément-de-la-Place, Les Pierres Blanches, St-Michel).

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Calas, 1949; Brébion, 1964).



***Rissoa torquata* nov. sp.**

Plate 111, fig. 1

*Type material* – Holotype NHMW 2016/0103/1567, height 3.0 mm, width 1.9 mm, **St-Clément-de-la-Place**; paratype 3 RGM.1348719, height 2.9 mm, width 1.8 mm, **Sceaux-d'Anjou**; paratype 1 NHMW 2016/0103/1568, height 2.9 mm, width 1.8 mm; paratype 2 NHMW 2016/0103/1569, height 2.7 mm, width 1.6 mm, **Renauleau**.

*Other material* – Maximum height 3.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1597 (3 juveniles). **Renauleau**: NHMW 2016/0103/1570 (4).

*Etymology* – Latin ‘*torques*, *-uis*’, noun, meaning torque, chain, necklace; describing the infrasutural band characteristic of the species. *Rissoa* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Rissoa* species with small robust shell, protoconch of two smooth whorls, four teleoconch whorls bearing indented subsutural band and raised suprasutural cord accentuating suture, no axial sculpture, last whorl globose with a few weak cords adapically and over base, smooth columella.

*Description* – Shell small, robust, conical spire. Protoconch of two whorls with smooth surface. Teleoconch of four convex whorls with periphery at abapical suture. Suture linear, deeply impressed. Spire whorls smooth except for single indented subsutural band and poorly delimited, slightly raised suprasutural cord, both accentuating suture. Last whorl globose, strongly convex mid-whorl; sculpture of two or three weak cords below suprasutural band, smooth mid-whorl, weak cords on base. Base slightly flattened, small umbilical chink. Aperture ovate, outer lip, roundly pointed abapically, thickened by poorly delimited labial varix, smooth within. Columella excavated, smooth. Columellar and parietal callus thickened forming narrow callus rim.

*Discussion* – *Rissoa torquata* nov. sp. is most similar to

the extant Mediterranean species *R. multicincta* Smriglio & Mariottini, 1995 in size, robustness and shape, but differs in having a relatively well-delimited subsutural band, and spiral cords on the base. In *R. multicincta* the sculpture is extremely weak and poorly delimited. Both of these species have a smooth columella. The present-day eastern Atlantic and Mediterranean species *Rissoa monodonta* Philippi, 1836 and *R. auriformis* Pallary, 1904 both differ in having a central columellar tooth. We note that *R. auriformis* also has a subsutural collar, but has a more elongate shell shape and a wider, more expanded aperture.

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

Genus *Powellisetia* Ponder, 1965

*Type species* (by original designation) – *Rissoa porcellana* Suter, 1908, present-day, New Zealand.

1965b *Powellisetia* Ponder, p. 104.

***Powellisetia europaea* nov. sp.**

Plate 112, figs 1-2

*Type material* – Holotype MNHN.F.A66706, height 1.8 mm, width 1.4 mm; paratype 1 NHMW 2016/0103/1575, height 1.7 mm, width 1.4 mm; paratype 2 NHMW 2016/0103/1576, height 1.6 mm, width 1.3 mm.

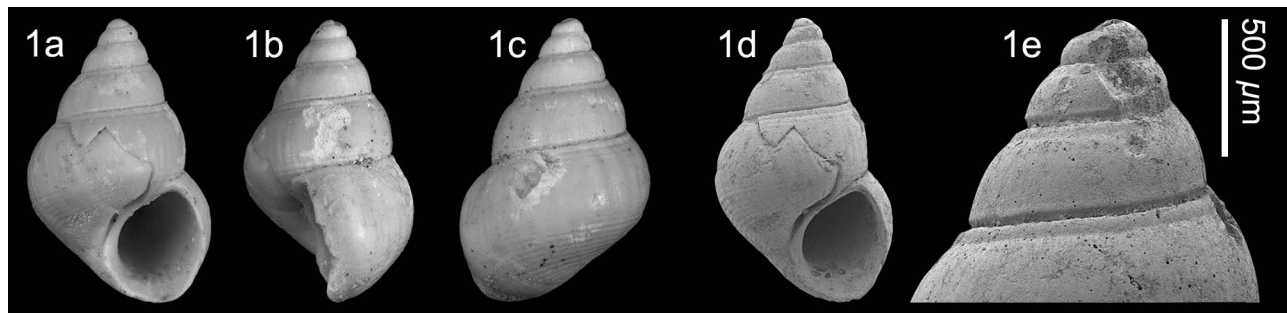
*Other material* – Maximum height 1.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1577 (8). **Renauleau**: NHMW 2016/0103/1613 (1).

*Etymology* – Named as being the first recognised European member of the genus. *Powellisetia* gender feminine.

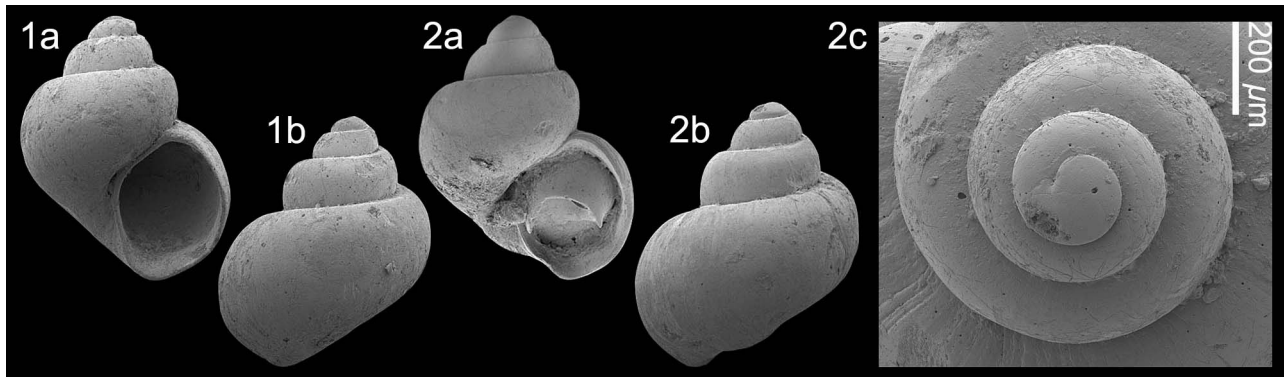
*Locus typicus* – Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Powellisetia* species of small size, with



**Plate 111.** *Rissoa torquata* nov. sp.; 1. **Holotype** NHMW 2016/0103/1567, height 3.0 mm, width 1.9 mm; 1e, detail of protoconch (1e, f, SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 112.** *Powellisetia europaea* nov. sp.; 1. **Holotype** MNHN.F.A66706, height 1.8 mm, width 1.4 mm; 2. **Paratype 1** NHMW 2016/0103/1575, height 1.7 mm, width 1.4 mm; 2c, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

scalate spire, devoid of sculpture, protoconch of about one whorl, teleoconch junction not sharply delimited, globose last whorl, small umbilical chink, relatively large aperture weakly pointed abapically.

*Description* – Shell minute, ovate, turbiniform, with scalate spire. Protoconch dome-shaped, of about one smooth whorl with large nucleus (dn = 140 µm, dpl = 240 µm). Protoconch/teleoconch junction not sharply delimited. Teleoconch consisting of three convex whorls with periphery at abapical suture. Suture linear, deeply impressed. Last whorl globose, rounded, with shoulder placed relatively high; base not delimited, small umbilical chink. Aperture relatively large, simple, weakly flared and pointed abapically. Peristome complete forming thin callus margin.

*Discussion* – Most members of this genus are antipodean, although a few species have been described from the South Atlantic (Ponder, 1983), and most inhabit temperate to cold water, although some warmer-water species have also been described (Kay, 1979). *Powellisetia europaea* nov. sp. is more turbiniform than most known species, which are more rissoiform, although *P. fallax* Kay, 1979 from Hawaii is almost identical in shape and in lacking sculpture. It differs from *P. europaea* in having the shoulder placed lower and in having a wider umbilicus. *Powellisetia subtenuis* (Powell, 1937) from New Zealand is also similar in shape, but the teleoconch is finely spirally striate.

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

Genus *Pusillina* Monterosato, 1884

*Type species* (by monotypy) – *Rissoa pusilla* Philippi, 1836 (junior secondary homonym of *R. pusilla* (Brocchi, 1814) [= *Turbo pusillus* Brocchi, 1814], renamed *Rissoa philippi* Aradas & Maggiore, 1844), present-day, Mediterranean.

1884b *Pusillina* Monterosato, p. 56.

1972 *Turboella* (*Mutiturboella*) Nordsieck, p. 196. Type species (by original designation): *Rissoa inconspicua* Alder, 1844, present-day, British Isles.

1972 *Turboella* (*Benzia*) Nordsieck, p. 197. Type species (by original designation): *Paludina benzi* Aradas & Maggiore, 1843, present-day, Mediterranean.

*Note* – It is difficult to ascribe species to the genera *Rissoa* Desmarest, 1814 or *Pusillina* Monterosato, 1884 in the absence of soft tissue, as they differ mainly in the character of their genitalia (Ponder, 1985a, p. 26). We ascribe the species below to *Pusillina* rather than *Rissoa* based on their small size, the very variable extent of their axial sculpture and the absence of spiral sculpture from some species, similar to several European fossil (see Lozouet, 2015) and extant (see Warén, 1996a, b) *Pusillina* species.

***Pusillina dollfusi* nov. sp.**

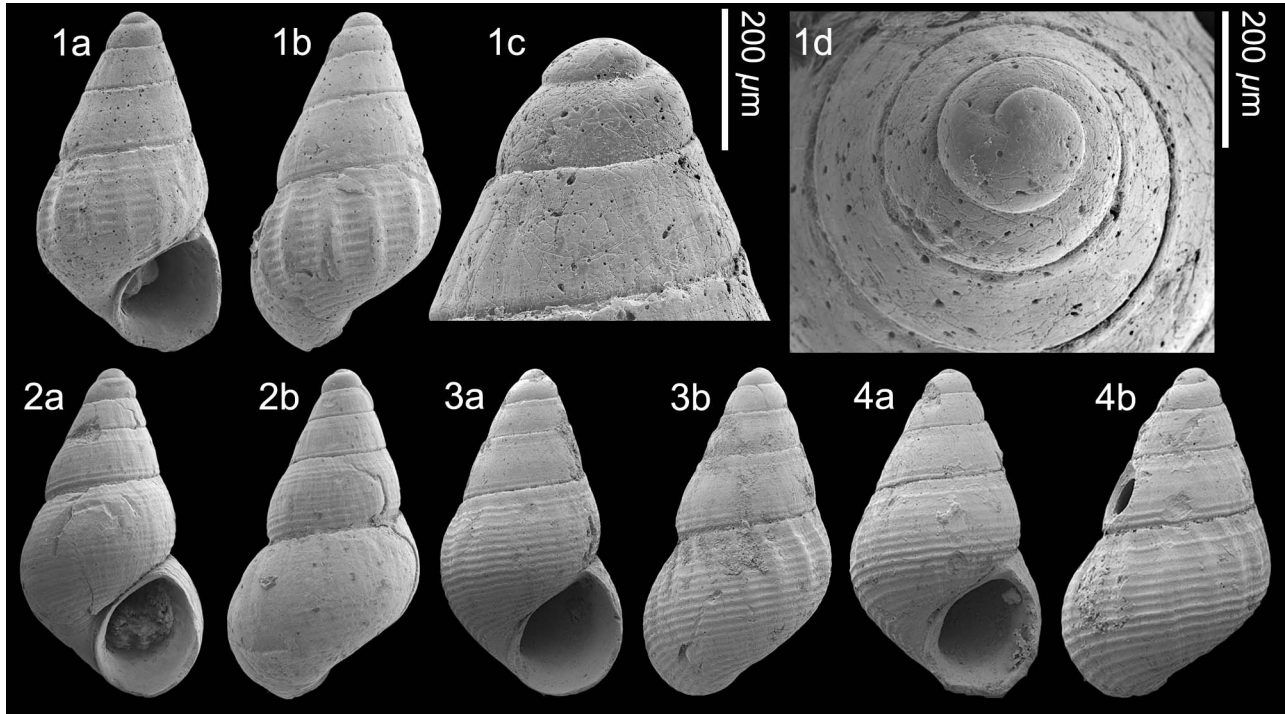
Plate 113, figs 1-4

*Type material* – Holotype MNHN.F.A57731, height 2.1 mm, width 1.3 mm; paratype 1 MNHN.F. A57909, height 2.5 mm, width 1.4 mm; paratype 2 NHMW 2016/0103/0532, height 2.3 mm, width 1.2 mm; paratype 3 NHMW 2016/0103/0533, height 1.9 mm, width 1.1 mm; paratype 4 RGM.1348594, height 2.2 mm; paratype 5 RGM.1348595, height 2.3 mm.

*Other material* – Maximum height 2.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0537 (50+), RGM.1348596 (23), RGM.1348670 (45), RGM.1348750 (50+), RGM.1348969 (5), LC (50+), FVD (50+).

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

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



**Plate 113.** *Pusillina dollfusi* nov. sp.; 1. **Holotype** MNHN.F.A57731, height 2.1 mm, width 1.3 mm; 1c-d, detail of protoconch; 2. **Paratype 1** MNHN.F. A57909, height 2.5 mm, width 1.4 mm; 3. **Paratype 2** NHMW 2016/0103/0532, height 2.3 mm, width 1.2 mm; 4. **Paratype 3** NHMW 2016/0103/0533, height 1.9 mm, width 1.1 mm (all SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Pusillina* species of small size, with moderately tall, conical spire, paucispiral protoconch of 1.8 smooth whorls, first teleoconch whorl straight-sided, last convex, sculptured by fine, close-set spiral cords, abapical cord strengthened, ribs on last whorl in some specimens that fade gradually at level of insertion of outer lip and do not extend onto base.

**Description** – Shell small, solid, rissoiform, with relatively tall conical spire. Protoconch paucispiral, dome-shaped, composed of 1.8 smooth whorls, with a large nucleus; Protoconch I of one whorl, sharply delimited, Protoconch II consisting of 0.8 convex whorl ( $dp = 400 \mu\text{m}$ ,  $hp = 230 \mu\text{m}$ ,  $dn = 150 \mu\text{m}$ ,  $dpl = 260 \mu\text{m}$ ). Transition with teleoconch sharply delimited. Teleoconch consisting of 3.5 whorls; first teleoconch whorl straight sided, with periphery at abapical suture, second whorl slightly swollen abapically, so that periphery is above suture. Suture linear, impressed. Axial sculpture variable; when present composed of 13-14 weak, orthocline rounded ribs, usually only developed on last whorl. Spiral sculpture of narrow close-set cords; abapical cord usually slightly stronger. Last whorl convex, with or without ribs; in ribbed specimens, sculpture not extending onto base, but terminating gradually at level of insertion of outer lip. Base not delimited, bearing narrow umbilical chink. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by varix, smooth

within. Columella short, weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus rim.

**Discussion** – As in many fossil and extant *Pusillina* species, the presence of axial sculpture and if present its strength, are highly variable. Ribbed and unribbed forms occur in roughly equal proportions at the type locality. The regularly conical spire commencing with a straight-sided teleoconch whorl with only the last whorl convex separates *Pusillina dollfusi* nov. sp. from its congeners. *Pusillina gallica* nov. sp., also from the Assemblage I fauna, is immediately separated by its multispiral protoconch, less regularly conical spire with more convex whorls and by the presence of broad axial ribs.

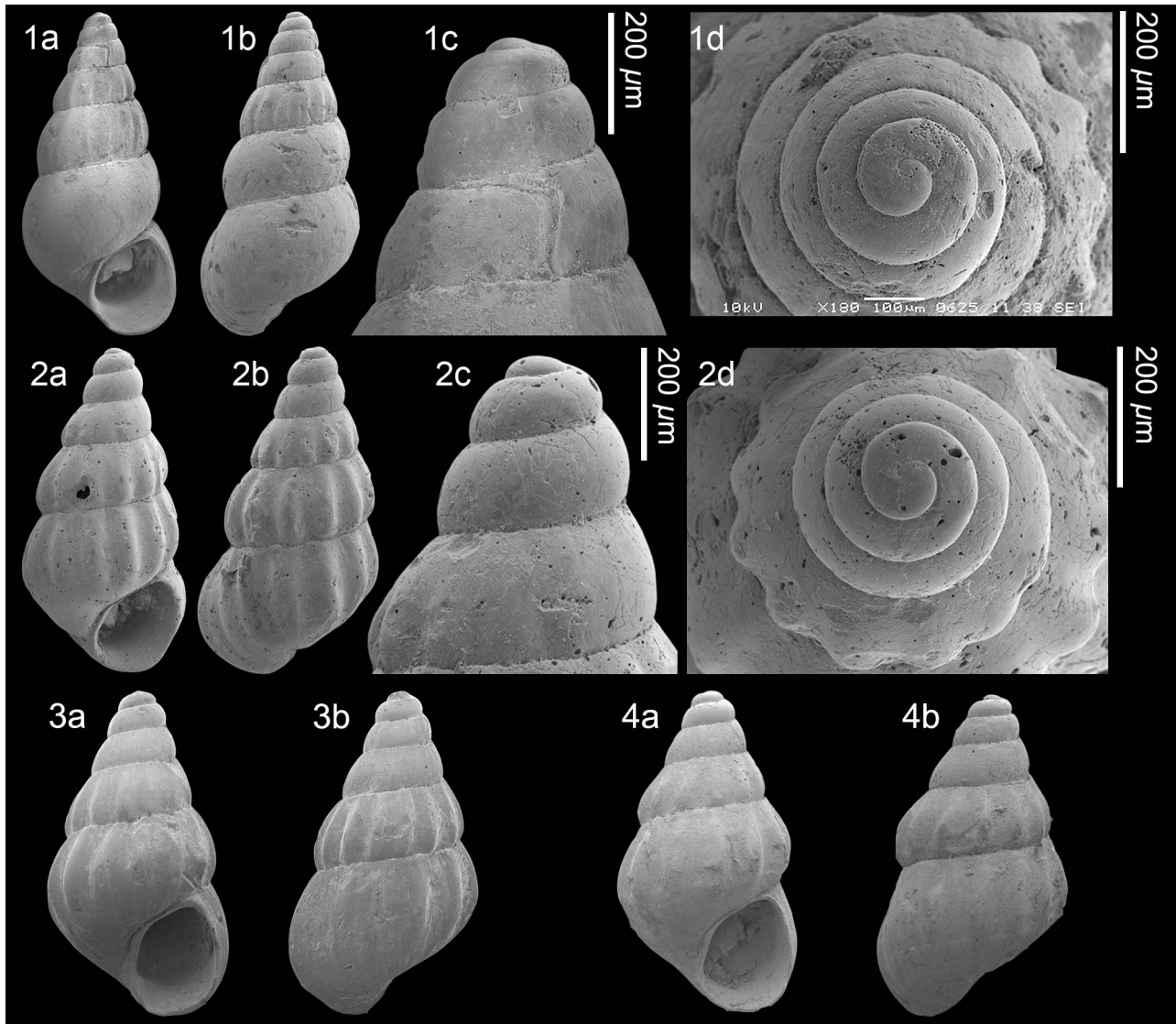
**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper).

***Pusillina gallica* nov. sp.**

Plate 114, figs 1-4

**Type material** – Holotype MNHN.F.A57729, height 2.7 mm, width 1.3 mm; paratype 1 MNHN.F.A57730, height 1.9 mm, width 950  $\mu\text{m}$ ; paratype 2 NHMW 2016/0103/0532, height 1.8 mm, width 1.0 mm; paratype 3 NHMW 2016/0103/0533, height 2.0 mm, width 1.1 mm; paratype 4 RGM.1348600, height 2.1 mm; paratype 5 RGM.1348601, height 2.3 mm, **St-Clément-de-la-Place**.





**Plate 114.** *Pusillina gallica* nov. sp.; 1. **Holotype** MNHN.F.A57729, height 2.7 mm, width 1.3 mm; 2. **Paratype 1** MNHN.F.A57730, height 1.9 mm, width 950 µm; 3. **Paratype 2** NHMW 2016/0103/0532, height 1.8 mm, width 1.0 mm; 4. **Paratype 3** NHMW 2016/0103/0533, height 2.0 mm, width 1.1 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Paratype 6 RGM.1348692, height 2.3 mm; paratype 7 RGM.1348693, height 2.4 mm, **Sceaux-d'Anjou**.

**Other material** – Maximum height 3.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0534 (50+), RGM.1348053 (3), RGM.1348602 (5), RGM.1348702 (50+), RGM.1348970 (2), LC (50+), FVD (50+). **Sceaux-d'Anjou**: RGM.1348694 (2), RGM.1348973 (4). **Renauleau**: NHMW 2016/0103/1397 (50+), RGM.1349006 (25), LC (35), FVD (18). **Beugnon**: RGM.1348438 (1).

**Etymology** – Named after the Roman province of Gaul, Latin: ‘*Gallia*’, a region of Western Europe encompassing present-day France. *Pusillina* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

**Diagnosis** – *Pusillina* species of small size, elongate shape, with multispiral protoconch of 2.5 whorls, smooth first teleoconch whorl, axial sculpture below consisting of 12-13 ribs, obsolete or persisting onto last whorl; when persisting, fading gradually at level of insertion of outer lip, not extending onto base.

**Description** – Shell small, elongate, rissoiform, with tall spire. Protoconch dome-shaped, composed of about 2.5 smooth whorls, with a small nucleus ( $dp = 300 \mu\text{m}$ ,  $hp = 310 \mu\text{m}$ ,  $dn = 50 \mu\text{m}$ ,  $dp1 = 120 \mu\text{m}$ ). Transition with teleoconch not sharply delimited. Teleoconch consisting of 3-4 convex whorls, with periphery below mid-whorl. Suture linear, impressed. Axial sculpture variable; first teleoconch whorl smooth; second whorl with 12-13 or-

thocline rounded ribs, most strongly developed on abapical half of whorls. Axial ribs weaken and disappear on penultimate whorl in some specimens, persist until the aperture in others. Last whorl convex, ribbed or smooth; in ribbed specimens, sculpture not extending onto base, but terminating gradually at level of insertion of outer lip. Base not delimited, bearing narrow umbilical chink. Aperture moderate size, ovate, outer lip somewhat flared abapically, thickened by varix, smooth within. Columella short, weakly excavated. Columellar and parietal callus thickened, sharply delimited, forming narrow callus.

*Discussion* – *Pusillina gallica* nov. sp. is most similar in shell shape and sculpture to the extant European species *P. philippi* (Aradas & Maggiore, 1844), but in that species the whorls are more convex and more swollen abapically and the axial ribs are strongly opisthocline and terminate rather abruptly at the level of the insertion of the outer lip. Most of the other extant European species are less slender than *P. gallica*; *P. marginata* (Michaud, 1830) has more strongly developed and more numerous axial ribs, as does *P. radiata* (Philippi, 1836), which also differs in having the axials extending, albeit weakened onto the base and in having weak spiral sculpture. Three French Atlantic Oligocene congeners, *P. grateloupi* (Vergneau-Saubade, 1968), *P. aquensis* Lozouet, 2015 and *P. protocarinata* Lozouet, 2015 all differ from *P. gallica* in having squatter shells and more numerous narrower ribs that stop abruptly above the base on the last whorl. *Pusillina gallica* is easily separated from *P. dollfusi* nov. sp. from the same deposits (see above) by its multispiral protoconch and absence of spiral sculpture.

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

### *Pusillina* sp.

Plate 115, figs 1-3

*Material and dimensions* – Maximum height 2.4 mm, width 1.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1777 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1714-1716 (3).

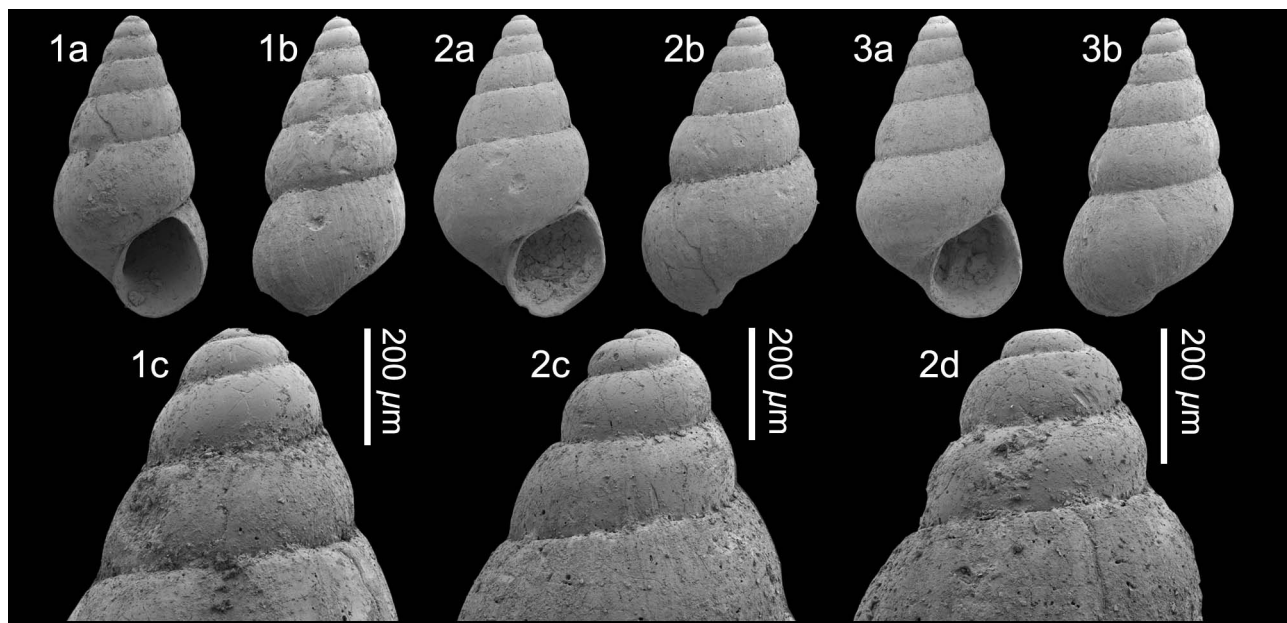
*Discussion* – Similar to *Pusillina gallica* nov. sp., but lacking any axial sculpture. However, the significant variation in shell shape and sculpture seen in the population of *P. gallica* from St-Clément-de-la-Place (see Pl. 114, figs 1-4) is enormous, and some specimens with almost no sculpture can also be found. We are therefore reluctant to describe this small species with such few shell characters with which to distinguish it.

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

Genus *Setia* H. & A. Adams, 1852

*Type species* (by subsequent designation, Schwartz von Mohrenstern, 1860) – *Rissoa pulcherrima* Jeffreys, 1848, present-day, British Isles.

- 1852 *Setia* H. & A. Adams, p. 359.
- 1884a *Parvisetia* Monterosato, p. 280. Type species (by monotypy): *Rissoa scillae* Aradas & Benoit, 1876, present-day, Mediterranean.
- 1917 *Rudolphosetia* Monterosato, p. 14. Type species (by monotypy): *Truncatella fusca* Philippi, 1841, present-day, Mediterranean.
- 1972 *Setia* (*Varisetia*) Nordsieck, p. 158. Type species



**Plate 115.** *Pusillina* sp.; 1. NHMW 2016/0103/1714, height 2.2 mm, width 1.1 mm, 1c detail of protoconch; 2. NHMW 2016/0103/1715, height 2.4 mm, width 1.3 mm, 2c, detail of protoconch; 3. NHMW 2016/0103/1716, height 2.4 mm, width 1.3 mm (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



(by original designation): *Rissoa quisquiliarum* Watson, 1886, present-day, Azores.

***Setia* sp.**

Plate 116, figs 1-2

**Material and dimensions** – Maximum height 2.4 mm, width 1.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1583-1584 (2), NHMW 2016/0103/1585 (17), RGM.1348754 (1). **Sceaux-d’Anjou:** RGM.1348760 (4).

**Description** – Shell small, rissoiform. Protoconch of 1.25 smooth whorls, with large nucleus (dp = 290 µm; dn = 110 µm, dp1 = 210 µm). Teleoconch consisting of about three strongly convex whorls with periphery just above abapical suture. Suture linear, impressed. Last whorl globose, evenly rounded. Aperture relatively wide, outer lip rounded, simple, slightly flared abapically, smooth within. Peristome thin, complete, forming narrow callus rim. Columella thickened abapically, slightly erect and everted.

**Discussion** – This species has few characters to separate it from several extant European smooth-shelled taxa placed by Verduin (1984) in the genus *Cingula* Fleming, 1818, but now transferred to *Setia* H. & A. Adams, 1852 (Gofas, 2004; WoRMS). Both *Setia* and *Cingula* have a paucispiral protoconch, but it is spirally sculptured in *Cingula* (Ponder, 1985a, pp. 33, 52). The type species, *S. pulcherrima* (Jeffreys, 1848) is closely similar, but has a squatter shell and the protoconch, although also composed of 1.25 whorls, seems slightly larger (dp = 350-400 µm; dn = 150-200 µm; Fretter & Graham, 1978, p. 161). *Setia amabilis* (Locard, 1886), another European species, has a less expanded aperture. *Setia* sp. is not abundant in the Assemblage I deposits, and the two specimens illustrated (Pl. 116, figs 1-2) show considerable variation in the number of teleoconch whorls and in spire height. We therefore await further material to better characterise this species.

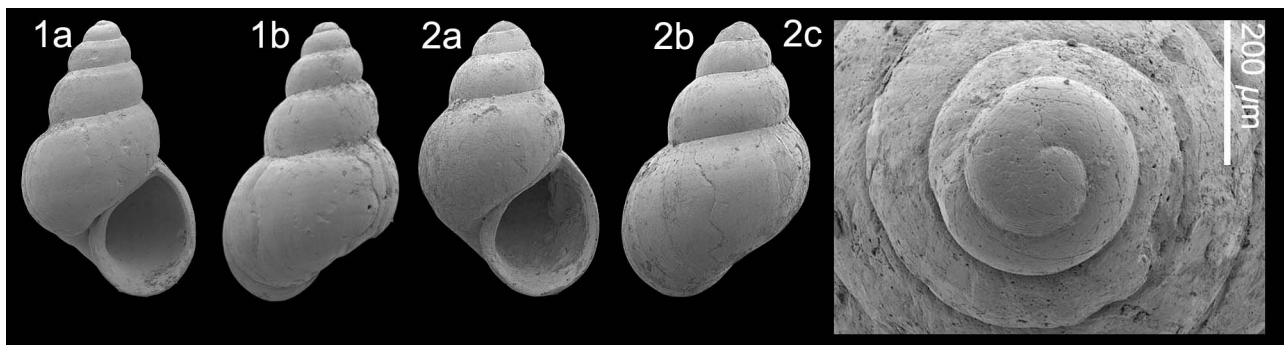
**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper).

Subfamily Rissoiinae Stimpson, 1865

Genus *Rissoina* d’Orbigny, 1840

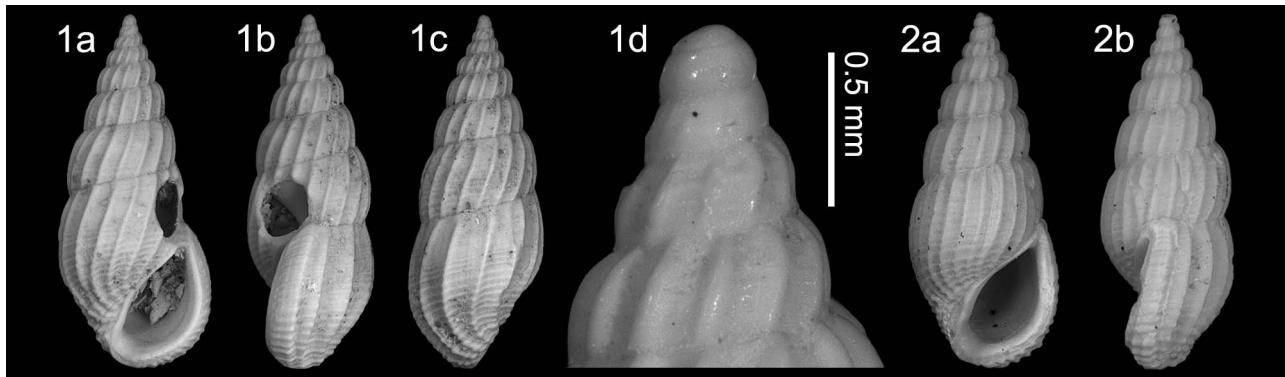
**Type species** (by monotypy) – *Rissoina inca* d’Orbigny, 1840, present-day, Peru.

- 1840 *Rissoina* d’Orbigny, pp. 394, 395, pl. 53.
- 1861 *Rissolina* Gould, p. 401. Type species (by subsequent designation, Nevill, 1885). *Rissoina plicatula* Gould, 1861, present-day, Japan.
- 1885 *Moerchiella* Nevill, p. 88. Type species (by original designation): *Rissoa gigantea* Deshayes, 1848, present-day, Indo-Pacific.
- 1893 *Pachyrissoina* Boettger, p. 104. Type species (by subsequent designation, Wenz, 1939): *Rissoina walkeri* E.A. Smith, 1893, present-day, Indo-Pacific.
- 1904 *Stiva* Hedley, p. 192. Type species (by original designation): *Stiva ferruginea* Hedley, 1904, present-day, New South Wales, Australia.
- 1955 *Caporista* Iredale, p. 81. Type species (by original designation): *Rissoina iredalei* Laseron, 1950, present-day, New South Wales, Australia.
- 1956b *Austrosina* Laseron, p. 393. Type species (by original designation): *Rissoina pulchella* Brazier, 1877, present-day, Queensland, Australia.
- 1956b *Costalynia* Laseron, p. 394. Type species (by original designation): *Rissoina cardinalis* Brazier, 1877, present-day, Queensland, Australia.
- 1956b *Fractoralla* Laseron, p. 398. Type species (by original designation): *Fractoralla praecida* Laseron, 1956, present-day, Queensland, Australia.
- 1956b *Peripetella* Laseron, p. 400. Type species (by original designation): *Peripetella queenslandica* Laseron, 1956, present-day, Queensland, Australia.
- 1956b *Condylicia* Laseron, p. 418. Type species (by original designation): *Condylicia collaxis* Laseron, 1956, present-day, Queensland, Australia.
- 1959 *Laseronia* Cotton, p. 355. Type species (by original designation): *Rissoina cretacea* Tenison Woods, 1878.
- 1965 *Sulcorissoina* Kosuge, p. 108. Type species (by original designation): *Rissoina imbricata* Gould, 1861, present-day, South China Seas.



**Plate 116.** *Setia* sp.: 1. NHMW 2016/0103/1583, height 2.4 mm, width 1.5 mm; 2. NHMW 2016/0103/1584, height 2.0 mm, width 1.3 mm; 2c, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.





**Plate 117.** *Rissoina exdecussata* Sacco, 1895; 1. NHMW 2016/0103/1497, height 7.5 mm, width 2.9 mm; 1d, detail of protoconch. La Presselière, Sceaux-d'Anjou; 2. NHMW 2016/0103/1499, height 5.7 mm, width 2.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Rissoina exdecussata* Sacco, 1895**

Plate 117, figs 1-2

- 1837 *Rissoa decussata* Dujardin, p. 277, pl. 19, fig. 23 (non Montagu, 1803).  
 \*1895b *Rissoina exdecussata* Sacco, p. 35 (nov. nom. pro *Rissoa decussata* Dujardin, 1837, non Montagu, 1803).  
 1916 *Rissoina exdecussata* Sacco – Cossmann & Peyrot, p. 541, pl. 16, figs 135-136.  
 1949 *Rissoina exdecussata* Sacco, 1893 – Glibert, p. 110, pl. 6, fig. 6.

*Material and dimensions* – Maximum height 7.5 mm, width 2.9 mm. **St-Clément-de-la-Place:** RGM.1348319 (1). **Sceaux-d'Anjou:** NHMW 2016/0103/1497 (1), NHMW 2016/0103/1704 (1). **Renauleau:** NHMW 2016/0103/1498 (5), NHMW 2016/0103/1499 (2), LC (4). **Beugnon:** RGM.1348422 (1), RGM.1348434 (2).

*Discussion* – *Rissoina exdecussata* Sacco, 1895 is extremely uncommon in the Assemblage I fauna. It differs from the Pliocene to present-day European eastern Atlantic and Mediterranean species *R. bruguieri* (Payraudau, 1826) in reaching a smaller maximum size and in having more numerous but weaker and more flexuous axial ribs, which are not as strongly interrupted or serrated by the spiral sculpture. The two are, nevertheless, very similar and most likely represent an evolutionary series.

*Distribution* – Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1916), Loire Basin, France (Dujardin, 1837; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).

***Rissoina rissoides* (Millet, 1865)**

Plate 118, figs 1-2

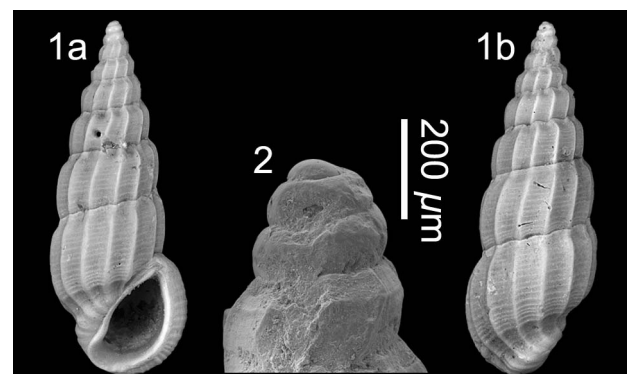
- 1854 *Melania Rissoides* Millet, p. 154 (nomen nudum).  
 1865 *Melania rissoides* Millet, p. 580.

1964 *Rissoina bistriata* var. *rissoides* Millet, 1854 [sic] – Brébion, p. 182, pl. 4, figs 37, 38.

*Type material* – Syntypes: Sceaux-d'Anjou, Thorigné and Renauleau, Musée d'Angers, France (fide Brébion, 1964, p. 183).

*Material and dimensions* – Maximum height 6.6 mm, width 2.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0387-0388 (2), NHMW 2016/0103/0389 (50+), RGM.1347944 (15), RGM.1348320 (10), RGM.1348848 (3), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0391 (50+), RGM.1347960 (15), RGM.1347973 (50+), RGM.1348055 (50+), RGM.1348061 (6), RGM.1348086 (13), RGM.1348373 (50+), RGM.1348518 (2), RGM.1348898 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0390 (50+), RGM.1348981 (50+), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0395 (5), RGM.1348415 (1), RGM.1348435 (9), RGM.1348444 (6), LC (2).

*Discussion* – The original description ‘*Melania rissoides*, Millet. Coq. petite, un peu allongée, obtuse au som-



**Plate 118.** *Rissoina rissoides* (Millet, 1865); 1. NHMW 2016/0103/0387, height 6.5 mm, width 2.4 mm; 2. NHMW 2016/0103/0388, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

met; composée de 6-7 tours de spire, couverts de côtes saillantes, verticales; ouverture oblique, allongée en pointe aiguë à ses extrémités, ventrue sur le bord droit et bordée d'un bourrelet extérieur. Longueur: 5-6 millimètres; diamètre: 2 millimètres. Th., Sc., Ren.' (Millet, 1865, p. 580) omits some important shell characters. The protoconch is multispiral, tall dome-shaped, composed of 3.5 smooth convex whorls. The whorls have a narrow, concave, poorly delimited subsutural ramp, weakly convex below to the suture. Sculpture consists of 12-13 sharp, slightly flexuous axial ribs and weak spiral cords visible only in the interspaces between the ribs. The last whorl is sculptured like the spire whorls, except that the spiral cords strengthen slightly, crowding towards the base. The base is sharply delimited, angular, concave, with the axial ribs persisting strongly developed over the base, which bears a prominent rounded siphonal fasciole medially.

Brébion (1964, p. 182) considered Millet's taxon a subspecies of *Rissoina bistrata* (Grateloup, 1847) from the lower Miocene Atlantic Aquitanian and Burdigalian of France, but that species differs from *R. rissoides* (Millet, 1865) in lacking the narrow, concave subsutural ramp, and in having more numerous and straighter axial ribs. Spiral sculpture is absent on the spire whorls in *R. bistrata*, and restricted to four strong narrow cords over the base and siphonal fasciole, overrunning the axials, forming small tubercles at the intersections.

Millet (1865, p. 580) recorded this species from Assemblage I localities (Thorigné, Sceaux-d'Anjou, Renauleau), to which Brébion (1964, p. 184) added St-Clément-de-la-Place, and we add Beugnon.

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

Genus *Zebinella* Mörch, 1875

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

1875 *Zebinella* Mörch, p. 47.

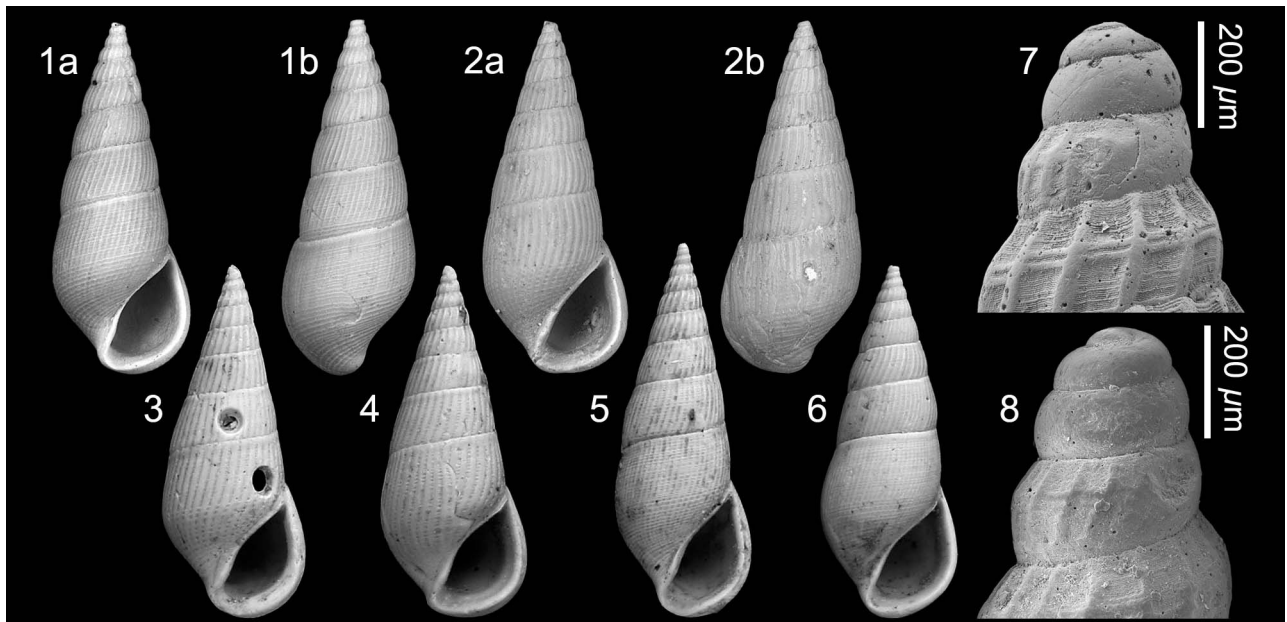
For generic synonymy see Van Dingenen *et al.* (2016, p. 144).

***Zebinella decussata sensu lato* (Montagu, 1803)**

Plate 119, figs 1-8

- \*1803 *Helix decussata* Montagu, p. 399, pl. 15, fig. 7.
- 1964 *Rissoina (Zebinella) decussata* (Montagu, 1803) – Brébion, p. 185, pl. 4, fig. 39.
- 2004a *Rissoina (Zebinella) decussata* (Montagu, 1803) *sensu lato* – Landau *et al.*, p. 53, pl. 12, fig. 2 (*cum syn.*).
- 2016 *Zebinella decussata sensu lato* (Montagu, 1803) – Landau *et al.*, p. 144, pl. 10, fig. 6 (*cum syn.*).

**Material and dimensions** – Maximum height 9.0 mm, width 3.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0396-0403 (8), NHMW 2016/0103/0404 (50+), RGM.1347968 (1), RGM.1348039 (32), RGM.1348313 (1), RGM.1348321 (12), RGM.1348624 (2), RGM.1348845



**Plate 119.** *Zebinella decussata sensu lato* (Montagu, 1803); 1. NHMW 2016/0103/0396, height 7.9 mm, width 3.0 mm; 2. NHMW 2016/0103/0397, height 8.3 mm, width 3.3 mm; 3. NHMW 2016/0103/0398, height 8.0 mm, width 3.2 mm; 4. NHMW 2016/0103/0399, height 7.9 mm, width 3.2 mm; 5. NHMW 2016/0103/0400, height 9.7 mm, width 3.2 mm; 6. NHMW 2016/0103/0401, height 8.8 mm, width 3.3 mm; 7. NHMW 2016/0103/0402, detail of protoconch (SEM image); 8. NHMW 2016/0103/0403, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

	<i>Z. punctatostriata</i>	<i>Z. decussata</i>	St-Clément-de-la-Place
size	up to 10 mm	usually up to 7 mm	7-9 mm
profile	slightly undulated in the last whorls by the subsutural depression	almost rectilinear	almost rectilinear to undulated
adapical whorls of teleoconch	angulated	not angulated	angulated
axial ribs	opisthocline and slightly curved; weakly prominent on last whorl	almost orthocline; rectilinear; prominent on last whorl	variable, both forms present
subsutural part of last whorl	depressed; axial ribs almost disappear	not depressed; axial ribs well marked	variable, both forms present
protoconch	3 whorls, diameter increases rapidly	2.5 whorls, diameter increases slowly	3.0-3.25 whorls; diameter increases moderately
sinusigera notch	deep	absent	absent

**Table 5.** Differences between *Zebinella punctatostriata*, *Z. decussata* (extant) and *Zebinella* (St-Clément-de-la-Place). Adapted from Rolán & Luque (2000, table 1).

(2), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0406 (50+), RGM.1347978 (26), RGM.1348026 (44), RGM.1348028 (50+), RGM.1348063 (49), RGM.1348077 (50+), RGM.1348085 (12), RGM.1348366 (50+), RGM.1348368 (50+), RGM.1348511 (50+), RGM.1348796 (20), RGM.1348896 (50+), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0405 (50+), RGM.1348980 (50+), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0407 (6), RGM.1348421 (17), RGM.1348445 (34).

*Discussion* – *Zebinella decussata* (Montagu, 1803) was considered a living amphiatlantic species, until Rolán & Luque (2000) separated the Caribbean form, *Z. decussata*, from the West African form, *Z. punctatostriata* (García-Talavera, 1975). The differences between the two are summarised in Table 5. *Zebinella decussata* (Montagu, 1803), or forms of it, has been recorded in the European fossil literature since the early Miocene (Sacco, 1895b, Bałuk, 1975, Landau *et al.*, 2013, Brébion, 1964, amongst others). Whether these fossil shells are the Caribbean or West African form, or a third species, has not been addressed. Numerous specimens are available from St-Clément-de-la-Place. Adult shells vary in height from 7.0-9.0 mm. The shape and sculpture of the early teleoconch whorls is consistent, but later whorls can be almost straight-sided (Pl. 119, figs 2, 3, 4) to somewhat concave in the subsutural area and more strongly convex below (Pl. 119, figs 1, 5). The axial sculpture is predominant in most specimens, but can weaken giving a fine even reticulate pattern on the last whorl (Pl. 119, fig. 6). The ribs on later whorls can extend between the sutures (Pl. 119, figs 2, 3), or weaken in the subsutural area (Pl. 119, figs 1, 5, 6). Also the number of ribs is variable (Pl. 119 figs 1, 5, 6 vs. figs 2, 3). In Table 5 we have summarised the differences between the two extant species and compared them to the specimens from St-Clément-de-la-Place:

It is possibly not surprising that this ancestral population from St-Clément-de-la-Place shows a combination of the

characters identified by Rolán & Luque (2000) to separate the present-day species. The size is intermediate, the protoconch is composed of a slightly greater number of whorls than either of the two extant species, the early whorls are angulated, as in the West African *Z. punctatostriata*, and the sinusigera notch shallow (Pl. 119, fig. 7) or absent (Pl. 119, figs 8), as in the Caribbean *Z. decussata*. The teleoconch shape and sculptural characters that separate the extant species are variable in the fossil form. We consider it excessive to erect yet another name for the fossil form and continue to use the name *Zebinella decussata sensu lato* (Montagu, 1803).

Brébion (1964, p. 186) recorded this species from Assemblage I localities (Renauleau, Sceaux-d'Anjou, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu) and the Assemblage IV locality of Gourbesville. Van Dingenen *et al.* (2016, p. 144) added the Assemblage III locality of Le Pigeon Blanc.

*Distribution* – Lower Miocene: (Burdigalian) Italy (Sacco, 1895b). Middle Miocene Paratethys, Poland (Bałuk, 1975), ?Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964); Proto-Mediterranean, Tortonian, Italy (Sacco, 1895b). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); central Mediterranean, Italy (Anfossi *et al.*, 1982; Chirli, 2006). Upper Pliocene: western Mediterranean, Estepona (Landau *et al.*, 2004a); central Mediterranean, Italy (Sacco, 1895b; Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914).

#### *Zebinella obsoleta* (Hörnes, 1856)

Plate 120, fig. 1

\*1856 *Rissoina obsoleta* Hörnes, p. 556, pl. 48, fig. 3.

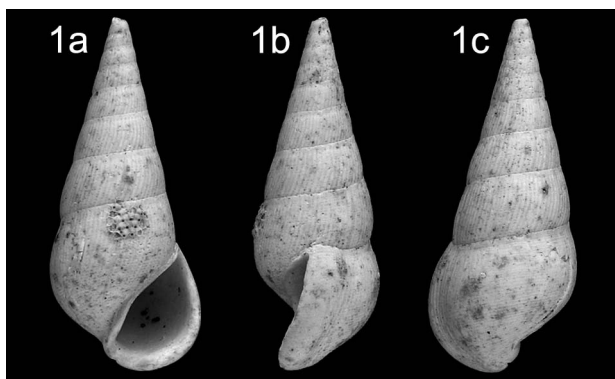


- 1854 *Rissoina Cochlearella* d'Orb. [sic] – Millet, p. 150 [non *R. cochlearella* (Lamarck, 1804)].  
 1964 *Rissoina (Zebinella) obsoleta* Partsch in Hörnes, 1856 – Brébion, p. 184.  
 2013 *Rissoina (Zebinella) obsoleta* Hörnes, 1856 – Landau *et al.*, p. 76, pl. 6, fig. 12, pl. 58, fig. 7 (*cum syn.*).

**Material and dimensions** – Maximum height 14.1 mm, width 5.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0408 (2), LC (15), FVD (9). **Sceaux-d'Anjou**: NHMW 2016/0103/0394 (13), RGM.1347977 (4), RGM.1348025 (5), RGM.1348029 (10), RGM.1348078 (5), RGM.1348369 (6), RGM.1348510 (14), LC (12), FVD (15). **Renauleau**: NHMW 2016/0103/0392 (1), NHMW 2016/0103/0393 (33), LC (50+), FVD (50+). **Beugnon**: RGM.1348418 (2), RGM.1348419 (1), RGM.1348420 (2), RGM.1348446 (7 fragments).

**Discussion** – *Zebinella obsoleta* (Hörnes, 1856) is probably the largest of the European Neogene rissoinids. It differs from *Z. decussata* (Montagu, 1803) and *Z. loueli* (Hörnes, 1856) by its larger size, the almost straight-sided spire whorls and in having the last whorl weakly angular at the base in most specimens. The protoconch is multispiral, composed of about three whorls (Landau *et al.*, 2013, pl. 58, fig. 7a). The teleoconch bears microsculpture of very fine spiral threads, visible only in the sculptural interspaces (Landau *et al.*, 2013, pl. 58, fig. 7b). Brébion (1964) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné, Renauleau, St-Clément-de-la-Place, St-Michel, Les Pierres Blanches, Beaulieu) and Assemblage II (Apigné, Le Temple du Cerisier, Carcé).

**Distribution** – Middle Miocene: Atlantic: Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Brébion, 1964), Cabela Basin, Portugal (Dollfus *et al.*, 1903); Proto-Mediterranean Sea (Tortonian), Italy (Sacco, 1895b).



**Plate 120.** *Zebinella obsoleta* (Hörnes, 1856); 1. NHMW 2016/0103/0392, height 6.5 mm, width 2.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Superfamily Truncatelloidea Gray, 1840  
 Family Caecidae Gray, 1850  
 Subfamily Caecinae Gray, 1850  
 Genus *Caecum* Fleming, 1813

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

1813 *Caecum* Fleming, p. 67.

**Note** – For this genus we follow the measurements as suggested by Porta *et al.* (1993, p. 3, fig. 2). L = total length; D = diameter aperture; d = diameter of shell at base of septum; Ls = height of septum.

***Caecum aartseni* Van Dingenen, Ceulemans & Landau, 2016**

Plate 121, figs 1-2

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

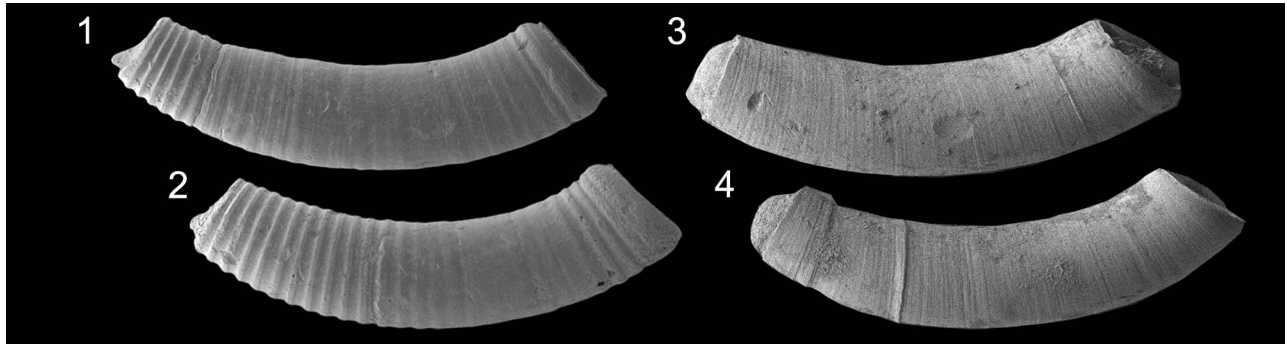
\*2016 *Caecum aartseni* Van Dingenen, Ceulemans & Landau, p. 144, pl. 10, figs 7-9, pl. 11, figs 3, 4.

**Material and dimensions** – Maximum height 3.1 mm; width 650  $\mu\text{m}$ . **St-Clément-de-la-Place**: NHMW 2016/0103/0332-333 (2), NHMW 2016/0103/0334 (50+), RGM.1347942 (6), RGM.1348040 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: RGM.1348889 (1). **Renauleau**: NHMW 2016/0103/1445 (4), LC (2).

**Discussion** – *Caecum aartseni* Van Dingenen, Ceulemans & Landau, 2016 is characterised by its pointed septum, in having a broad ring bordering the aperture, sculpture of 13-17 widely-spaced rings at the posterior end, 5-6 closer-set rings at the anterior end, with a smooth area between, without any axial sculpture and no discernable microsculpture. The species is common at St-Clément-de-la-Place, where the largest specimen has the following dimensions: L = 3.1, D = 605  $\mu\text{m}$ , d = 450  $\mu\text{m}$ , Ls = 126  $\mu\text{m}$ . The shell is slightly larger than the largest specimen from the Assemblage III locality of Le Pigeon Blanc, but the relative proportions and sculpture are the same. For further discussion and comparison see Van Dingenen *et al.* (2016, p. 145).

Brébion (1964, p. 216) recorded this species from Assemblage I localities (Beaulieu, St-Michel), to which we add St-Clément-de-la-Place, Assemblage II (Apigné, Vieux Chartres) and Assemblage III (Le Pigeon Blanc).

**Distribution** – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016).



**Plate 121.** *Caecum aartseni* Van Dingenen, Ceulemans & Landau, 2016; 1. NHMW 2016/0103/0332, height 3.1 mm, width 650  $\mu\text{m}$ ; 2. NHMW 2016/0103/0333, height 2.7 mm, width 700  $\mu\text{m}$ . Le Grand Chauvereau, St-Clément-de-la-Place. *Caecum glabrum* (Montagu, 1803); 3. NHMW 2016/0103/1442, height 2.3 mm, width 520  $\mu\text{m}$ ; 4. NHMW 2016/0103/1443, height 2.2 mm, width 470  $\mu\text{m}$  (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Caecum glabrum* (Montagu, 1803)**

Plate 121, figs 3-4

- \*1803 *Dentalium glabrum* Montagu, p. 197.
- 1848 *Caecum glabrum* Mont. – Wood, p. 117, pl. 20, fig. 6.
- 1896b *Brochina glabra* (Montg.) – Sacco, p. 3, pl. 1, fig. 2.
- 1912 *Caecum glabrum* Mtg. – Cerulli-Irelli, p. 168, pl. 25, figs 28, 29.
- 1923 *Caecum glabrum* (Montagu) – Harmer, p. 848, pl. 64, fig. 33.
- 1949 *Caecum* cf. *glabrum* Montagu, 1803 – Glibert, p. 130, pl. 8, figs 2a-b.
- 1954 *Caecum glabrum* (Montagu, 1803) – Van Regteren Altena, p. 29, pl. 6, fig. 57.
- 1978 *Caecum glabrum* (Montagu, 1803) – Fretter & Graham, p. 234, fig. 195.
- 1997a *Caecum glabrum* (Montagu, 1803) – Marquet, p. 18, pl. 4, fig. 4.
- 1998 *Caecum glabrum* (Montagu, 1803) – Marquet, p. 71, fig. 46.
- 2001 *Caecum* (*Brochina*) *glabrum* (Montagu, 1803) – Silva, p. 168, pl. 6, fig. 22.

**Material and dimensions** – Maximum height 2.3 mm, width 520  $\mu\text{m}$ . **St-Clément-de-la-Place:** NHMW 2016/0103/1786 (3). **Renauleau:** NHMW 2016/0103/1442-1443 (2), NHMW 2016/0103/1444 (3), LC (2). **Beugnon:** RGM. 1348416 (3).

**Discussion** – *Caecum glabrum* (Montagu, 1803) is characterised by its relatively small size (for present-day specimens 2.5 mm x 0.5 mm; Fretter & Graham, 1978), its smooth shell lacking concentric sculpture, and its evenly convex septum. In the fossil assemblages this species has a reliable record in the North Sea Basin and along the European eastern Atlantic frontage from the Middle Miocene to present-day. In the Mediterranean, whilst recorded by early authors (Sacco, 1896b; Cerulli-Irelli, 1912), we have not found more recent references. *Caecum glabrum* seems to be uncommon wherever it

occurs in the fossil assemblages (Glibert, 1949, p. 130; Marquet, 1997a, p. 19).

**Distribution** – Lower Miocene: Proto-Mediterranean, Italy (Sacco, 1896b). Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper); Proto-Mediterranean, Italy (Sacco, 1896b). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1923). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1923), Belgium (Marquet, 1997a, 1998); Atlantic, Mondego Basin (Silva, 2001). Pliocene (indeterminate): North Sea Basin, Netherlands (Van Regteren Altena, 1955); Proto-Mediterranean, Italy (Sacco, 1896b). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912). Upper Pleistocene: Atlantic, Scotland (Harmer, 1923). Present-day: Eastern Atlantic, Norway, into Mediterranean (Fretter & Graham, 1978).

Genus *Parastrophia* de Folin, 1869

**Type species** (by typification of replaced name) – *Moreletia cornucopiae* de Folin, 1869, present-day, China.

- 1861 *Spirolidium* O.G. Costa, p. 64. Type species (by monotypy): *Spirolidium mediterraneum* O.G. Costa, 1861, present-day, Mediterranean.
- 1869 *Moreletia* de Folin, p. 119. Type species (by monotypy): *Moreletia cornucopiae* de Folin, 1869, present-day, China. Junior homonym of *Moreletia* Gray, 1855 [Pulmonata].
- 1869 *Parastrophia* de Folin, p. 174. *Nom. nov. pro Moreletia* de Folin, 1869, *non* Gray, 1855.
- 1905 *Pseudoparastrophia* Di Staso, p. 434. Type species (by monotypy): *Pseudoparastrophia levigata* Di Staso, 1905, present-day, Mediterranean.
- 1957 *Pedumicra* Iredale & Laseron, pp. 98, 104. Type species (by original designation): *Strebloceras cygnicollis* Hedley, 1904, present-day, Queensland, Australia.

- 1957 *Gladioceras* Iredale & Laseron, pp. 98, 105. Type species (by original designation): *Gladioceras armorum* Iredale & Laseron, 1957, present-day, Queensland, Australia.

***Parastrophia asturiana* de Folin, 1870**

Plate 122, figs 1-2

- 1861 *Spirolidium Mediterraneum* O.G. Costa, p. 64 (*nomen dubium*).
- \*1870 *Parastrophia asturiana* de Folin, p. 218, pl. 29, fig. 7.
- 1884a *Spirolidium Mediterraneum* O.G. Costa – Monterosato, p. 22.
- 1884b *Spirolidium Mediterraneum* O.G. Costa – Monterosato, p. 77.
- 1884 *Parastrophia Folini* Bucquoy, Dautzenberg & Dollfus, p. 233, fig. 5.
- 1905 *Pseudoparastrophia levigata* Di Staso, p. 434.
- 1954 *Paratrophia garganica* Montcharmont-Zei, p. 120, pl. 1.
- 1971 *Paratrophia garganica* Montcharmont-Zei – De Castro-Coppa, p. 11, pl. 1, fig. 18, pl. 2, figs 1-6.
- 1980 *Parastrophia mediterranea* (O.G. Costa) – Panetta, p. 279, pl. 3, fig. 3.
- 1980 *Parastrophia asturiana* de Folin – Panetta, p. 279, pl. 1, fig. 1.
- 1991 *Parastrophia mediterranea* (O.G. Costa, 1861) – Poppe & Goto, p. 98, pl. 12, fig. 10.
- 1993 *Parastrophia garganica* Montcharmont-Zei, 1954 – Porta *et al.*, p. 8, pl. 3, fig. 9.
- 1996 *Parastrophia asturiana* de Folin, 1870 – Giannuzzi Savelli *et al.*, p. 16, fig. 538.
- 1996 *Parastrophia* (*Parastrophia*) *asturiana* de Folin, 1870 – Bandel, p. 71, pl. 9, figs 8, 9, pl. 10, figs 1-3, 5-7.
- 2001 *Parastrophia* (*Parastrophia*) *asturiana* de Folin, 1869 [*sic*] – Silva, p. 171, pl. 7, figs 5-7.
- 2001 *Parastrophia asturiana* de Folin, 1870 – Baroncelli, p. 231, pl. 2, fig. 3.
- 2002 *Parastrophia asturiana* de Folin, 1870 – Chirli & Bogi, p. 20, pl. 1, figs 12-13.
- 2006 *Parastrophia asturiana* de Folin, 1870 – Chirli, p. 68, pl. 28, figs 11-14.

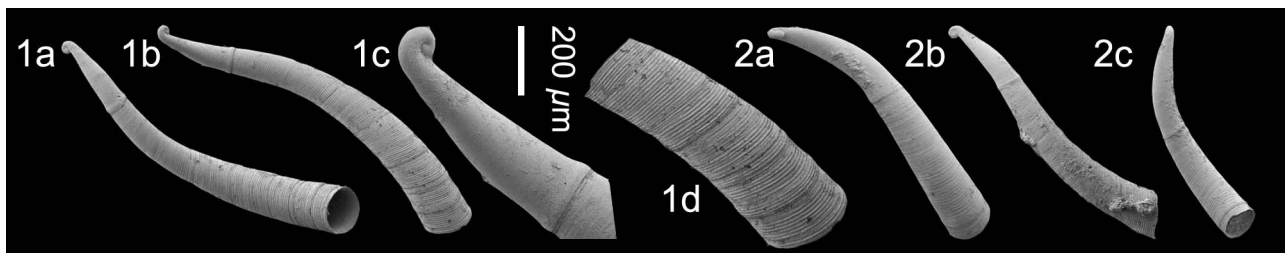
**St-Clément-de-la-Place:** RGM.1348036 (1). **Sceaux-d'Anjou:** RGM.1348242 (1), RGM.1348892 (1). **Renauleau:** NHMW 2016/0103/1708-1709 (2), LC (1). **Beugnon:** RGM.1348417 (2).

*Discussion* – The specimens from Renauleau have a protoconch of about 690  $\mu\text{m}$ , with an apertural diameter of about 215  $\mu\text{m}$ , and an apical whorl diameter of 100  $\mu\text{m}$ . This is slightly smaller than the measurements given by Silva (2001, fig. 3.41) for the specimens from the upper Pliocene lower Piacenzian of the Mondego Basin of Portugal (880-950  $\mu\text{m}$ ; 260  $\mu\text{m}$ ; 140-160  $\mu\text{m}$  respectively), but then almost all the species from Assemblage I are small compared with other populations.

The teleoconch has a length of about 3.0 mm, and is sculptured with close-set fine concentric rings starting immediately after the protoconch-teleoconch boundary. It is now accepted that the extant taxa *Spirolidium mediterraneum* O.G. Costa, 1861, *Parastrophia folini* Bucquoy, Dautzenberg & Dollfus, 1884 and *Pseudoparastrophia levigata* Di Staso, 1905 are all synonyms of *Parastrophia asturiana* de Folin, 1870 (Van Aartsen & Fehr-De Wal, 1975; Ruggieri, 1982; Bandel, 1996; Gofas in WoRMS, 2018). Van Aartsen & Fehr-De Wal (1975) argued that the earlier name of *Spirolidium mediterraneum* O.G. Costa, 1861 was invalid as it was based on embryonic forms. However, basing a name on an embryonic form does not invalidate the name. At present *S. mediterraneum* is considered a *nomen dubium*, as it is unclear whether the poorly drawn shell represents a juvenile *Parastrophia* or a juvenile *Caecum* that has not yet shed the embryonic shell (Serge Gofas, personal communication BML, 2018).

*Paratrophia garganica* Montcharmont-Zei, 1954 was erected based on material from the Quaternary of Italy and said to differ in having the first portion of the shell devoid of sculpture. Ruggieri (1982) and Silva (2001) argued that the smooth portion described by these authors was the first 0.6 mm after the apical whorl, which was still protoconch and not teleoconch, and that *P. asturiana* also has the post-apical whorl portion of the protoconch smooth, concluding that *P. garganica* was also a junior synonym of *P. asturiana*. *Parastrophia radwanskii* Bałuk, 1975 from the middle Miocene lower Badenian Paratethys of Poland seems to differ in having a relatively wide aperture, but more material would be required to confirm this.

*Material and dimensions* – Maximum height 3.6 mm.



**Plate 122.** *Parastrophia asturiana* de Folin, 1870; 1. NHMW 2016/0103/1708, height 3.6 mm, 1c, detail of protoconch, 1d detail of teleoconch sculpture; 2. NHMW 2016/0103/1709 height 2.2 mm (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli & Bogi, 2002; Chirli, 2006). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); central Mediterranean, Italy (Ruggieri, 1982; Baroncelli, 2001). Pleistocene: eastern Mediterranean, Spain (Porta *et al.*, 1993); central Mediterranean, Italy (Monteharmont-Zei, 1954; De Castro-Coppa, 1971). Present-day: Atlantic coasts of Europe from Bay of Biscay into the Mediterranean (Ruggieri, 1982, Poppe & Goto, 1991).

Family Elachisnidae Ponder, 1985b  
Genus *Pseudocirsope* Boettger, 1907

*Type species* (by monotypy) – *Lacuna galeodina* Boettger, 1907, Miocene, Romania.

1907 *Pseudocirsope* Boettger, pp. 152, 153.

***Pseudocirsope delphinuloides* (Millet, 1865)**

Plate 123, figs 1-3

- 1854 *Phasianella Delphinuloides* Millet, p. 158 (*nomen nudum*).  
\*1865 *Phasianella delphinuloides* Millet, p. 584.  
1874 *Lacuna Bourgeoisii* Tournouër, p. 288, pl. 9, fig. 2.  
1886 *Lacuna (Epheria) Bourgeoisii* Tourn. – Dollfus & Dautzenberg, p. 139.  
1907 *Phasianella delphinuloides* Millet – Couffon, p. 183.  
1915 *Lacuna Basteroti* [sic] Bronn – Couffon, p. 42. [*non Pseudocirsope basterotina* (Bronn, 1831)].  
1938 *Lacuna (Epheria) Bourgeoisii* Tournouër [sic] – Peyrot, p. 115.  
1949 *Lacuna (Pseudocirsope) bourgeoisii* Tournouër, 1874 – Glibert, p. 85, pl. 5, fig. 3.  
1964 *Lacuna (Pseudocirsope) bourgeoisii* Tournouër, 1874 – Brébion, p. 139.  
1964 *Lacuna (Pseudocirsope) basteroti* [sic] Bronn, 1831 – Brébion, p. 140, pl. 4, fig. 1 [*non Pseudocirsope basterotina* (Bronn, 1831)].  
2004 *Lacuna bourgeoisii* (Tournouër [sic]) [sic], 1874 – Bogi & Chirli, p. 90, fig. 1i-l.

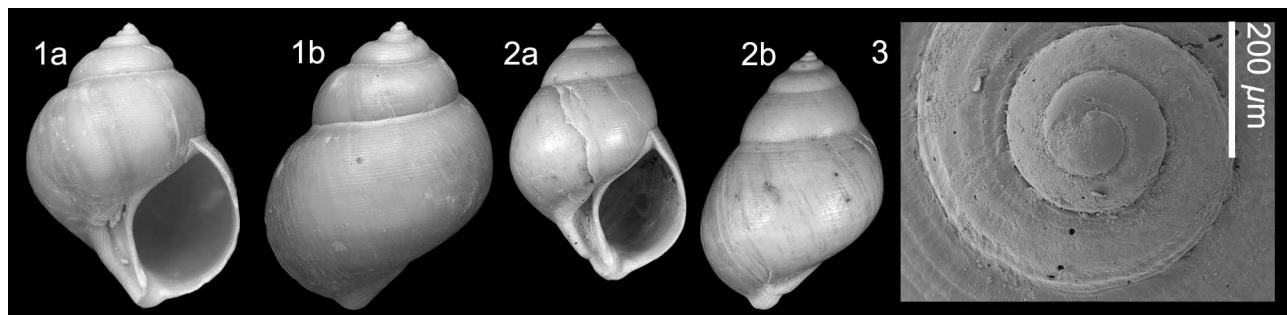
2008 *Lacuna bourgeoisii* Tournouër, 1874 – Chirli, p. 3, pl. 1, figs 1-5.

*Material and dimensions* – Maximum height 7.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0538-540 (3), NHMW 2016/0103/0541 (50+), RGM.1309572 (4), RGM.1347939 (1 juvenile), RGM.1348054 (3), RGM.1348850 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0542 (50+), RGM.1347937 (1), RGM.1347976 (29), RGM.1348027 (10 + 6 juveniles), RGM.1348079 (9 + 3 juveniles), RGM.1348512 (29), RGM.1348762 (3), RGM.1348903 (10), LC (30), FVD (50+). **Renauleau**: NHMW 2016/0103/1464 (32), RGM.1348991 (12), LC (50+), FVD (50+). **Beugnon**: RGM.1348496 (1), RGM.1348504 (2).

*Original description* – ‘*Phasianella delphinuloides*, Millet. *Coq. petite, ovoïde, composée de 6 tours de spire bombés, lisses. Ouverture ovale, arrivant en pointe légèrement sinueuse à ses extrémités. Fente ombilicale allongée, élargie au milieu. Longueur: 6 millimètres; diamètre: 5 millimètres. Sc. Rare*’ (Millet, 1865, p. 584).

*Discussion* – *Lacuna bourgeoisii* Tournouër, 1874 is a junior subjective synonym of *Phasianella delphinuloides* Millet, 1865. The original description adequately describes this species, however, the spire whorls are not smooth, but finely striate, although in some specimens this sculpture is worn giving the whorl surface a smooth appearance. We add that the umbilicus is relatively broad and bordered by a prominent rounded periumbilical cord. The protoconch is composed of about two whorls, with a medium-sized nucleus, although it is difficult to be precise, as the protoconch-teleoconch boundary is not sharply delimited in the material at hand (Pl. 123, fig. 3).

Glibert (1949, p. 86) drew attention to the globose shell shape typical of this species to distinguish it from its congeners, recording the apical angle for the middle Miocene forms as 80°. We note that whilst most specimens do indeed have a wide apical angle, even up to 90° and a strongly globose shell (Pl. 123, fig. 1), others are more elongate, with a narrower apical angle of 70° and a less strongly globose last whorl (Pl. 123, fig. 2). It is these narrower forms Couffon (1915) and Brébion (1964)



**Plate 123.** *Pseudocirsope delphinuloides* (Millet, 1865); 1. NHMW 2016/0103/0538, height 5.0 mm, width 3.8 mm; 2. NHMW 2016/0103/0539, height 6.8 mm, width 4.7 mm; 3. NHMW 2016/0103/0540, detail of protoconch (SEM image). Le Grand Chauvereu, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

identified as *Pseudocirsope basterotina* (Bronn, 1831), found in the Pliocene of the Mediterranean, which has the same shell shape, but is separated by its narrower umbilicus, which lacks the strong periumbilical keel seen in *P. delphinuloides* (see Landau *et al.*, 2004a, pl. 4, fig. 9). Glibert (1949, p. 86, pl. 5, fig. 4) identified a shell from the middle Miocene of the Loire Basin as *P. miocenica* (Sacco, 1895). This taxon was erected by Sacco (1895b, p. 16) for the shell illustrated by Hörnes (1856, pl. 44, fig. 11) from the middle Miocene of the Paratethys as *Lacuna basterotina* Bronn. It is difficult to draw too many conclusions from Glibert's figures, which in our opinion show a somewhat worn shell with an abraded, polished surface. Moreover, the differences given by Glibert (1949, p. 87), that *P. miocenica* differs from *P. basterotina* in having a smooth polished surface is incorrect, as surface sculpture was clearly illustrated by Hörnes. We have not seen this species, but it seems to differ from *P. delphinuloides* in being even more slender than the slender form of *P. delphinuloides* and in being higher-spined.

*Pseudocirsope eburnaeformis* (Sandberger, 1859) from the Rupelian lower Oligocene of Germany is closely similar, but differs in being taller spired and in having an even more strongly developed and prominent periumbilical keel.

We note that *P. delphinuloides* (as *P. basterotina*) has recently been recorded from the Mediterranean Pliocene (Bogi & Chirli, 2004; Chirli, 2008). We agree that the specimens illustrated by these authors seem to be conspecific with those from the upper Miocene of NW France. The protoconch of the Italian specimens is given at 2.3 whorls (Chirli, 2008, p. 3). As stated above, the protoconch-teleoconch boundary in the French material is unclear, but it also consists of about two whorls.

**Distribution** – Middle Miocene: Loire Basin (Tournouër, 1874, Dollfus & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Couffon, 1907, 1915; Bré-bion, 1964). Lower Pliocene: central Mediterranean, Italy (Bogi & Chirli, 2004; Chirli, 2008).

Family Hydrobiidae Stimpson, 1865  
Subfamily Hydrobiinae Stimpson, 1865  
Genus *Hydrobia* Hartmann, 1821

**Type species** (by subsequent designation, Gray, 1847b) – *Cyclostoma acutum* Draparnaud, 1805, present-day, France.

- 1821 *Hydrobia* Hartmann, p. 258.
- 1826 *Leachia* Risso, p. 102. Type species (by subsequent designation, Monterosato, 1884a): *Leachia viridescens* Risso, 1826 [= *Hydrobia acuta* (Draparnaud, 1805)], present-day, France.
- 1843 *Littorinella*, Braun, p. 148. Type species (by subsequent designation, Nevill, 1885): *Cyclostoma acutum* Draparnaud, 1805, present-day, France.
- 1847 *Littorinella* Herrmannsen, 616. Unnecessary emendation of *Littorinella* Braun, 1843.
- 1877 *Thalassobia* Mabille, pp. 214, 220. Type species (by subsequent designation, Martens, 1879): *Cyclostoma acutum* Draparnaud, 1805, present-day, France.

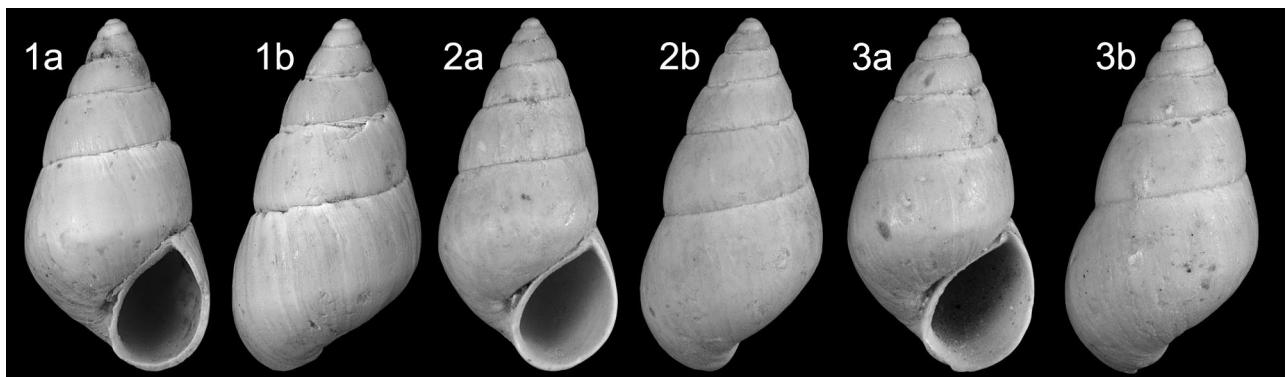
#### ***Hydrobia tournoueri* Sandberger, 1875**

Plate 124, figs 1-3

- \*1875 *Hydrobia Tournoueri* Sandberger, p. 522, pl. 26, fig. 7.
- 1886 *Bithinella* [*sic*] *Tournoueri* (Mayer) – Dollfus & Dautzenberg, p. 139.
- 1920 *Bithinella* [*sic*] *Tournoueri* (Mayer) – de Morgan, p. 330, fig. 25.
- 1949 *Bythinella tournoueri* Mayer, 1875 – Glibert, p. 93, pl. 5, fig. 14.

**Material and dimensions** – Maximum height 4.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0548-0550 (3), NHMW 2016/0103/0551 (9), RGM.1309571 (1). **Renauveau**: NHMW 2016/0103/1623 (2), LC (1).

**Discussion** – This species has been placed by most authors in the genus *Bythinella* Moquin-Tandon, 1856. However, *Bythinella* species are spring-dwellers (Bichain



**Plate 124.** *Hydrobia tournoueri* Sandberger, 1875; 1. NHMW 2016/0103/0548, height 4.3 mm, width 2.3 mm; 2. NHMW 2016/0103/0549, height 5.0 mm, width 2.5 mm; 3. NHMW 2016/0103/0550, height 4.1 mm, width 2.2 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*et al.*, 2007) and this species is now included in the genus *Hydrobia* Hartmann, 1821 (Neubauer, 2015), with which it fits much better based on its shell characters. As can be seen in the series illustrated (Pl. 124, figs 1-3), there is little intraspecific variation and it cannot be confused with any other species in the assemblage.

**Distribution** – Middle Miocene: Loire Basin (Dollfus & Dautzenberg, 1886; de Morgan, 1920; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).

Genus *Peringia* Paladilhe, 1874

**Type species** (by subsequent designation, Clessin, 1880) – *Turbo ulvae* Pennant, 1777, present-day, British Isles.

- 1842 *Sabinea* G.B. Sowerby II, p. 250. Type species (by monotypy): *Turbo ulvae* Pennant, 1777, present-day, British Isles. Junior homonym of *Sabinea* Owen, 1835 [Crustacea].
- 1847a *Sabanaea* Leach in Gray, p. 270. Incorrect subsequent spelling.
- 1847b *Sabanea* Gray, p. 159. Incorrect subsequent spelling.
- 1854 *Sabinaea* H. & A. Adams, p. 334. Incorrect subsequent spelling.
- 1874 *Peringia* Paladilhe, p. 7.

***Peringia fontannesi* (Dollfus & Dautzenberg, 1886)**  
Plate 125, figs 1-2

- \*1886 *Bithinella* [sic] *Fontannesi* Dollfus & Dautzenberg, p. 139.
- 1886 *Bithinella* [sic] *Benoisti* Dollfus & Dautzenberg, p. 139.
- 1920 *Peringia Fontannesi* (Dollf. et Dautz.) – de Morgan, p. 330, fig. 25.
- 1920 *Peringia Benoisti* (Dollf. et Dautz.) – de Morgan, p. 331, fig. 26.
- 1949 *Hydrobia (Sabinea) fontannesi* Dollfus & Dautzenberg, 1886 – Glibert, p. 92, pl. 5, fig. 10.

- 1949 *Hydrobia (Sabinea) fontannesi benoisti* Dollfus & Dautzenberg, 1886 – Glibert, p. 92, pl. 5, fig. 13.

**Material and dimensions** – Maximum height 2.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0545-0546 (2), NHMW 2016/0103/0547 (10). **Sceaux-d’Anjou**: NHMW 2016/0103/0612 (2), RGM.1348244 (1). **Renauleau**: NHMW 2016/0103/1452 (7), LC (2).

**Discussion** – As noted by Glibert (1949, p. 92), *Peringia fontannesi* (Dollfus & Dautzenberg, 1886) is highly variable in its relative height/width ratio, with more pointed and squatter forms present in one population. The same author pointed out that transitional forms occurred between *P. fontannesi* and *P. benoisti* (Dollfus & Dautzenberg, 1886), which is just a squatter more inflated form. We do not consider the subspecific status afforded to *benoisti* by Glibert justified and consider *P. benoisti* a synonym of *P. fontannesi*, as first revisers choosing the latter name as the name to be used for this species (ICZN, 1999, Art. 24.2.1).

**Distribution** – Middle Miocene: Loire Basin (Dollfus & Dautzenberg, 1886; de Morgan, 1920; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).

Family Iravadiidae Thiele, 1928

Genus *Ceratia* H. Adams & A. Adams, 1852

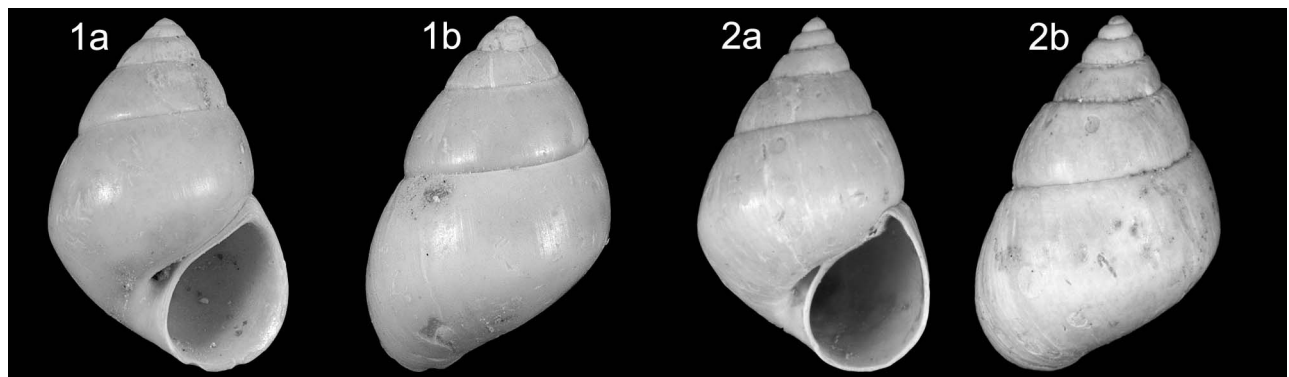
**Type species** (by monotypy) – *Rissoa proxima* Forbes & Hanley, 1850, present-day, British Isles.

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

***Ceratia ligeriana* (Peyrot, 1938)**

Plate 126, fig. 1

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

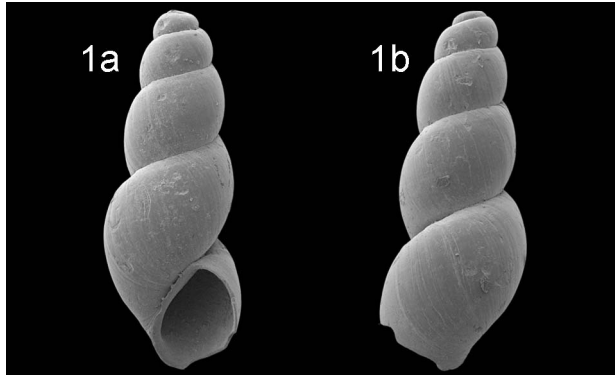


**Plate 125.** *Peringia fontannesi* (Dollfus & Dautzenberg, 1886); 1. NHMW 2016/0103/0545, height 4.0 mm, width 2.7 mm; 2. NHMW 2016/0103/0546, height 4.2 mm, width 2.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



2016 *Ceratia ligeriana* (Peyrot, 1938) – Van Dingenen *et al.*, p. 146, pl. 10, figs 11, 12, pl. 11, fig. 6 (*cum syn.*).

*Material and dimensions* – Maximum height 2.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0321 (1), NHMW 2016/0103/0712 (8), RGM.1348668 (3). **Renauveau**: NHMW 2016/0103/1612 (4), LC (1).



**Plate 126.** *Ceratia ligeriana* (Peyrot, 1938); 1. NHMW 2016/0103/0321, height 2.4 mm, width 900  $\mu\text{m}$  (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – Glibert (1949) was correct to separate this middle Miocene to lower Pliocene French Atlantic form as a distinct species. He named the new species *Cingula* (*Ceratia*) *falunica*, but later realised that it is a junior synonym of *Cingula* (*Setia*) *ligeriana* Peyrot, 1938 (Glibert, 1962, p. 51). In shape and in having a truncated apex it resembles the present-day Atlantic and Mediterranean species *Ceratia proxima* (Forbes & Hanley, 1850), but differs in having no trace of spiral sculpture. In having a smooth teleoconch it resembles the middle Miocene to present-day Atlantic and Mediterranean species *Hyalia vitrea* (Montagu, 1803), but this has a taller protoconch resulting in a more tapered apex. Both Glibert (1949) and Fretter & Graham (1978) argued that the presence/absence of sculpture was insufficient reason to separate *Ceratia* H. Adams & A. Adams, 1852 and

*Hyalia* H. Adams & A. Adams, 1852. Ponder (1984) tentatively separated the genera based on shell characters: absence of spiral sculpture and a more elevated protoconch in *Hyalia*, some differences in the central radular tooth, and differences in the end of the foot. The intermediate shell morphology makes it difficult to assign *C. ligeriana* to one or other genus, or if indeed they should be separated. We maintain it in *Ceratia*, as originally suggested by Glibert (1949).

*Distribution* – Middle Miocene: Loire Basin (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

Genus *Pseudonoba* Boettger, 1902

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

1902 *Pseudonoba* Boettger, p. 145.

*Pseudonoba* aff. *striata* (Hörnes, 1856)

Plate 127, figs 1-2

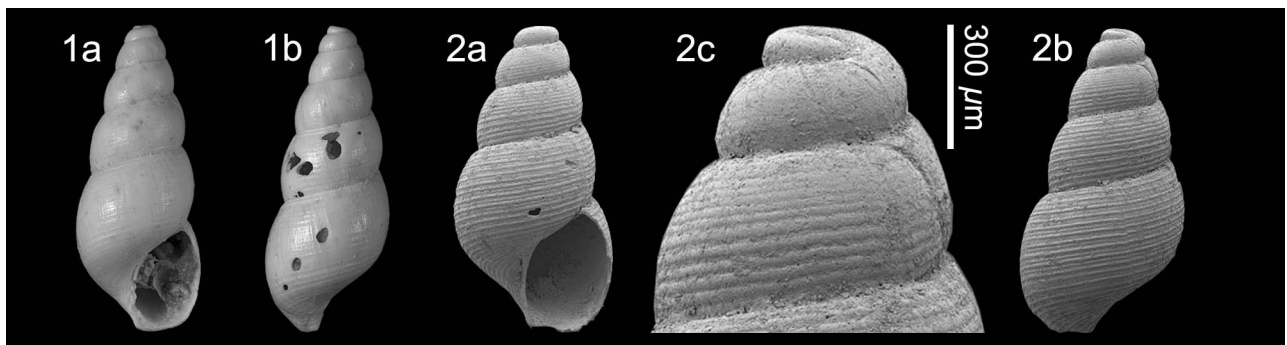
aff. \*1856 *Chemnitzia striata* Hörn., Hörnes, p. 541 (*partim*, pl. 43, fig. 21 only).

aff. 2013 *Pseudonoba* aff. *striata* (Hörnes, 1856) – Landau *et al.*, p. 78, pl. 7, fig. 1, pl. 58, fig. 9.

2016 *Pseudonoba* aff. *striata* (Hörnes, 1856) – Van Dingenen *et al.*, p. 147, pl. 11, fig. 7.

*Material and dimensions* – Maximum height 4.4 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/0688 (1). **Renauveau**: NHMW 2016/0103/1578 (1), NHMW 2016/0103/1618 (3).

*Discussion* – These shells seem to represent the same species as that illustrated by Van Dingenen *et al.* (2016, pl. 11, fig. 7) as *Pseudonoba* aff. *striata* (Hörnes, 1856) from the lower Pliocene Assemblage III locality of Le Pigeon Blanc. The planorbid, depressed protoconch com-



**Plate 127.** *Pseudonoba* aff. *striata* (Hörnes, 1856); 1. NHMW 2016/0103/0688, height 4.4 mm, width 1.8 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene. 2. NHMW 2016/0103/1578, height 2.7 mm, width 1.4 mm; 1c, detail of protoconch (SEM image). Renauveau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

posed of about two whorls places this shell within the Iravadiidae Thiele, 1928. The teleoconch sculpture is similar to that of *Pseudonoba striata* (Hörnnes, 1856) (see Landau *et al.*, 2013, pl. 7, fig. 1, pl. 58, fig. 9), composed of numerous spiral cords, but in this species the cords are narrower. Both the shell from Assemblage I and that from Le Pigeon Blanc seem thinner-shelled than the European iravadiid genera *Pseudonoba*, *Rhombostoma* G. Seguenza, 1876 and *Erentozia* Landau, Harzhauser, İslamoğlu & Silva, 2013. We await further material to better characterise this species. We note that the shells from the lower Pliocene of Italy identified by Chirli (2006, pl. 20, figs 11-13) as *Onoba tarifensis* Hoenselaar & Moolenbeek, 1987 has a protoconch that looks more iravadiid than rissoiid and it is very similar to the French species discussed here. Rolán (2008, p. 241) discussed the close superficial similarity between certain European iravadiids and *Onoba* species.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

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

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

1888 *Bouryia* Cossmann, p. 290.

For generic synonymy see Van Dingenen *et al.* (2016, p. 148).

***Bouryia cylindrica* (Cossmann & Peyrot, 1918)**

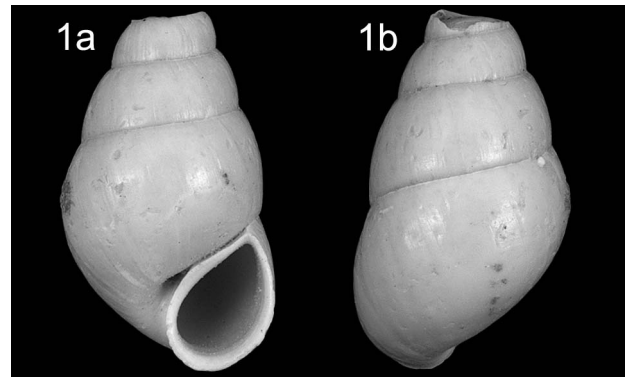
Plate 128, fig. 1

\*1918 *Nystia cylindrica* Cossmann & Peyrot, p. 422, pl. 16, figs 45, 46.

2016 *Bouryia cylindrica* (Cossmann & Peyrot, 1918) – Van Dingenen *et al.*, p. 148, pl. 12, fig. 2 (*cum syn.*).

*Material and dimensions* – Maximum height 4.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0543 (1), NHMW 2016/0103/0544 (5), RGM.1348249 (3).

*Discussion* – *Bouryia cylindrica* (Cossmann & Peyrot, 1918) is found only at St-Clément-de-la-Place, where it is uncommon. The illustrated specimen is squatter and with less convex whorls than that figured from the middle Miocene Loire Basin of France (Glibert, 1949, pl. 5, fig. 15), but otherwise shows the characters of the species clearly: relatively convex whorls, deep suture, truncated apex and small aperture. *Bouryia pontileviensis* (de Morgan, 1920), also from the middle Miocene of the Loire Basin, differs in having fewer and less convex whorls, a



**Plate 128.** *Bouryia cylindrica* (Cossmann & Peyrot, 1918); 1. NHMW 2016/0103/0543, height 4.6 mm; width 2.6 mm; Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

less impressed suture and a smaller aperture. The older species *B. falunica* Cossmann, 1895 from the Aquitanian lower Miocene of the Aquitaine Basin has a smaller, almost regularly cylindrical shell shape, with superficial sutures and weakly convex whorls.

*Distribution* – Middle Miocene: Loire Basin (Cossmann & Peyrot, 1918; de Morgan, 1920; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

Family Tornidae Sacco, 1896 (1884)  
Subfamily Torninae Sacco, 1896 (1884)  
Genus *Discopsis* de Folin, 1870

*Type species* (by original designation) – *Discopsis omalos* de Folin, 1870, present-day, Gulf of Mexico.

1870 *Discopsis* de Folin, p. 205.

*Note* – The shells of this genus are characterised by being small, strongly depressed lentiform in shape, the dorsal surface smooth or with axial ribs and only one prominent peripheral carina, the venter with axial ribs, one or more spiral cords and a wide umbilicus (Rolán & Rubio, 2002), although some species lack the cords on the venter (i.e. *Discopsis rarus* Rolán & Rubio, 2002).

Although it has been suggested that *Discopsis* de Folin, 1870 is possibly a synonym of *Cochliolepis* Stimpson, 1858 (Bouchet & Gofas, 2013, in WoRMS), Rubio & Rolán (2011) argued for the distinction of these two genera based on shell and opercular characters. Furthermore, they considered that *Discopsis* should be placed in the Torninae Sacco, 1896, whereas *Cochliolepis* belonged within the Vitrinellinae Bush, 1897. Many of the Miocene European species classically placed in the genus *Tornus* Turton & Kingston, 1830 should be transferred to *Discopsis*; i.e. *Tornus trigonostoma* (de Basterot, 1825), *T. europaeus* (de Stefani, 1888), *T. pseudotriostoma* (Boettger,

1907), *Tornus canui* de Morgan, 1920, *Tornus falunicus* de Morgan, 1920, *Tornus pontileviensis* de Morgan, 1920.

***Discopsis pseudocanui* nov. sp.**

Plate 129, fig. 1

*Type material* – Holotype MNHN.F.A57702, diameter 1.6 mm, height 380  $\mu\text{m}$ ; paratype 1 NHMW 2016/0103/0260, diameter 2.0 mm, height 400  $\mu\text{m}$ ; paratype 2 RGM.1309635.

*Other material* – Maximum diameter 2.0 mm, height 400  $\mu\text{m}$ . **St-Clément-de-la-Place:** NHMW 2016/0103/0261 (8). **Renaleau:** NHMW 2016/0103/0262 (32), RGM.1349010 (2), LC (25), FVD (14). **Beugnon:** NHMW 2016/0103/0263 (6).

*Etymology* – Name reflecting the close similarity to *Discopsis canui* (de Morgan, 1920). *Discopsis* gender masculine.

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

*Stratum typicum* – Tortonian, upper Miocene.

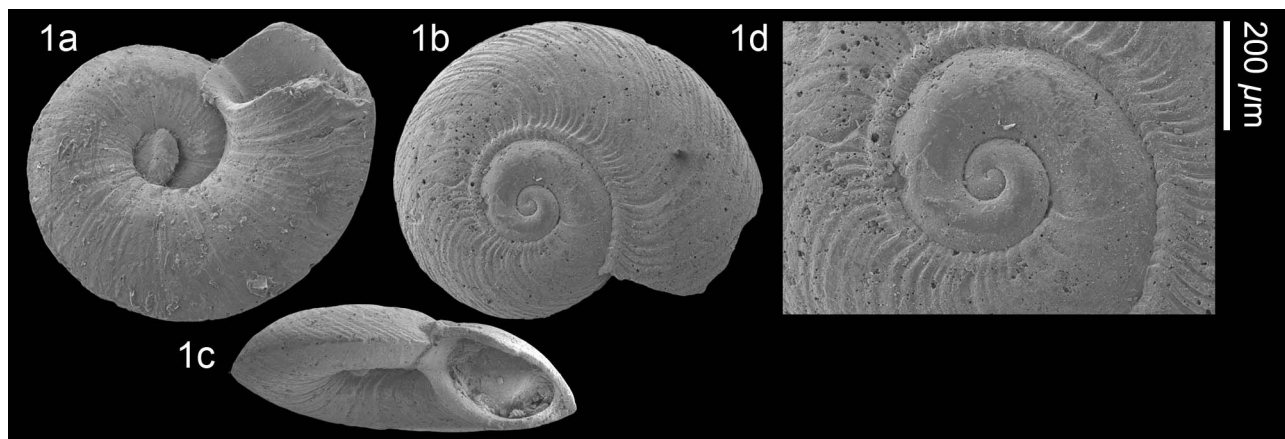
*Diagnosis* – *Discopsis* species of small size, with strongly depressed lentiform shell shape, multispiral protoconch composed of 2.5 whorls, single teleoconch whorl, dorsum bearing single cord running just below suture, from which radiate crowded, sinuous axial riblets, periphery angulated, but not delimited, weakly convex base bearing weak axial sculpture, wide non-delimited umbilicus.

*Description* – Shell small, depressed lentiform. Protoconch multispiral, planorbid, composed of 2.5 smooth whorls (dp = 600  $\mu\text{m}$ ; dn = 40  $\mu\text{m}$ , dp1 = 90  $\mu\text{m}$ ). Junction with teleoconch sharply delimited by sinuous scar. Teleoconch of one strongly depressed whorl. Suture deeply impressed. Dorsal sculpture of one strong spiral cord placed immediately below suture and crowded sinuous

axial riblets, most strongly developed on adapical half of whorl. Periphery angular, but not delimited by cord. Base depressed, weakly convex bearing weak axial growth lines. Umbilicus wide, not sharply delimited. Aperture strongly tangential, outer lip simple, columella smooth, strongly tilted abaxially. Columellar and parietal callus thickened, narrow.

*Discussion* – *Discopsis pseudocanui* nov. sp. is extremely similar to *D. canui* (de Morgan, 1920) from the middle Miocene of the Loire Basin of France. Both species have a single dorsal spiral cord immediately below the suture, although this is more strongly developed in *D. pseudocanui*, and a wide, non-delimited umbilicus. However, *D. canui* has a paucispiral protoconch composed of a single whorl, with a large nucleus and 2.2 teleoconch whorls, whereas *D. pseudocanui* has a multispiral protoconch of 2.5 whorls, with a small nucleus and only one teleoconch whorl. Both species are closely similar in their strongly depressed shell shape to *Discopsis trigonostoma* (de Basterot, 1825), widespread in the European middle Miocene (Glibert, 1949; Janssen, 1984; Wienrich, 2001) but that species differs in having a carina delimiting the umbilicus. *Discopsis trigonostoma* also has a multispiral protoconch composed of about 2.5 whorls (Wienrich, 2001, pl. 65, fig. 4a). We note that the middle Miocene Paratethyan shells recorded as *D. trigonostoma* (Strausz, 1966) are not this species, but *D. pseudotinostoma* (Boettger, 1907), which differs from *D. trigonostoma* mainly in having a much narrower umbilicus. *Discopsis pseudotinostoma* has a protoconch of just over two whorls (Bałuk, 1975, p. 99). *Discopsis falunicus* (de Morgan, 1920), also from the middle Miocene Loire of the Basin of France, differs in having the single dorsal cord seen in *D. canui* placed further away from the suture, almost mid-dorsum and like, *D. trigonostoma* and *D. pseudotinostoma* has a cord delimiting the base. Like *D. canui*, *D. falunicus* also seems to have a paucispiral protoconch of just over one whorl, with a large nucleus.

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



**Plate 129.** *Discopsis pseudocanui* nov. sp.; 1. **Holotype** MNHN.F.A57702, diameter 1.6 mm, height 380  $\mu\text{m}$ ; 1d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



Genus *Tornus* Turton & Kingston, 1830

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

1830 *Tornus* Turton & Kingston, No. 73, unnumbered page.

For generic synonymy see Van Dingenen *et al.* (2016, p. 148).

***Tornus pedemontanus* Pavia, 1980**

Plate 130, fig. 1

- \*1980a *Tornus pedemontanus* Pavia, p. 212, pl. 2, figs 3, 8-10, 13.
- 1992 *Tornus pedemontanus* Pavia, 1980 – Cavallo & Repetto, p. 58, fig. 97.
- 2006 *Tornus pedemontanus* Pavia, 1980 – Chirli, p. 78, pl. 32, figs 1-6.
- 2013 *Tornus pedemontanus* Pavia, 1981 [sic] – Landau *et al.*, p. 12, pl. 3, fig. 8.

*Material and dimensions* – Maximum diameter 3.8 mm, height 3.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0264 (1), NHMW 2016/0103/0265 (2), RGM.1309643 (2). **Renauleau:** NHMW 2016/0103/0266 (50+), RGM.1349008 (6), LC (50+), FVD (50+). **Beugnon:** NHMW 2016/0103/0267 (6), RGM.1348425 (1 juvenile).

*Discussion* – We consider these shells from the Assemblage I localities to be conspecific with *Tornus pedemontanus* Pavia, 1980, originally described from the lower Pliocene of Italy. The specimen illustrated (Pl. 130, fig. 1) is indistinguishable in sculpture from the Italian specimens figured by Chirli (2006, pl. 32, figs 1-6). In most of the specimens from France the mid-basal cord is not as strongly developed as it is in the specimen illustrated. The figured specimen is also relatively high-spired for the species, other specimens are more depressed, but these differences are part of the intraspecific variability. Moroni & Ruggieri (1985) described *Tornus pedemontanus primitivus* from the upper Miocene of Italy. It is

extremely similar to *Tornus pedemontanus* Pavia, 1980, but differs in being smaller, in having a slightly narrower umbilicus, which is bordered by a weaker carina and in lacking a mid-basal carina. Interestingly, the specimens from the upper Pliocene Assemblage III locality of Le Pigeon Blanc are *T. primitivus* rather than *T. pedemontanus* (Van Dingenen *et al.*, 2016, p. 148). As they both occur in the late Moocene, we prefer to consider the two separate at full species rank.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al.*, 2013); central Mediterranean, Italy (Pavia, 1980a; Chirli, 2006). Upper Pliocene: central Mediterranean, Italy (Cavallo & Repetto, 1992).

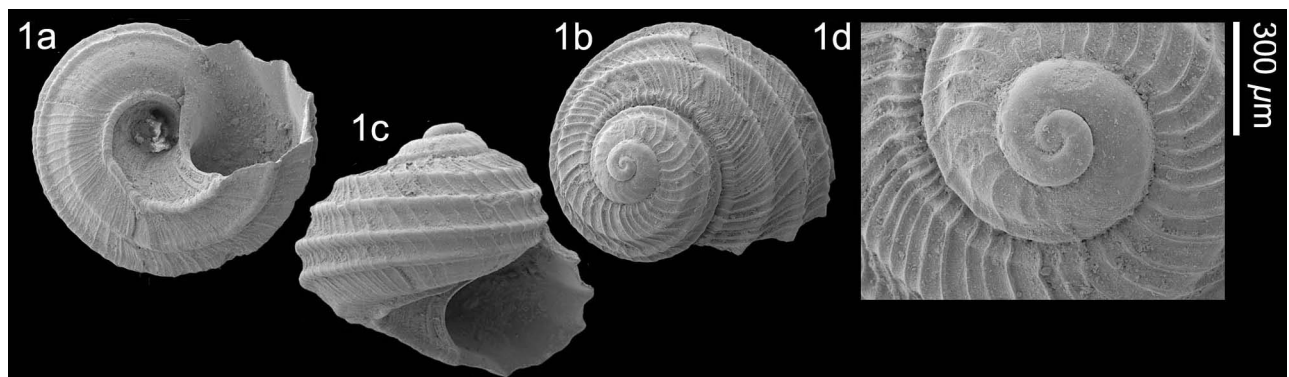
***Tornus subcarinatus* (Montagu, 1803)**

Plate 131, fig. 1

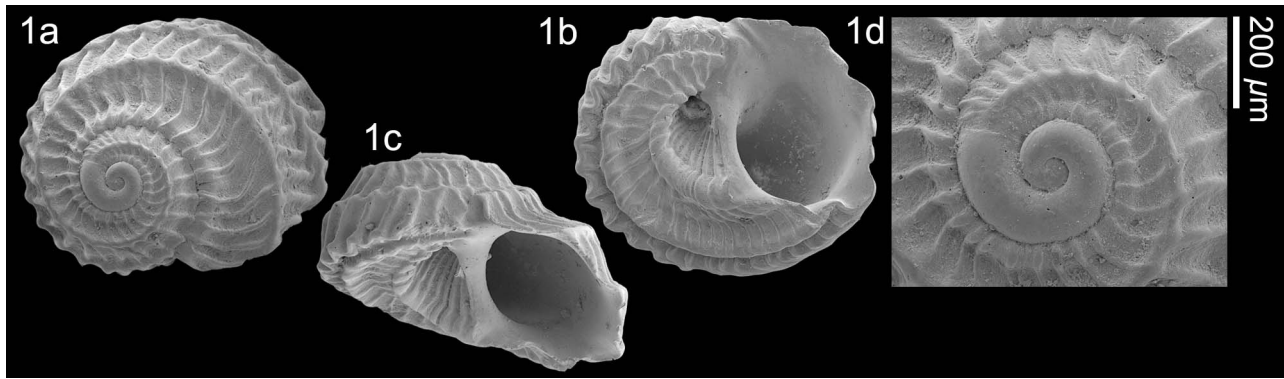
- \*1803 *Helix subcarinata* Montagu, p. 438, pl. 7, fig. 9.
- 1918 *Tornus Dollfusi* Cossmann, p. 346, pl. 2, figs 67-69.
- 1964 *Tornus dollfusi* Cossmann, 1918 – Brébion, p. 186.
- 2016 *Tornus subcarinatus* (Montagu, 1803) – Van Dingenen *et al.*, p. 149, pl. 11, fig. 9, pl. 12, fig. 3 (*cum syn.*).

*Material and dimensions* – Maximum diameter 2.0 mm, height 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0268 (1), NHMW 2016/0103/0269 (50+), RGM.1309644 (45), LC (20), FVD (15). **Sceaux-d'Anjou:** NHMW 2016/0103/0272 (1), RGM.1347935 (1), RGM.1348891 (1). **Renauleau:** NHMW 2016/0103/0270 (27), RGM.1349009 (3), LC (12), FVD (10). **Beugnon:** NHMW 2016/0103/0271 (19).

*Discussion* – Van Dingenen *et al.* (2016, p. 149) highlighted the problem with the *Tornus subcarinatus* (Montagu, 1803) species concept as accepted at present, in which specimens with paucispiral and multispiral protoconchs are considered conspecific. They concluded that there were two species: an Atlantic species *T. subcarinatus*, with a multispiral protoconch of about 2.1-2.25 whorls, with a



**Plate 130.** *Tornus pedemontanus* Pavia, 1980; 1. NHMW 2016/0103/0264, diameter 3.8 mm, height 3.1 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 131.** *Tornus subcarinatus* (Montagu, 1803); 1. NHMW 2016/0103/0268, diameter 2.0 mm, height 1.2 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

small nucleus (counting including first half whorl: Rolán & Rubio, 2002, figs 5, 6; Van Aartsen *et al.* 1998, fig. 7), and a Mediterranean species that is at present unnamed with a paucispiral protoconch of 1.25-1.4 whorls, with a larger nucleus (Rolán & Rubio, 2002, figs 13, 14; Van Aartsen *et al.*, 1998, fig. 7). The protoconch diameter also differs between the two species, Atlantic specimens have a diameter of 420-480 µm, Mediterranean specimens 330-350 µm. There seems to be a sharp delimitation between these species today with specimens from Tarifa belonging to the Atlantic form and specimens from Tanger to the Mediterranean form (Van Aartsen *et al.*, 1998, p. 136).

Van Dingenen *et al.* (2016, p. 149) concluded that the lower Pliocene specimens from NW France were conspecific with present-day Atlantic species *T. subcarinatus*, with similar protoconch characters (dn=2.4, dp = 440 µm, dn = 37 µm, dp1 = 100 µm; Van Dingenen *et al.*, 2016, pl. 11, fig. 9d).

Cossmann (1918) described specimens from the upper Pliocene-Pleistocene Assemblage IV locality of Gourbesville, NW France as *T. dollfusi*, which we consider a junior subjective synonym of *T. subcarinatus*. Glibert (1949) described the specimens from the middle Miocene of the Loire Basin of France as a distinct subspecies; *T. subcarinatus minor*, differing from the nominate subspecies only in being smaller. Brébion (1964, p. 186) united all the NW French specimens from the middle Miocene of the Loire Basin and the upper Miocene to Pleistocene 'Redonian' deposits under the name *T. dollfusi* and considered *T. subcarinatus minor* a synonym. Brébion noted that the upper Miocene Assemblage I and II specimens were smaller than the Assemblage IV specimens and gave as the most important distinguishing character between *T. dollfusi* and *T. subcarinatus* the weaker carinae in the latter. The specimen figured from the Assemblage I locality of St-Clément-de-la-Place (Pl. 131, fig. 1) does indeed have strongly developed carinae, but not significantly more so than the specimens from Tarifa illustrated by Rolán & Rubio (2002, figs 7-11). It is true that on average the middle and upper Miocene NW French specimens are smaller than the Pliocene to present-day ones, but we see no merit in separating them as a distinct subspecies, as there is some overlap; the maximum diam-

eter of the Assemblage I specimens is in the lower range given by Rolán & Rubio (maximum diameter 2.0-30 mm; 2002, fig. 8). Moreover, the protoconch dimensions are quite similar to the present-day specimens [Pl. 131, fig 1d: n= 2.1, dp = 440 µm, dn = 60 µm, dp1 = 150 µm vs. dp = 420-480 µm (Rolán & Rubio, 2002, p. 8) for present-day specimens, although we note the nucleus is slightly bigger in the French Tortonian specimens 60 µm vs. 40 µm]. We therefore also consider *T. subcarinatus minor* a junior subjective synonym of *T. subcarinatus*.

**Distribution** – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); NSB, Coraline Crag, England (Wood, 1848; Harmer, 1923; central Mediterranean, Italy (Chirli, 2006). Upper Pliocene: Red Crag, England (Wood, 1848; Harmer, 1923). Upper Pliocene-Pleistocene: Atlantic, NW France (Cossmann, 1918; Brébion, 1964). Pleistocene (indeterminate): Atlantic, British Isles (Harmer, 1923); NSB, The Netherlands (Van Regteren Altena *et al.*, 1954); Present-day: Atlantic coasts of Europe from British Isles to Tarifa (Fretter & Graham, 1978).

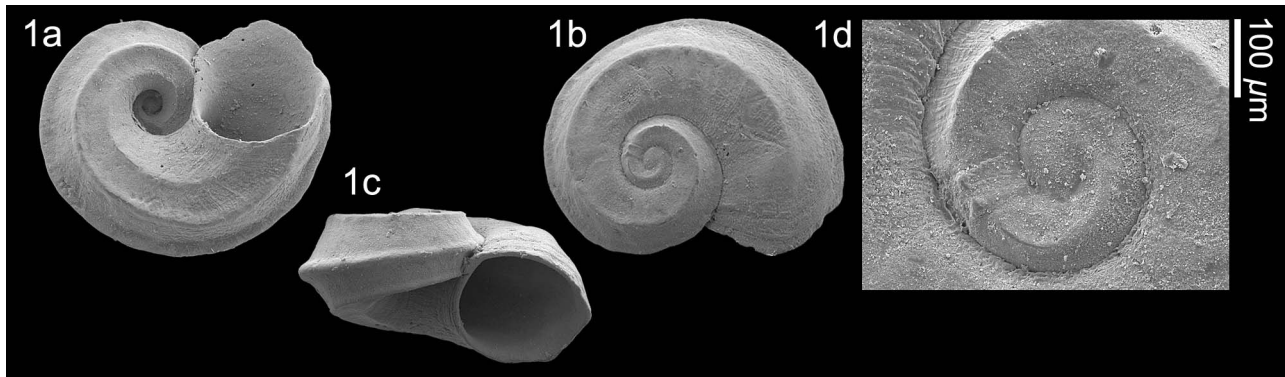
#### *Tornus superlatus* nov. sp.

Plate 132, fig. 1

**Type material** – Holotype NHMW 2016/0103/1579, diameter 1.5 mm, height 730 µm, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/1609, diameter 1.6 mm, height 740 µm; paratype 2 NHMW 2016/0103/1610, diameter 600 µm, height 430 µm, **Renauleau**. Paratype 3 NHMW 2016/0103/1735, diameter 650 µm, height 440 µm, **Sceaux-d'Anjou**.

**Other material** – **St-Clément-de-la-Place**: NHMW 2016/0103/1784 (4). **Renauleau**: LC (1).

**Etymology** – Latin '*superlatus*, -a, -um', adjective meaning exaggerated, reflecting the very strongly keeled sculpture. *Tornus* gender masculine.



**Plate 132.** *Tornus superlatus* nov. sp.; 1. **Holotype** NHMW 2016/0103/1579, diameter 1.5 mm, height 730  $\mu\text{m}$ ; 1d, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Tornus* species of minute size, with strongly keeled paucispiral protoconch, teleoconch of 1.6 whorls angular at upper, peripheral, peribasal and periumbilical keels, but lacking further spiral sculpture, whorl profile concave between keels, smooth umbilicus.

*Description* – Shell minute, circular, depressed. Protoconch paucispiral, composed of 1.5 whorls; nucleus smooth, post-nuclear whorl strongly keeled mid-whorl ( $dp = 270 \mu\text{m}$ ;  $dn = 75 \mu\text{m}$ ). Protoconch/teleoconch boundary sharply delimited by scar. Teleoconch composed of 1.6 whorls, strongly angled at upper, peripheral, peribasal and periumbilical keels, whorl profile concave between keels. Suture deeply impressed. No further spiral sculpture apart from keels. Umbilicus relatively wide, smooth within. Aperture circular, somewhat angled at keels, strongly oblique in profile.

*Discussion* – *Tornus superlatus* nov. sp. is characterised by its strongly keeled teleoconch whorls, making the last whorl sharply angular at the shoulder, mid-whorl, base and umbilicus and by the absence of axial and secondary spiral sculpture. None of the extant eastern Atlantic *Tornus* species revised by Rolán & Rubio (2002) have their axial sculpture completely lacking, nor do any of the fossil species encountered. Most of the fossil species lacking axial sculpture placed by previous authors in *Tornus*, such as *Delphinula trigonostoma* de Basterot, 1825, are here placed in the genus *Discopsis* (see above). *Tornus caraboboensis* (Weisbord, 1962) from the Pliocene to present-day southern Caribbean (Rubio *et al.*, 2011) is similar in shell profile; the spire is a little more elevated, but the keels are placed in the same positions as in *T. superlatus* making the last whorl sharply angular, but the Caribbean shell has axial sculpture. *Tornus superlatus* is superficially similar in shape and sculpture to some of the present-day eastern Atlantic *Circulus* species revised by Oliver & Rolán

(2011). However, *Circulus* species have a multispiral protoconch.

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

Subfamily Teinostomatinae Cossmann, 1917

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

*Type species* (by subsequent designation, Cossmann, 1918) – *Teinostoma politum* A. Adams, 1853, present-day, Philippines.

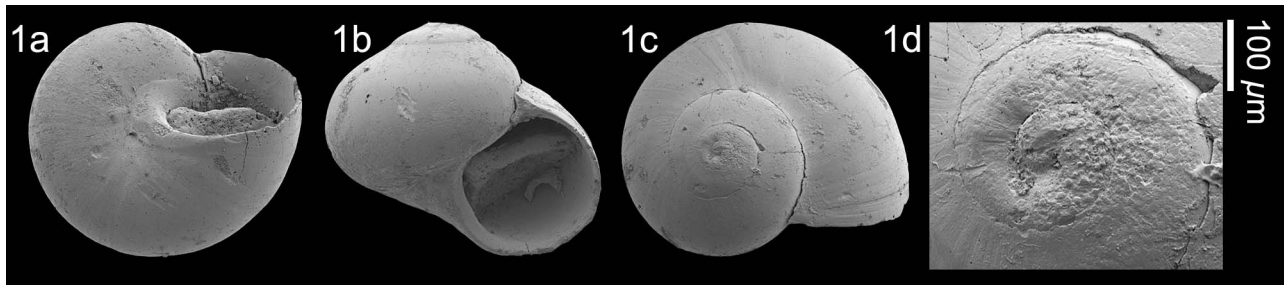
- 1853 *Teinostoma* H. & A. Adams, p. 122.
- 1857 *Pseudorotella* Fischer, p. 52. Type species (by monotypy): *Trochus semistriatus* d'Orbigny, 1842, present-day, Caribbean.
- 1863 *Calceolina* A. Adams, p. 267. Type species (by monotypy): *Neritina pusilla* C.B. Adams, 1850, present-day, Jamaica. Junior homonym of *Calceolina* Rafinesque, 1815 [Cnidaria].
- 1885 *Tinostoma* Fischer, p. 834. Unjustified emendation.
- 1918 *Calceolata* Iredale, pp. 28, 32. Type species (by typification of replacement name): *Neritina pusilla* C.B. Adams, 1850, present-day, Jamaica. *Nom. nov. pro Calceolina* A. Adams, 1863, *non* Rafinesque, 1815 [Cnidaria].
- 1945 *Teinostoma (Annulicallus)* Pilsbry & McGinty, p. 7. Type species (by monotypy): *Teinostoma lituipalmarum* Pilsbry & McGinty, 1945, present-day, Florida, USA.
- 1945 *Teinostoma (Ellipetylus)* Pilsbry & McGinty, p. 8. Type species (by monotypy): *Teinostoma coccolitoris* Pilsbry & McGinty, 1945, present-day, Florida, USA.

***Teinostoma obesum* nov. sp.**

Plate 133, fig. 1

*Type material* – Holotype NHMW 2016/0103/1580, dia-





**Plate 133.** *Teinostoma obesum* nov. sp.; 1. **Holotype** NHMW 2016/0103/1580, diameter 1.6 mm, height 1.3 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

meter 1.6 mm, height 1.3 mm; paratype 1 NHMW 2016/0103/1581, diameter 1.2 mm, height 1.0 mm; paratype 2 RGM.1309562; paratype 3 NHMW 2016/0103/1766, diameter 1.3 mm, height 1.1 mm.

*Other material* – Known only from type series.

*Etymology* – Latin ‘*obesus*, -a, -um’, adjective meaning fat, reflecting the inflated last whorl for the genus. *Teinostoma* gender neuter.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Teinostoma* species of minute size, with globose shell for genus, teleoconch of about 2.5 smooth whorls, columellar callus moderately thickened, not greatly expanded, closing umbilicus.

*Description* – Shell minute, globose. Protoconch of about one whorl, surface abraded. Protoconch/teleoconch junction not preserved. Teleoconch of 2.5 whorls separated by suture becoming more deeply impressed abapically, smooth, except for indistinct axial growth lines. Last whorl globose, rounded at periphery. Aperture rounded, outer lip simple, thin. Columella slightly thickened. Columella callus moderately thickened, not greatly expanded, closing umbilicus completely.

*Discussion* – *Teinostoma obesum* nov. sp. is immediately separated from most of its congeners by virtue of its rather globose shell. Most *Teinostoma* species are far more flattened. *Teinostoma neritoides* Cossmann & Peyrot, 1917 from the Burdigalian lower Miocene of the Aquitaine Basin of France has a similar shell shape, but a far more widely expanded columellar callus. *Teinostoma ciskae* Faber, 1995 from the present-day Caribbean also has a similar shell shape, but has the teleoconch covered in rows of pits.

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

Genus *Circulus* Jeffreys, 1865

*Type species* (by monotypy) – *Delphinula duminyi* Requier, 1848 (= *Valvata striata* Philippi, 1836), present-day, Mediterranean.

1865 *Circulus* Jeffreys, p. 315.

1961 *Soyorota* Habe, p. 425. Type species (by monotypy): *Pygmaeorota soyoae* Habe, 1961 present-day, Japan.

#### ***Circulus planorbillus* (Dujardin, 1837)**

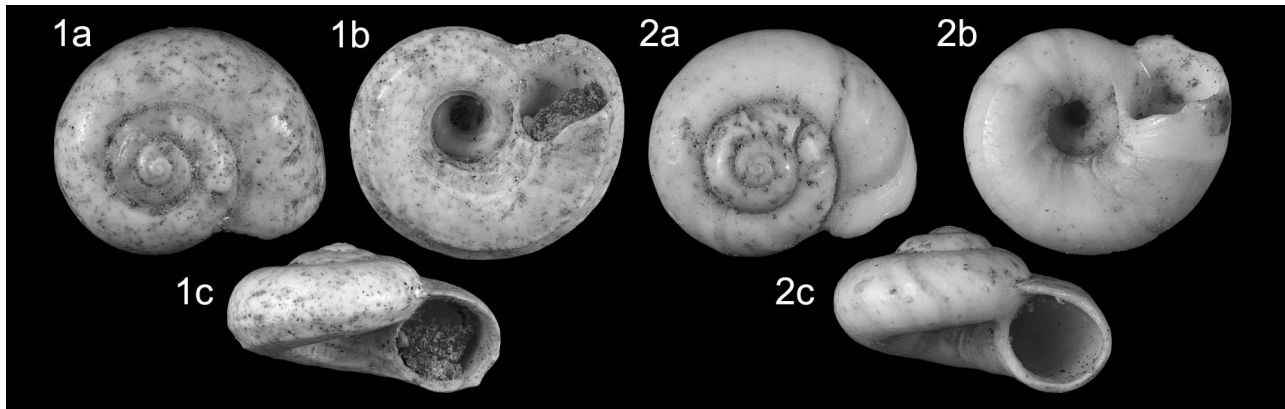
Plate 134, figs 1-2

- \*1837 *Solarium planorbillus* Dujardin, p. 282, pl. 19, fig. 13.
- 1917 *Tornus planorbillus* Duj – Cossmann & Peyrot, p. 237, pl. 7, figs 57-62.
- 1949 *Circulus planorbillus* (Dujardin, 1837) – Glibert, p. 70, pl. 4, fig. 4.

*Material and dimensions* – Maximum diameter 2.7 mm, height 1.4 mm. **Beugnon:** NHMW 2016/0103/1456-1457 (2), NHMW 2016/0103/1458 (50+).

*Discussion* – In the Assemblage I localities, we have found this species only at Beugnon. Like the middle Miocene Loire Basin specimens discussed by Glibert (1949, p. 70), all the specimens at hand are worn. Those illustrated here are the best preserved. The weak peripheral and peribasal carinae and the two or three cords within the umbilicus described by Cossmann & Peyrot (1917, p. 238) are moderately well developed in one specimen (Pl. 134, fig. 1), but almost obsolete in the other (Pl. 134, fig. 2), showing a similar range of variability as that illustrated by Cossmann & Peyrot (1917, pl. 7, figs 57-62) for the middle Miocene of the Aquitaine Basin. We have tried to photograph the protoconch using SEM, but it is worn in even the best specimens and the protoconch/teleoconch boundary is not preserved.

*Distribution* – Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1917), Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper).



**Plate 134.** *Circulus planorbillus* (Dujardin, 1837); 1. NHMW 2016/0103/1456, diameter 2.6 mm, height 1.3 mm; 2. NHMW 2016/0103/1457, diameter 2.5 mm, height 1.4 mm. Beugnon, Maine-et-Loire, NW France, Tortonian, upper Miocene.

### *Circulus striatus* (Philippi, 1836)

Plate 135, figs 1-3

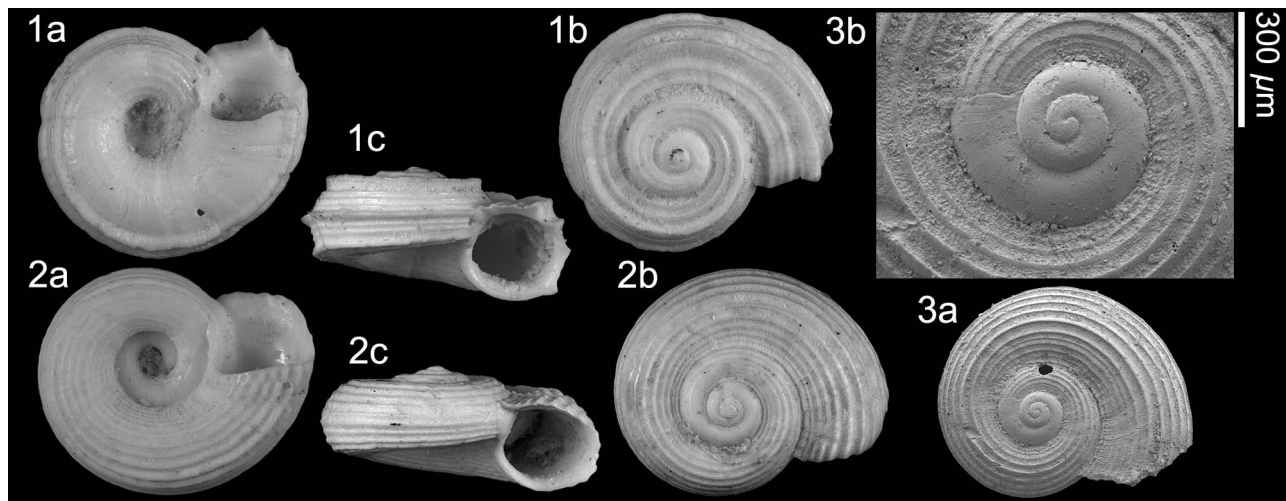
- \*1836 *Valvata striata* Philippi, p. 137, pl. 9, fig. 3.
- 1842 *Adeorbis striatus* Wood, p. 530.
- 1842 *Adeorbis tricarinatus* Wood, p. 530 (*nomen nudum*).
- 1848 *Adeorbis striatus* S. Wood – Wood, p. 137, pl. 15, fig. 7.
- 1848 *Adeorbis tricarinatus* S. Wood – Wood, p. 138, pl. 15, fig. 6.
- 1898 *Circulus striatus* (Philippi) – Almera & Bofill, p. 194, pl. 6, fig. 16.
- 1916 *Adeorbis striatus* Phil. – Cerulli-Irelli, p. 186, pl. 21, figs 19, 20.
- 1916 *Adeorbis striatus* var. *triangulata* De Rayn. – Cerulli-Irelli, p. 187, pl. 21, figs 21, 22.
- 1923 *Adeorbis tricarinatus* S.V. Wood – Harmer, p. 759, pl. 60, fig. 24.
- 1923 *Circulus striatus* (Philippi) – Harmer, p. 759, pl. 60, fig. 25.
- 1954 *Circulus striatus* (Philippi, 1836) – Van Regteren Altena *et al.*, p. 61, pl. 3, fig. 25.
- 1957 *Circulus striatus* Philippi, 1836 – Glibert, p. 21, pl. 1, fig. 18.
- non 1959 *Circulus striatus* (Philippi, 1836) – Anderson, p. 64, pl. 3, fig. 8 [= *Circulus subcirculus* (Cossmann & Peyrot, 1916)].
- non 1967 *Circulus striatus* (Philippi, 1836) – Janssen, p. 127, pl. 2, fig. 6 [= *Circulus subcirculus* (Cossmann & Peyrot, 1916)].
- 1975 *Circulus striatus* (Philippi, 1843 [sic]) – Pavia, p. 128, pl. 2, figs 4, 6, 9, 12.
- 1978 *Circulus striatus* (Philippi, 1836) – Fretter & Graham, p. 227, fig. 190.
- 1980 *Circulus striatus* (Philippi, 1836) – Martinell, p. 123, pl. 1, figs 11, 12.
- 1985 *Circulus striatus* (Philippi, 1836) – González-Delgado, p. 68, pl. 2, figs 9-11.
- 1992 *Circulus striatus* (Philippi, 1836) – Cavallo & Repetto, p. 54, fig. 087.
- 1996 *Circulus striatus* (Philippi, 1836) – Giannuzzi-

Savelli *et al.*, p. 118, figs 514-515.

- 1996 *Circulus tricarinatus* (Wood, 1848) – Giannuzzi-Savelli *et al.*, p. 118, fig. 516.
- 1997a *Circulus striatus* (Philippi, 1836) – Marquet, p. 18, pl. 4, fig. 2.
- 1998 *Circulus striatus* (Philippi, 1836) – Ferrero *et al.*, p. 48, 52, pl. 1, fig. 4.
- 1998 *Circulus striatus* (Philippi, 1836) – Marquet, p. 69, fig. 44.
- 2001 *Circulus striatus* (Philippi, 1836) – Silva, p. 155, fig. 3.33, pl. 6, figs 1, 2.
- 2006 *Circulus striatus* (Philippi, 1836) – Chirli, p. 55, pl. 24, figs 6-14.
- 2010 *Circulus striatus* (Philippi, 1836) – Moths *et al.*, fig. 26a, b.
- 2011 *Circulus striatus* (Philippi, 1836) – Landau *et al.*, p. 12, pl. 3, fig. 10.

*Material and dimensions* – Maximum diameter 3.5 mm, height 1.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0350 (5), LC (2). **Sceaux-d'Anjou:** NHMW 2016/0103/0353 (1), NHMW 2016/0103/0354 (7), RGM. 1309688 (2), RGM.1348974 (1), LC (1). **Renaleau:** NHMW 2016/0103/1459 (1), NHMW 2016/0103/0351 (50+), RGM.1349007 (7), LC (35), FVD (24). **Beugnon:** NHMW 2016/0103/1755 (1), NHMW 2016/0103/0352 (6).

*Discussion* – Oliver & Rolán (2011, p. 13) discussed the spirally striate form *Valvata striata* Philippi, 1836 and the strongly tricarinate form *Adeorbis tricarinatus* Wood, 1848 and noted that both extremes plus intermediate forms were found together in a small geographical area. They argued that these observations supported the position that they represent extreme forms of a single species, *Circulus striatus*. We can make the same observation based on the Assemblage I specimens, which also show these two extreme forms (Pl. 135, figs 1-3) together with intermediates. *Circulus subcirculus* (Cossmann & Peyrot, 1917) from the lower Miocene Aquitanian of the Aquitaine Basin of France is similar. The specimen illustrated by Lozouet *et al.* (2001, pl. 11, fig.1) has a strongly elevated peripheral carina, more so



**Plate 135.** *Circulus striatus* (Philippi, 1836); 1. NHMW 2016/0103/1755, diameter 2.5 mm, height 1.1 mm. Beugnon; 2. NHMW 2016/0103/0353, diameter 3.2 mm, height 1.4 mm. La Presselière, Sceaux-d'Anjou; 3. NHMW 2016/0103/1459, diameter 2.0 mm, height 1.0 mm; 3b, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

than in the carinate form of *C. striatus*, but weak shoulder and peribasal carinae. It has pustular microsculpture on the teleoconch, also seen in *C. striatus* (Pl. 135, fig. 3b). More material is required to separate these two taxa clearly.

**Distribution** – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1923), Kattendijk Formation, Belgium (Glibert, 1957; Marquet, 1997a, 1998); Atlantic, Guadalquivir Basin, Spain (González-Delgado, 1985; Landau *et al.*, 2011); western Mediterranean: Spain (Almera & Bofill, 1898; Martinell, 1980); central Mediterranean, Italy (Pavia, 1975; Chirli, 2006). Upper Pliocene: Mondego Basin (Silva, 2001); central Mediterranean, Italy (Cavallo & Repetto, 1992; Ferrero *et al.*, 1998). Lower Pleistocene: North Sea Basin, The Netherlands (Van Regteren Altena *et al.*, 1954); central Mediterranean, Italy (Cerulli-Irelli, 1916). Present-day: eastern Atlantic frontage coasts of Ireland, into Mediterranean (Fretter & Graham, 1978).

Superfamily Vanikoroidea Gray, 1840

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

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

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

1842 *Macromphalus* Wood, p. 537.

For generic synonymy see Van Dingenen *et al.* (2016, p. 160).

***Macromphalus bourgeoisi* (de Morgan, 1915)**

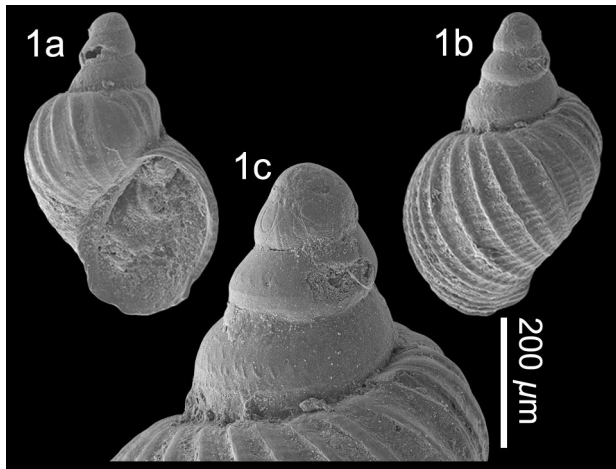
Plate 136, fig. 1

- \*1915 *Escharella Bourgeoisi* de Morgan, p. 230, fig. 13.
- 1925 *Michreschara (Dialystostoma) Bourgeoisi* de Morgan – Cossmann, p. 173.
- 1938 *Michreschara Bourgeoisi* de Morgan – Peyrot, p. 90.

**Material and dimensions** – Maximum height 1.0 mm, width 650 µm. **Sceaux-d'Anjou:** NHMW 2016/0103/0360 (1). **Renauleau:** NHMW 2016/0103/1446 (1), LC (3).

**Discussion** – The specimen from Sceaux-d'Anjou fits well with the description and illustration of the type from the French middle Miocene of the Loire Basin of France (de Morgan, 1915, p. 230, fig. 13). In the specimen from Sceaux-d'Anjou the protoconch is composed of closer to four whorls than the three described by de Morgan. It bears a fine abapical spiral thread, above which lie numerous short axial riblets (Pl. 136, fig. 1c). This agrees with the original description: ‘*Embryon lisse sur un tour et demi, le reste de la protoconque étant finement costulé*’ (de Morgan, 1915, p. 230). The teleoconch sculpture consists of prominent sharp prosocline axial ribs and fine spiral cords. The umbilicus is reduced to a narrow, elongate chink. *Macromphalina roberti* (de Morgan, 1915), also from the middle Miocene of the Loire Basin is similar, but differs in having stronger spiral ribs resulting in coarser sculpture, a more globose last whorl and a wider umbilicus. According to the original description (de Morgan, 1915, p. 229) the protoconch is also multispi-





**Plate 136.** *Macromphalus bourgeoisi* (de Morgan, 1915); 1. NHMW 2016/0103/0360, height 1.0 mm, width 650  $\mu\text{m}$ ; 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ral, but smooth. *Macromphalus reticulatus* Wood, 1842, which occurs in the north-western French Assemblage III locality of Le Pigeon Blanc (Van Dingenen *et al.*, 2016, p. 160) is immediately separated by its paucispiral protoconch consisting of about 1-1.25 globose whorls, with a large nucleus, suggestive of non-planktotrophic development.

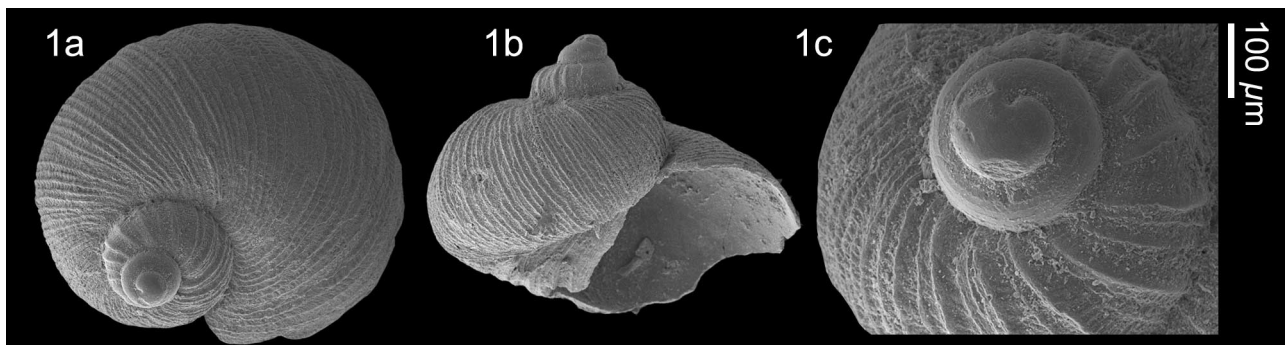
*Distribution* – Middle Miocene: Atlantic, Loire Basin, France (de Morgan, 1915; Peyrot, 1938). Upper Miocene: Atlantic (Tortonian) NW France (this paper).

Genus *Macromphalina* Cossmann, 1888

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

1888 *Macromphalina* Cossmann, p. 184.

For generic synonymy see Van Dingenen *et al.* (2016, p. 161).



**Plate 137.** *Macromphalina morgani* nov. sp.; 1. **Holotype** NHMW 2016/0103/0361, height 1.1 mm, width 1.5 mm; 1c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Macromphalina morgani* nov. sp.**

Plate 137, fig. 1

*Type material* – Holotype NHMW 2016/0103/0361, height 1.1 mm, width 1.5 mm (incomplete), **Sceaux-d'Anjou**; paratype 1 RGM.1348245, height 1.0 mm; paratype 2 RGM.1348246, height 1.1 mm, **St-Clément-de-la-Place**.

*Other material* – **St-Clément-de-la-Place**: RGM.1348247 (6 juveniles and fragments). **Sceaux-d'Anjou**: NHMW 2016/0103/0612 (7). **Renauleau**: NHMW 2016/0103/1447 (4), LC (1).

*Etymology* – Named after Jacques Jean Marie de Morgan (1857-1924), French mining engineer, geologist, and archaeologist, in recognition of his work on the middle Miocene assemblages of the Loire Basin (France). *Macromphalina* gender feminine.

*Locus typicus* – Renauleau, Maine-et-Loire, NW France.

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Macromphalina* species, with small shell, protoconch of two whorls, Protoconch II bearing spiral threads, teleoconch sculptured by raised axial ribs, widely spaced on first half teleoconch whorl, crowded abapically, and close-set spiral threads visible only in inter-spaces between ribs.

*Description* – Shell small, auriculiform. Protoconch elevated, composed of two whorls, with a medium-sized nucleus; Protoconch I smooth, Protoconch II bearing five spiral threads ( $dp = 250 \mu\text{m}$ ,  $hp = 240 \mu\text{m}$ ,  $dn = 80 \mu\text{m}$ ,  $dp1 = 150 \mu\text{m}$ ). Transition with teleoconch abrupt, marked by beginning of axial sculpture. Teleoconch consisting of 1.5 rapidly expanding whorls, with periphery at abapical suture. Suture linear, impressed. Axial sculpture of lamellar axial ribs; 11 relatively widely spaced ribs on first half teleoconch whorl, at half-whorl abrupt crowding of ribs, so that last whorl bears about 90 ribs. Spiral sculpture of weak close-set threads, visible only in inter-spaces between ribs. Last whorl strongly depressed, with rounded periphery, base rounded, bearing wide, poorly delimited umbilicus, sculpture similar to dorsum. Aper-

ture wide. Outer lip and columella missing.

**Discussion** – *Macromphalina morgani* nov. sp. is most similar to *Macromphalina bouryi* (Dautzenberg, 1912) [*non Vanikoro (Micromphalina) bouryi* de Morgan, 1915, which is a secondary homonym, renamed *Macromphalina massicardi* Van Dingenen, Ceulemans & Landau, 2016], an extant West African species, but this species differs from *M. morgani* in having a multispiral protoconch of 2.5 whorls with a small nucleus, which is entirely sculptured. Protoconch I has a sculpture of micropustules, whereas Protoconch II has spiral threads with netting in the interspaces (Rubio & Rolán, 1994, fig. 10), which is absent in *M. morgani*. *Macromphalina cossmanni* (Dollfus & Dautzenberg, 1886) from the middle Miocene of the Loire Basin of France differs in being less depressed and having axial sculpture only on the first half teleoconch whorl; abapically the whorls are smooth. *Macromphalina pontileviensis* (de Morgan, 1915) differs in having a smooth protoconch and the axial sculpture after the first half teleoconch whorl is rather irregular and varicose. *Macromphalina massicardi*, also from the Loire Basin, differs in having carinate teleoconch whorls.

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

Family Eulimidae Philippi, 1853

**Note** – The family Aclididae Sars, 1878 used in previous parts of this series was synonymised with Eulimidae Philippi, 1853 by Bouchet & Rocroi (2017).

Genus *Aclis* Lovén, 1846

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

1846 *Aclis* Lovén, p. 148.

For generic synonymy see Van Dingenen *et al.* (2016, p. 157).

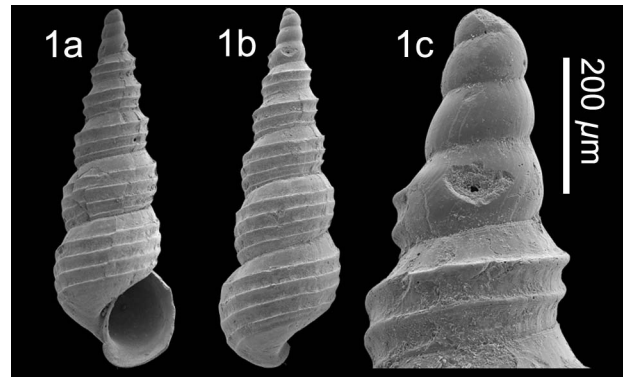
### *Aclis ascaris* (Turton, 1819)

Plate 138, fig. 1

\*1819 *Turbo Ascaris* Turton, p. 217.

2013 *Aclis ascaris* (Turton, 1819) – Landau *et al.*, p. 142, pl. 20, fig. 11 (*cum syn.*).

**Material and dimensions** – Maximum height 2.6 mm, width 1.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0314 (1), NHMW 2016/0103/0315 (50+), RGM.1347941 (1), RGM.1348037 (39). **Sceaux-d'Anjou**: NHMW 2016/0103/0316 (1), RGM.1348888 (2). **Renau-leau**: NHMW 2016/0103/0315 (8), LC (2). **Beugnon**: RGM.1348473 (3).



**Plate 138.** *Aclis ascaris* (Turton, 1819); 1. NHMW 2016/0103/0314, height 2.5 mm, width 895  $\mu\text{m}$ ; 1c, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

**Discussion** – The tall multispiral protoconch, well preserved in the specimen illustrated from St-Clément-de-la-Place (Pl. 138, fig. 1c), is similar to that illustrated from present-day shells by Giannuzzi-Savelli *et al.* (1999, fig. 104). Two similar European species of *Aclis* with spiral cords are known, *A. minor* (Brown, 1827) and *A. ascaris* (Turton, 1819). Most specimens of *Aclis ascaris* are smaller than *A. minor* (3 mm vs. 7 mm), with a broader, flattened subsutural ramp as opposed to evenly convex whorls as seen in *A. minor*, and the umbilicus is reduced to a narrow slit in *A. ascaris*. These characters are well illustrated in the figured specimen. The extant European species *A. trilineata* Watson, 1897 (= *Pherusa carinata* Chaster, 1896, non *Aclis carinata* Smith, 1871 = *Aclis verduini* Van Aartsen, Menkhorst & Gittenberger, 1984) from the Alboran Sea also has spiral sculpture, but is immediately distinguished by its paucispiral protoconch. *Aclis pacaudi* Van Dingenen, Ceulemans & Landau, 2016 from the lower Pliocene Assemblage III locality of Le Pigeon Blanc differs from all its spirally sculptured European congeners discussed above in having a more slender shell and in having more numerous but less elevated cords, which appear only on the later teleoconch whorls. All the other species have the cords appearing at the protoconch/teleoconch boundary.

**Distribution** – Middle Miocene: Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: North Sea Basin (Wood, 1848). Upper Pliocene: North Sea Basin (Marquet, 1997b, 1998); central Mediterranean (Sosso & Dell'Angelo, 2010). Recent: Scandinavia to the Mediterranean (Giannuzzi-Savelli *et al.*, 1999).

Genus *Eulima* Risso, 1826

**Type species** (by subsequent designation, Herrmannsen,

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

1826 *Eulima* Risso, p. 123.

For generic synonymy see Van Dingenen *et al.* (2016, p. 158).

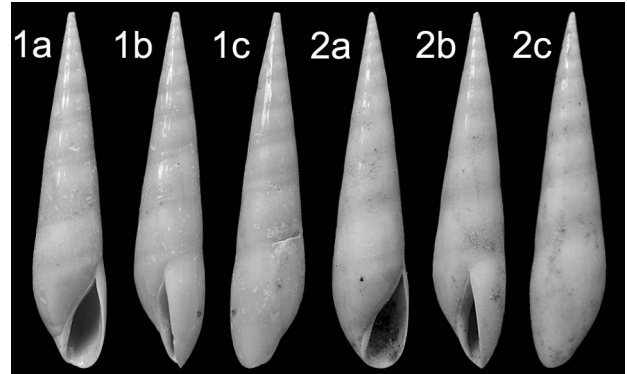
***Eulima taurinensis* (Sacco, 1892)**

Plate 139, figs 1-2

- \*1892 *Subularia subulata* var. *taurinensis* Sacco, p. 596, pl. 1, fig. 21.
- 1938 *Eulima (Subularia) taurinensis* Sacco – Peyrot, 1938.
- 1964 *Leiostraca taurinensis* Sacco, 1892 – Brébion, p. 270.
- 1984 *Sulcosubularia taurinensis* Sacco, 1892 – Ferrero Mortara *et al.*, pl. 9, fig. 7.

**Material and dimensions** – Maximum height 10.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0592-0595 (4), NHMW 2016/0103/0596 (25), RGM.1347943 (2 + 6 fragments), RGM.1348318 (8), LC (12), FVD (17). **Sceaux-d’Anjou:** NHMW 2016/0103/0695 (35), RGM.1347970 (1 fragment), RGM.1348516 (2), RGM.1348642 (2), RGM.1348880 (7), LC (1). **Renauleau:** NHMW 2016/0103/0609 (17), LC (12), FVD (9). **Beugnon:** RGM.1348474 (3), LC (1).

**Discussion** – Pending an in-depth review of the European Neogene Eulimidae we follow Glibert (1949, p. 175) and Brébion (1964, p. 270) in calling these middle and upper Miocene Atlantic forms *Eulima taurinensis* (Sacco, 1892). It is far from clear if they are indeed conspecific with the type from the lower Miocene of the Turin Hills, as the holotype illustrated by Ferrero Mortara *et al.* (1984, pl. 9, fig. 7) is poorly preserved. Nevertheless, the Assemblage I specimens are all small, hardly exceeding 10 mm in height, slightly less than the maximum height for the middle Miocene Loire Basin specimens (maximum 12 mm; Glibert, 1949, p. 176). The spire angle is 17.4-18.6°, slightly wider than the 15° mentioned by Glibert. Peyrot (1938) also noted when comparing the middle Miocene specimens to the present-day *E. subulata* (Donovan, 1804) [= *E. glabra* (Da Costa, 1778)] that the Miocene shells were more slender, the suture was more oblique and that the aperture was less regularly ovate and more oblique in profile. According to Fretter & Graham (1982, p. 412) the maximum size for *E. glabra* is 10 mm, similar to the Assemblage I shells and the apical angle is 20-22° (although it can vary from 17-23°). The other differences mentioned by Peyrot (1938) are difficult to interpret. Warén (1984) highlighted the importance of protoconch type. Unfortunately, despite several attempts at SEM, none of the protoconchs are well preserved. We can, however, be fairly certain that this is not the same species as that illustrated by Van Dingenen *et al.* (2016, pl. 13, fig. 10) from the upper Pliocene Assemblage III locality of Le Pigeon Blanc



**Plate 139.** *Eulima taurinensis* (Sacco, 1892); 1. NHMW 2016/0103/0592, height 8.9 mm, width 1.0 mm; 2. NHMW 2016/0103/0593, height 8.8 mm, width 940  $\mu$ m. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

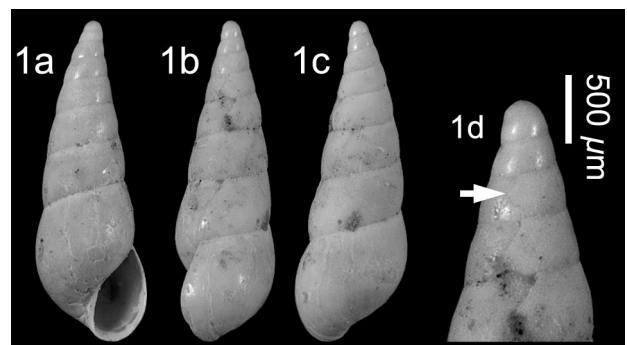
as *Eulima* sp. That species is unusually large (up to 20.6 mm) and slender (apical angle of about 17-18°) and has almost flat-sided spire whorls and an elongate aperture. Brébion (1964, p. 270) recorded this species from Assemblage I, II, and IV. We can confirm the Assemblage I records (Thorigné, Les Pierres Blanches, Renauleau, Sceaux-d’Anjou, St-Clément-de-la-Place, St-Michel, Beau-lieu), but exclude the other records until they have been confirmed.

**Distribution** – Lower Miocene: Proto-Mediterranean (Sacco, 1892). Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

***Eulima* (s.l.) sp.**

Plate 140, fig. 1

**Material and dimensions** – Maximum height 5.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1599 (1), NHMW 2016/0103/1560 (1). **Renauleau:** NHMW 2016/0103/1619 (3).



**Plate 140.** *Eulima* (s.l.) sp.; 1. NHMW 2016/0103/1599, height 5.3 mm, width 1.9 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Discussion** – A few specimens belong to a small ‘*Eulima*’ species with a relatively blunt, smooth multispiral protoconch of about three whorls, the teleoconch whorls are weakly convex, not particularly elevated, the aperture is of moderate size and the outer lip is convex in profile and lacks an abapical notch. We hesitate to go further than to say these characters do not match any of the European extant species.

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

Genus *Vitreolina* Monterosato, 1884

**Type species** (by subsequent designation, Crosse, 1885) – *Eulima incurva* Bucquoy, Dautzenberg & Dollfus, 1883, present-day, Mediterranean.

1884b *Vitreolina* Monterosato, p. 100.

***Vitreolina* cf. *subbrevis* (d’Orbigny, 1852)**

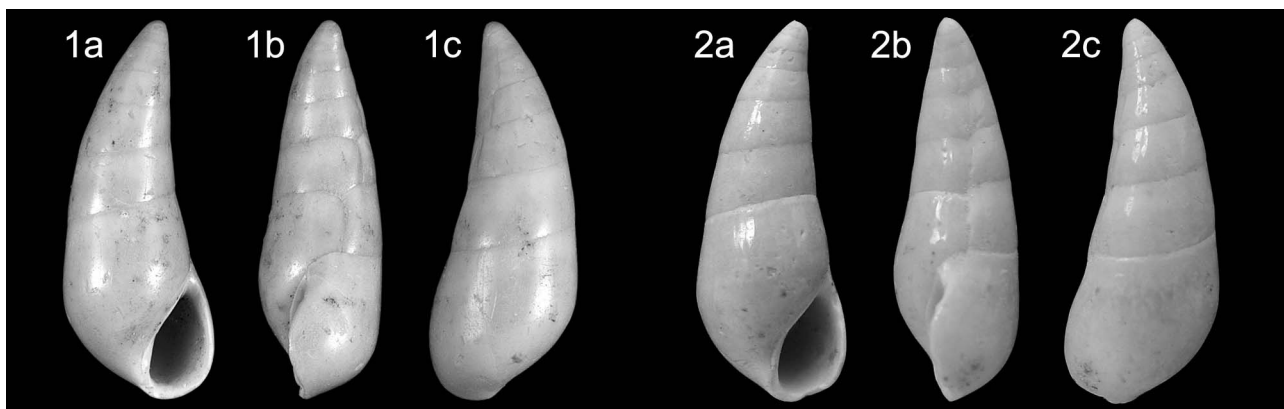
Plate 141, figs 1-2

- cf. \*1852 *Eulima subbrevis* d’Orbigny, 1852.  
 ?non1892 *Eulima polita* var. *subbrevis* (d’Orb.) – Sacco, p. 586, pl. 1, fig. 4.  
 1917 *Eulima (Vitreolina) subbrevis* d’Orbigny – Cossmann & Peyrot, p. 271, pl. 8, figs 44-47.  
 1949 *Melanella (Balcis) subbrevis* Orbigny, 1852 – Glibert, p. 177, pl. 12, fig. 1.  
 1964 *Melanella (Balcis) subbrevis* d’Orbigny, 1852 – Brébion (*partim*), p. 278.  
 ?non1984 *Eulima polita* var. *subbrevis* d’Orbigny, 1852 – Ferrero Mortara *et al.*, p. 586, pl. 9, fig. 1.

**Material and dimensions** – Maximum height 5.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0586 (1), NHMW 2016/0103/0601 (1), NHMW 2016/0103/0587 (18). **Sceaux-d’Anjou**: NHMW 2016/0103/0611 (10), RGM.1348520 (1), RGM.1348643 (6).

**Discussion** – The European fossil Eulimidae are in need of specialist review. Lozouet *et al.* (2001, p. 53) noted that *Eulima subbrevis* d’Orbigny, 1852 was described based on Italian Pliocene material. The poor figure given by Sacco (1892, pl. 1, fig. 2) is of little help, but the specimen was refigured by Ferrero Mortara *et al.* (1984, pl. 9, fig. 1). We doubt that the Assemblage I specimens are conspecific with those of Italy, but we are fairly certain they are the same species as that discussed by Cossmann & Peyrot (1917), Glibert (1949) and Brébion (1964). On the other hand, the lower Miocene shell from the Aquitaine Basin illustrated by Lozouet *et al.* (2001, pl. 19, fig. 9) as *Melanella* cf. *subbrevis* seems to have a more slender apex than what we understand here as *Vitreolina subbrevis* (d’Orbigny, 1852). Lozouet (1986, p. 338) argued for placement in the genus *Amamibalcis* Kuroda & Habe, 1950, a genus with a Japanese type species, later doubted by Lozouet *et al.* (2001a, p. 53). According to Warén (1984, p. 29, figs 25, 26) species of the genus *Amamibalcis* have indistinct but rather coarsely striated shells, which is not seen in the French specimens. Moreover, we note that according to Warén’s figure, whilst *Amamibalcis* also has a *Vitreolina*-type scar that resembles an uneven sinusoidal curve that dips at the false suture, the scars are randomly placed on successive whorls, whereas in the *Vitreolina* species we have observed the scars are either aligned or wind around the shell symmetrically (Bouchet & Warén, 1986, figs 1032, 1033).

As we understand this species, *V. subbrevis* (d’Orbigny, 1852) is characterised by its stocky, regularly curved shell with a relatively blunt apex. The incremental scars are prominent and markedly staggered in an anticlockwise direction from the last whorl adapically. The outer lip is weakly sinuous in side view, with the apex placed mid-whorl. Several European extant *Vitreolina* species were figured by Giannuzzi-Savelli *et al.* (1999, figs 297-322), of which the most similar are *V. incurva* (Bucquoy, Dautzenberg & Dollfus, 1883) and *V. philippi* (de Rayneval & Ponzi, 1854), both of which differs in having a relatively broader last whorl, a taller spire and a more pointed apex. Brébion (1964, p. 279) recorded this species from numerous Assemblage I localities (Renauleau, Sceaux-d’Anjou, Thorigné, Chalonnès, Lillion, St-Clément-de-la-Place,



**Plate 141.** *Vitreolina* cf. *subbrevis* (d’Orbigny, 1852); 1. NHMW 2016/0103/0585, height 5.5 mm, width 2.2 mm; 2. NHMW 2016/0103/0601, height 5.5 mm, width 2.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Les Pierres Blanches, Thorigné, Beaulieu) and Assemblage II (Apigné). He also recorded it from Assemblage III, but despite extensive collecting this species was not recorded by Van Dingenen *et al.* (2016), and therefore Assemblage III is excluded from the distribution.

**Distribution** – Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1917), Loire Basin (Glibert, 1949). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964).

***Vitreolina* sp.**

Plate 142, figs 1-3

**Material and dimensions** – Maximum height 10.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0602-604 (3), NHMW 2016/0103/0605 (6), RGM.1348627 (4), RGM.1348722 (5), LC (2). **Sceaux-d'Anjou:** NHMW 2016/0103/0697 (5), RGM.1347952 (2 incomplete), RGM.1348521 (2), RGM.1348645 (4), LC (1). **Renauleau:** NHMW 2016/0103/1490 (15), LC (3).

**Discussion** – We have placed this species in the genus *Vitreolina* Monterosato, 1884 based on the shell shape, the *Vitreolina*-type scar that resembles an uneven sinusoidal curve that dips at the false suture, and the position of the scars staggered along the right side of the shell. *Vitreolina* sp. differs from *V. subbrevis* (d'Orbigny, 1852) in being larger (maximum height 9.0 mm vs. 5.5 mm), in being taller-spired with more numerous whorls and in having a sharper, more produced and pointed apex. Unfortunately the apices tend to be abraded making the protoconch/teleoconch boundary unclear, but the protoconch of *Vitreolina* sp. is composed of more numerous whorls than that of *V. subbrevis*, which has a blunt apex. *Vitreolina knudseni* Bouchet & Warén, 1986 from the Azores is similar in shape, but has a narrower, longer aperture and a slightly pinched outer lip, not seen in *Vitreolina* sp. *Vitreolina incurva* (Bucquoy, Dautzenberg & Dollfus, 1883) is smaller (maximum height about 3 mm; Giannuzzi-Savelli *et al.*, 1999, p. 106), with fewer spire whorls and a broader apex, but not as broad as in

*V. subbrevis*. *Vitreolina philippi* (de Rayneval & Ponzi, 1854) is again smaller (maximum height about 4.4 mm; Giannuzzi-Savelli *et al.*, 1999, p. 106), but differs most significantly in the position of the apex of the outer lip, which is positioned high, well above mid-lip, accentuating the sinusoid outline of the lip, whereas in *Vitreolina* sp. the apex is at or just below mid-whorl.

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

Genus *Melanella* Bowdich, 1822

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

1822 *Melanella* Bowdich, p. 27.

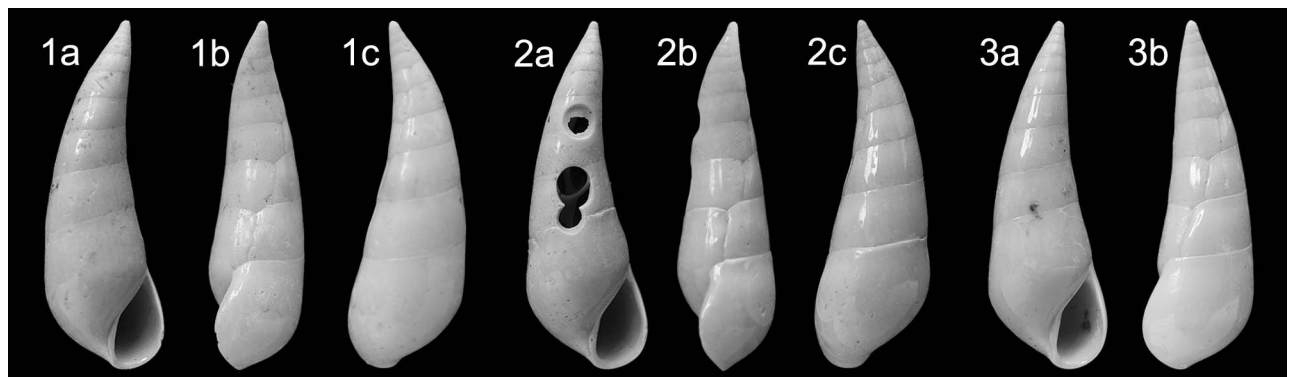
For generic synonymy see Van Dingenen *et al.* (2016, p. 159).

***Melanella alba* (Da Costa, 1778)**

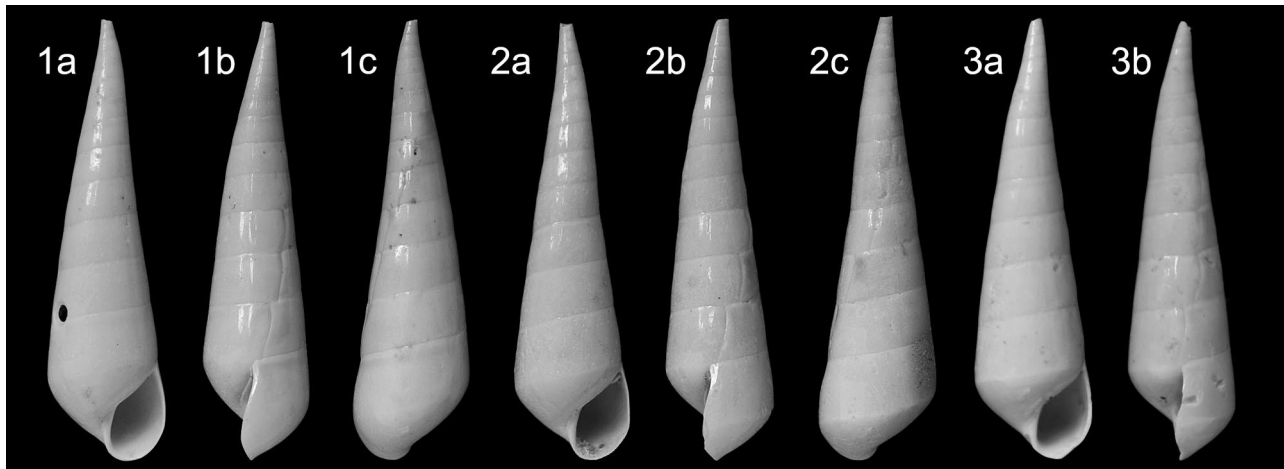
Plate 143, figs 1-3

- \*1778 *Strombiformis albus* Da Costa, p. 116.
- 1964 *Melanella polita* Linné 1776 [sic] – Brébion, p. 273, pl. 7, fig. 3 [*non Melanella polita* (Linnaeus, 1758)].
- 2006 *Melanella alba* (Da Costa, 1778) – Landau *et al.*, p. 62, pl. 19, fig. 1 (*cum syn.*).
- 2016 *Melanella alba* (Da Costa, 1778) – Van Dingenen *et al.*, p. 159, pl. 14, fig. 1.
- 2018 *Melanella alba* (da Costa, 1778) – Menkhorst & Wesselingh, p. 38, fig. 1.

**Material and dimensions** – Maximum height 20.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0597-0598 (1), NHMW 2016/0103/0600 (15), RGM.1348303 (1), RGM.1348317 (50+), RGM.1348720 (33), RGM.1348844 (20), LC (8), FVD (15). **Sceaux-d'Anjou:** NHMW 2016/0103/0696 (25), RGM.1348292 (1), RGM.1348294 (6), RGM.1348335 (5), RGM.1348372 (3), RGM.1348517



**Plate 142.** *Vitreolina* sp.; 1. NHMW 2016/0103/05602, height 9.0 mm, width 3.0 mm; 2. NHMW 2016/0103/0603, height 10.3 mm, width 3.3 mm; 3. NHMW 2016/0103/0604, height 8.4 mm, width 2.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 143.** *Melanella alba* (Da Costa, 1778); 1. NHMW 2016/0103/0597, height 20.2 mm, width 5.1 mm; 2. NHMW 2016/0103/0598, height 18.6 mm, width 4.7 mm; 3. NHMW 2016/0103/0599, height 13.8 mm, width 3.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(12), RGM.1348644 (1), RGM.1348931 (8), LC (5), FVD (16). **Renauleau:** LC (5). **Beugnon:** RGM.1348447 (7), RGM.1348475 (2).

*Discussion* – Warén (1988) discussed the confusion surrounding *Strombiformis albus* Da Costa, 1778 and *Turbo politus* Linnaeus, 1758, with which it has often been confused. *Melanella alba* is characterised by its very fine reticulate mesh sculpture, visible only under magnification and reflected light. The synonymy and distribution include only records in which the presence of this microsculpture has been confirmed. This microsculpture is exceedingly fine in the Assemblage I specimens and only visible under careful examination with reflected light.

Today this is primarily an Atlantic species, rare in the Mediterranean, where it does not reach as large a size as in the Atlantic (Warén, 1988). The shells from the Assemblage I localities are similar in size to the present-day Atlantic population described by Fretter & Graham (1982, p. 416).

Brébion (1964, p. 274) reported this species as *Melanella polita* from many Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches).

*Distribution* – Middle Miocene: NSB, Netherlands (Janssen, 1984). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); NSB, Coralline Crag, England (Harmer, 1920), Kattendijk Formation, Belgium (Marquet, 1998). Upper Pliocene: NSB, Red Crag, England (Harmer, 1920), Atlantic, Mondego Basin, Portugal (Landau *et al.*, 2006); western Mediterranean, Estepona, Spain (Landau *et al.*, 2006). Pliocene (unspecified): North Sea Basin, The Netherlands (Van Regteren Altena *et al.*, 1955; Menkhorst & Wesselingh, 2018). Pleistocene: Atlantic, St Erth, England (Harmer, 1920). Present-day: Atlantic, from Norway and into the Mediterranean (Fretter & Graham, 1982). Ectoparasite on the holothurian

*Neopentadactyla mixta* (Cabiocch *et al.*, 1978).

#### *Melanella* sp. 1

Plate 144, figs 1-3

1964 *Melanella* cf. *similis* d'Orbigny, 1852 – Brébion, p. 276, pl. 7, fig. 5.

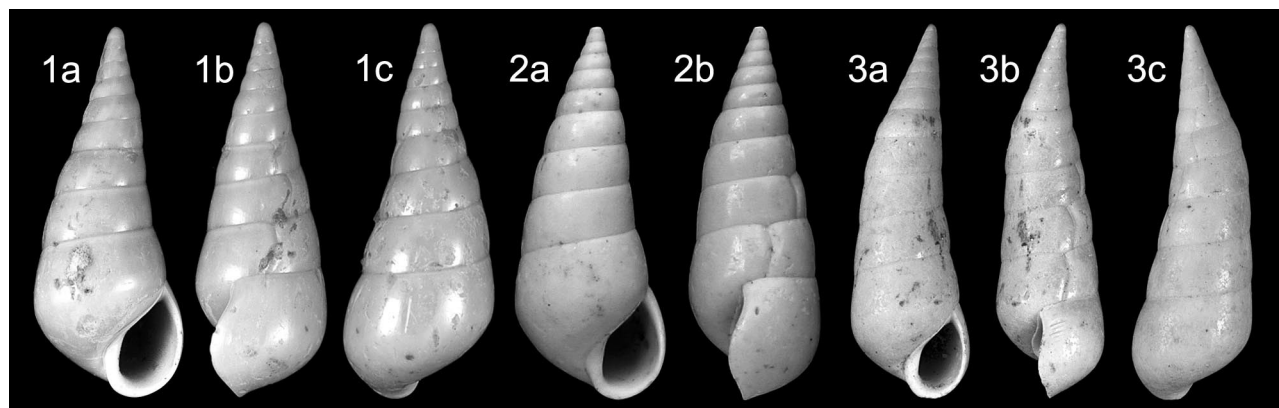
*Material and dimensions* – Maximum height 8.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0588-0590 (3), NHMW 2016/0103/0591 (30), RGM.1348721 (4). **Sceaux-d'Anjou:** NHMW 2016/0103/0610 (16), RGM.1348295 (1), RGM.1348646 (8).

*Discussion* – *Melanella* sp. 1 is characterised by its irregularly twisted spire, its unusually convex whorls for the genus and its low spire whorls, separated by a weakly oblique suture. In most specimens the incremental growth scars on the last three teleoconch whorls are staggered, above this their position is irregular. The outer lip is sinuoid in side view, with the apex of the lip just below mid-whorl. There is some degree of variability in the inflation of the later spire whorls, as shown by the series illustrated (Pl. 144, figs 1-3) and the convexity of the spire whorls. The most similar European species is the extant Mediterranean species *M. boscii* (Payraudeau 1826), which also has convex spire whorls (Giannuzzi-Savelli *et al.*, 1999, figs 264-266), but in this species the spire seems a little more scalate, the whorls less convex and in the syntype (MNHN-IM-2000-5641; <http://coldb.mnhn.fr/catalognumber/mnhn/im/2000-5641>) the position of the scars seems to be random on all whorls.

Brébion (1964, p. 276) recorded this species from the Assemblage I locality of St-Clément-de-la-Place, to which we add Sceaux-d'Anjou.

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





**Plate 144.** *Melanella* sp. 1; 1. NHMW 2016/0103/0588, height 6.3 mm, diameter 1.7 mm; 2. NHMW 2016/0103/0589, height 7.1 mm, diameter 2.0 mm 1. NHMW 2016/0103/0590, height 8.5 mm, diameter 1.8 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

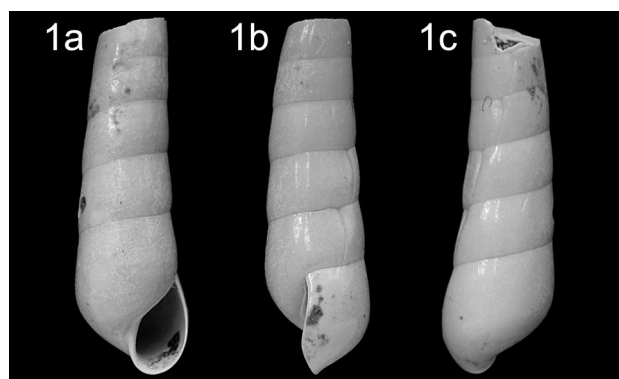
***Melanella* sp. 2**

Plate 145, fig. 1

*Material and dimensions* – Height 20.1 mm (incomplete).  
**St-Clément-de-la-Place:** NHMW 2016/0103/0606 (1).

*Discussion* – The most striking feature of this species is its size. The fragment at hand suggests a reconstructed shell height of about 30 mm. This is larger than usual for the family and far larger than any other eulimid in the Assemblage. The spire seems to have been exceedingly tall, as the rate of growth of the whorls preserved is low. The spire whorls are tall, weakly convex and slightly inflated abapically, forming the whorl periphery. The incremental scars winding up the shell on the right hand side are strongly staggered. The aperture is medium-sized for the group and the outer lip is weakly sinusoid with the apex placed below mid-aperture. We can find no other European eulimid to compare to this species.

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



**Plate 145.** *Melanella* sp. 2; 1. NHMW 2016/0103/0606, height 20.1 mm, diameter 6.3 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

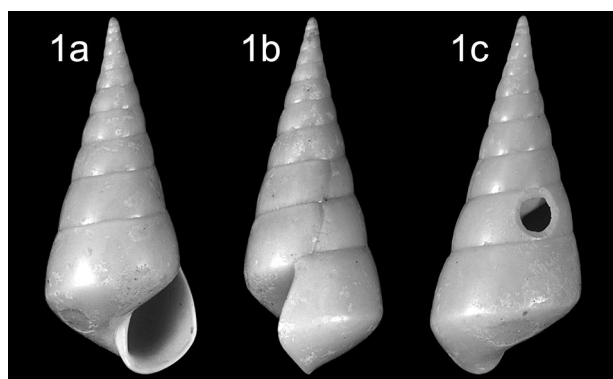
***Melanella* sp. 3**

Plate 146, fig. 1

1964 *Melanella conjugens* Sacco, 1892 – Brébion, p. 275, pl. 7, fig. 4 (?Sacco, 1892).

*Material and dimensions* – Height 7.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0607 (1), NHMW 2016/0103/0608 (4). **Sceaux-d'Anjou:** RGM.1348371 (1).

*Discussion* – *Melanella* sp. 3 is characterised by its coeloconoid spire profile, relatively pointed apex and convex spire whorls. The incremental growth scars on the right side of the shell wind continuously up the shell. The last whorl is broad for the genus, indeed the last whorls resemble those of a *Niso* species, but there is no basal perforation. This is probably the same species as illustrated by Brébion (1964, pl. 7, fig. 4) as *Melanella conjugens* Sacco, 1892, in which case he recorded this species from the Assemblage I localities of Sceaux-d'Anjou and St-Michel, to which we add St-Clément-de-la-Place. Sacco's type specimens from the Pliocene of Astigiana, Italy has not been reillustrated since it was originally described



**Plate 146.** *Melanella* sp. 3; 1. NHMW 2016/0103/0607, height 6.2 mm, diameter 2.6 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

and we have not seen any specimens of this Italian species. They seem to share a similar shell profile, however the original figure is small and does not give much detail. We are therefore unable to confirm whether they are conspecific and prefer not to include Sacco's reference in the chresonymy and distribution.

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

Superorder Latrogastropoda  
Superfamily Calyptraeoidea Lamarck, 1809  
Family Calyptraeidae Lamarck, 1809  
Genus *Calyptrea* Lamarck, 1799

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

1799 *Calyptrea* Lamarck, p. 78.

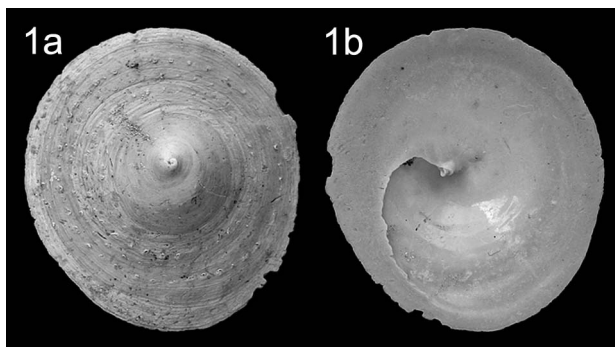
For generic synonymy see Van Dingenen *et al.* (2016, p. 121).

***Calyptrea chinensis* (Linnaeus, 1758)**

Plate 147, fig. 1

- \*1758 *Patella chinensis* Linnaeus, p. 1257.
- 1854 *Caliptraea* [sic] *Mamillaris* Millet, p. 165.
- 1864 *Caliptraea* [sic] *mamillaris* Millet, p. 680 (*non* Broderip, 1834).
- 1964 *Calyptrea chinensis* Linné, 1766 [sic] – Brébion, p. 313.
- 2013 *Calyptrea chinensis* (Linnaeus, 1758) – Landau *et al.*, p. 95, pl. 9, fig. 7, pl. 61, fig. 6 (*cum syn.*).
- 2016 *Calyptrea chinensis* (Linnaeus, 1758) – Van Dingenen *et al.*, p. 121, pl. 4, fig. 1.

*Material and dimensions* – Maximum height 3.0 mm, diameter 14.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0552 (1), NHMW 2016/0103/0553 (4), RGM.1347921 (8 fragments), RGM.1347926 (50+), RGM.



**Plate 147.** *Calyptrea chinensis* (Linnaeus, 1758); 1. NHMW 2016/0103/0552, height 3.0 mm, diameter 14.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1348031 (50+), RGM.1348829 (4 juveniles), FVD (1). **Sceaux-d'Anjou**: NHMW 2016/0103/0554 (1), RGM.1347927 (8 fragments and juveniles), RGM.1347930 (13), RGM.1347947 (37), RGM.1347955 (9), RGM.1347983 (6). **Renauleau**: NHMW 2016/0103/1406 (1), LC (12 + 4 juveniles), FVD (7). **Beugnon**: RGM.1348404 (1 + 1 juvenile), RGM.1348405 (5 + 1 juvenile), RGM.1348406 (1 juvenile), RGM.1348407 (1).

*Discussion* – This species is extremely variable in both sculpture and profile, although most specimens are relatively constant within a population. The specimens from St-Clément-de-la-Place are small and very flat, only the centre slightly mammillate, with finely squamous surface sculpture. The specimens from Sceaux-d'Anjou are also small, but more conical and elevated.

Brébion (1964, p. 315) recorded this species from Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu), Assemblage III localities (Le Pigeon Blanc, Le Girondor, La Gauvinière, Palluau, La Dixmérie) and Assemblage IV localities (St-Jean-la-Poterie, Gourbesville, Le Bosq d'Aubigny).

*Distribution* – Lower Miocene: Paratethys (Aquitanian): Vienna Basin, Austria (Schaffer, 1912); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: NSB (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964), Netherlands (Janssen, 1984). Middle Miocene: Atlantic (Langhian-Serravallian): Aquitaine Basin, France, (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1923; Bałuk, 1975), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966), Ukraine (Zelinskaya *et al.*, 1968), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Burdigalian-Langhian): northeastern Spain (Solsona, 1998), (Serravallian): Karaman Basin, Turkey (Fischer, 1866; Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), Cacela Basin, Portugal (Glibert, 1963); Proto-Mediterranean Sea (Tortonian and Messinian): Italy (Sacco, 1896b; Venzo & Pelosio, 1963). Lower Pliocene: NSB, Coralline Crag, England (Wood, 1848; Harmer, 1916), Belgium (Glibert, 1958; Marquet, 1998); Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al.*, 2011) Morocco (Lecointre, 1952); northeastern Spain (Martinell, 1979), Roussillon Basin, France (Fontannes, 1879); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967; Caprotti, 1974), Tunisia (Fekih, 1975). Upper Pliocene: NSB, Red Crag, England (Wood, 1848; Harmer, 1916), Belgium (Glibert, 1958; Marquet, 1998); Atlantic, Pombal Basin, Portugal (Silva, 2001), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a); central Mediterranean, Italy (Malatesta, 1974; Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Brébion, 1964). Pleistocene: Atlantic, British

Isles (Glibert, 1963), Morocco (Lecointre, 1952); central Mediterranean, Italy (Cerulli-Irelli, 1912; Taviani *et al.*, 1998), Sicily (Glibert, 1963). Present-day: northeastern Atlantic, British Isles to Zaire, Madeira and Canaries, Mediterranean, Black Sea (Poppe & Goto, 1991).

Genus *Crepidula* Lamarck, 1799

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

1799 *Crepidula* Lamarck, p. 78.

For generic synonymy see Van Dingenen *et al.* (2016, p. 121).

### *Crepidula gibbosa* DeFrance, 1818

Plate 148, fig. 1

- \*1818 *Crepidula gibbosa* DeFrance, p. 397.
- 1854 *Crepidula Mutabilis* Millet (*pars*), p. 166 (*nomen nudum*).
- 1865 *Crepidula mutabilis* Millet (*pars*), p. 598.
- 1964 *Crepidula gibbosa* DeFrance, 1818 – Brébion, p. 316.
- 2013 *Crepidula gibbosa* DeFrance, 1818 – Landau *et al.*, p. 96, pl. 9, figs 8, 9 (*cum syn.*).
- 2016 *Crepidula gibbosa* DeFrance, 1818 – Van Dingenen *et al.*, p. 121, pl. 4, fig. 2 (*cum syn.*).

*Material and dimensions* – Maximum length 12.3 mm, width 7.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1758 (1). **Sceaux-d’Anjou**: NHMW 2016/0103/1683 (1), RGM.1347950 (5), RGM.1347971 (1), RGM.1347982 (2). **Renaleau**: LC (4).

*Discussion* – *Crepidula gibbosa*, DeFrance, 1818 has a more elevated, convex dorsum than *C. unguiformis*, which usually has a concave dorsum. Moreover, *C. gibbosa* has a straight septum and lacks the central depression seen in *C. unguiformis*. For further discussion see Landau *et al.* (2004a, p. 72).



**Plate 148.** *Crepidula gibbosa* DeFrance, 1818; 1. NHMW 2016/0103/1683, length 12.3 mm, width 7.3 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

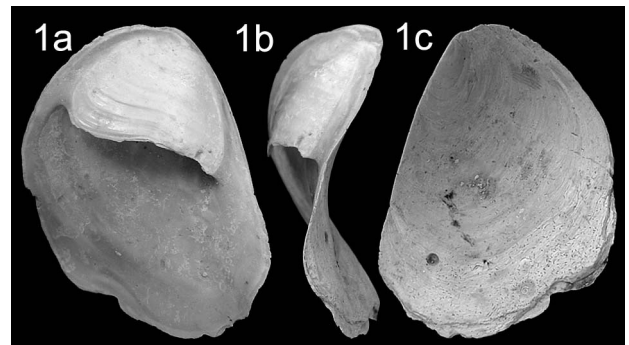
Brébion (1964, p. 316) recorded this species from numerous Assemblage I localities (Renaleau, Sceaux-d’Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Beaulieu) and Assemblage IV (Bosq-d’Aubigny), we record it from Assemblage III (Le Pigeon Blanc).

*Distribution* – Middle Miocene: Atlantic: (Langhian and Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964); Proto-Mediterranean Sea, Po valley, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al.*, 2011). Lower upper Pliocene: Atlantic, Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a); central Mediterranean, Italy (Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: NW France (Glibert, 1963). Present-day: Mediterranean, below low tide line, often on other molluscs (Poppe & Goto, 1991).

### *Crepidula unguiformis* Lamarck, 1822

Plate 149, fig. 1

- \*1822 *Crepidula unguiformis* Lamarck, p. 25.
- 1854 *Crepidula Mutabilis* Millet (*pars*), p. 166 (*nomen nudum*).
- 1865 *Crepidula mutabilis* Millet (*pars*), p. 598.
- 1964 *Crepidula (Janacus) crepidula* Linné 1766 [*sic*] – Brébion, p. 317.
- 2004a *Crepidula unguiformis* Lamarck, 1822 – Landau *et al.*, p. 73, pl. 15, fig. 5 (*cum syn.*).
- 2011 *Crepidula unguiformis* Lamarck, 1822 – Landau *et al.*, p. 15, pl. 4, fig. 13 (*cum syn.*).
- 2013 *Crepidula unguiformis* Lamarck, 1822 – Landau *et al.*, p. 96, pl. 9, fig. 10 (*cum syn.*).
- 2016 *Crepidula unguiformis* Lamarck, 1822 – Van Dingenen *et al.*, p. 122, pl. 4, fig. 3.



**Plate 149.** *Crepidula unguiformis* Lamarck, 1822; 1. NHMW 2016/0103/0560, height 7.2 mm, diameter 27.6 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



*Material and dimensions* – Maximum height 7.2 mm, diameter 38.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0560 (1), NHMW 2016/0103/0561 (18). **Sceaux-d’Anjou**: NHMW 2016/0103/0644 (5), RGM.1347920 (11), RGM.1347951 (17), RGM.1347957 (5). **Renauleau**: LC (8), FVD (5). **Beugnon**: RGM.1348402 (2 juveniles), RGM.1348403 (1 juvenile).

*Discussion* – *Crepidula unguiformis* Lamarck, 1822 is often found inside the aperture of other shells that were occupied by hermit crabs. Its shape is therefore very variable, determined by the substrate. Some specimens develop a corrugated shell, following the contour of internal lirae, if present inside the aperture of their host shell. The specimens from St-Clément-de-la-Place are all smooth and strongly concave. For further discussion see Landau *et al.*, (2004a, p. 73).

Brébion (1964, p. 317) recorded this species from Assemblage I localities (Sceaux-d’Anjou, Thorigné, St-Michel), Assemblage III (Le Pigeon Blanc, Palluau) and Assemblage IV (Bosq-d’Aubigny).

*Distribution* – Lower Miocene: Atlantic (Aquitainian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1919). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Anderson, 1964), Netherlands (Janssen, 1984). Middle Miocene: northeastern Atlantic (Langhian and Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Bałuk, 1975), Hungary (Strausz, 1966); Proto-Mediterranean Sea, northeastern Spain (Solsona, 1998); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), (Tortonian): Cabela Basin, Portugal (NHMW collection); Proto-Mediterranean Sea, Po valley, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016), Guadalquivir Basin, Spain (González-Delgado, 1988; Landau *et al.*, 2011); western Mediterranean, Roussillon Basin, France (Fontannes, 1879), northeastern Spain (Solsona, 1998); central Mediterranean, Italy (Sacco, 1896b; Palla, 1967), Tunisia (Fekih, 1975). Lower-upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Zbyszewski, 1959; Silva, 2001), Morocco (Lecointre, 1952); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2004a), central Mediterranean, Italy (Sacco, 1896b; Chirli, 1988; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Lower-upper Pleistocene: central Mediterranean, Sicily (Glibert, 1963). Present-day: Mediterranean, below low tide line to 100 m depth, often on other molluscs (Pope & Goto, 1991).

Superfamily Cypraeoidea Rafinesque, 1815

Family Cypraeidae Rafinesque, 1815

Subfamily Pustulariinae Gill, 1871

Tribe Zonariini Schilder, 1932

Genus *Schilderia* Tomlin, 1930

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

1930 *Schilderia* Tomlin, p. 24.

For generic synonymy see Van Dingenen *et al.* (2016, p. 126).

*Note* – The genus *Schilderia* Tomlin, 1930 is one of the few ‘Redonian’ gastropod groups that has received attention recently, albeit as a sideline, in a paper concentrating on the Cypraeidae and Ovulidae of the Oligocene and lower Miocene of south-western France (Dolin & Lozouet, 2004). This genus represents an important and easily recognisable component of the Assemblage I fauna, being plentiful in some of the deposits like Renauleau, from which we have hundreds of specimens. *Schilderia* survived into the lower Pliocene Assemblage III (*i.e.* at the Le Pigeon Blanc deposits), but is represented by rare fragments (Van Dingenen *et al.*, 2016, p. 126).

Dolin & Lozouet (2004) described five species from the ‘Messinian’ of Brigné, which we interpret here as Renauleau (Brigné includes the localities of Renauleau and Beugnon, but cypraeids are exceedingly uncommon at Beugnon; see Geological setting). We have tabulated a resumé of the distinguishing shell characters, according to these authors (Table 6).

We note that Dolin & Lozouet (2004) base all the species, except *S. laurietae* on a relatively small number of specimens and that no information on interspecific variability was given. We are therefore led to deduce that the number of fossular, labial and columellar denticles was considered species-specific and constant. Therefore, these authors suggest a scenario in which we had five small-shelled *Schilderia* species coexisting, which can be separated based on precise and invariable shell characters.

Cypraeid taxonomy is notoriously difficult and the argument between ‘lumpers’ and ‘splitters’ will continue. However, the phrasing above may reveal the present authors’ scepticism over this scenario. We have extensive cypraeid collecting experience in Europe and elsewhere and have found that the size can vary more than threefold within a population and the shape can be quite different in a single species from a single locality, and may even depend on, as Schilder (1961) noted, for example, where on the reef the animal lived. The number of columellar and labial teeth is rarely constant in a given species, which is why authors such as Schilder (1935, p. 327) developed the normalised tooth count (*i.e.* the number of teeth in a hypothetical shell 25 mm in length).

To better understand the genus, we examined the living representative *Schilderia achatidea* (Gray in G.B. Sowerby I, 1837), which ranges from the northern At-

species no. specimens	size in mm	fossula shape no. denticles	columellar denticles	labial denticles
<i>S. brebioni</i> N = 7	H = 19.6, D = 12.3 lozenge-shaped	small, reduced, spoon-shaped shallow 3 large subobsolete	16 short, delimited by angulation	20 regularly spaced, short, restricted to edge
<i>S. fasciolaria</i> N = 4	H = 28.7, D = 17.6 solid, tapered	hardly developed, weakly concave, smooth 2 large	20 short, delimited by angulation	20 (+3) regularly spaced, restricted to edge
<i>S. incognita</i> N = 3	H = 23.2, D = 14.5 solid, ovate	poorly developed, almost flat, smooth 5 small	13 large, strongly delimited by angulation	18 (+2) irregularly spaced, extending weakly over ½ lip
<i>S. lauriatae</i> N = 18	H = 21.1, D = 13.6 fragile, ovate	weakly concave, spoon-shaped 7 irregular obsolete	16 small, delimited by angulation, forming ridge posteriorly	16 (+3) regularly spaced, extending weakly over lip
<i>S. veronicata</i> N = 1	H = 26.1, D = 16.6 Solid, ficiform	flat and deep 6 small	19 small but thick and elongated, delimited by angulation	18 (+2) strong, regularly spaced, relatively elongated

**Table 6.** Shell characters for *Schilderia* Tomlin, 1930 species from the Assemblage I localities of NW France (based on Dolin & Lozouet, 2004).

lantic coast of Spain to West Africa and into the western Mediterranean (Lorenz & Hubert, 2000). Heiman (2006) looked at the variability in present-day populations and found differences in shell shape and the degree of development of the columellar teeth between different populations. He suggested separating the West African population as a distinct subspecies, a position not supported by Lorenz & Hubert (2000) or Bouchet & Gofas (2011; WoRMS), which brings us back to the different position taken between ‘lumpers’ and ‘splitters’. For the purposes of this paper, the importance is that neither the shape nor the number of columellar teeth is constant in *S. achatidea*. Interestingly, Heiman did not mention the labial teeth, but counting the teeth on numerous specimens and illustrations of *S. achatidea* at hand, it is certainly not constant.

We have over 1000 specimens of *Schilderia* from Renauleau, of which we took morphometric measurements from 333 specimens (all specimens in NHMW coll.). The first inconsistency we encountered between our observations and those made by Dolin & Lozouet (2004) concerns the columellar teeth. In the description of all five of these author’s species the columellar count is given as an absolute number. Of the 333 specimens from Renauleau measured, only in 76 (23%) were the denticles developed along the entire columella. The gradual disappearance of columellar teeth towards the apex is a generic character (Lorenz & Hubert, 2000, p. 107). The second problem was the number of labial teeth. According to Dolin & Lozouet (2004) we should have cohorts with either 16, 18 or 20 denticles. We found that the number of denticles ranged from 15-24. If we take the size of the shell into consideration, *i.e.*, the normalised tooth count (see above), this ranged from 15-23 (Fig. 1).

The third problem was with the shell shape. Dolin & Lozouet (2004) used ‘ficiform’ or ‘lozenge-shaped’ as a sep-

arating character. This could be expressed as globosity [(H/W)/L]. When this is plotted, no obvious groups become apparent (Fig. 2). There was also no grouping when globosity was plotted against the normalised number of columellar teeth (Fig. 3). In general, the smaller specimens are more lozenge-shaped and the larger ones more ficiform, but specimens can be aligned from small lozenge-shaped to large ficiform with numerous intermediates.

The shape of the fossula, and the presence or absence of denticles on the inner edge, was also examined in the Renauleau specimens. The fossula is relatively shallow to almost flat and invariably poorly delimited with a variable number of denticles developed at the inner edge, and although we could find specimens that matched the descriptions of the five species described by Dolin & Lozouet (2004), not only in these characters by also shape and dentition, there were also many intermediates.

One observation we can make, is that all specimens in which colour is preserved, which is about 10%, have a dorsal blotch placed on the left side of the mid-line and a spire blotch, regardless of any other shell characters.

Dolin & Lozouet (2004, p. 44) discussed a sixth species from the ‘Redonian’ assemblages, *Cypraea andegavensis* Defrance, 1826 and noted that the type was lost and designated a neotype from La Presselière, Sceaux-d’Anjou. We also have material at hand from this locality. These specimens are all relatively small and lozenge-shaped, with a relatively greater number of teeth than average for the Renauleau population, but these parameters overlap with those from Renauleau (see Figs. 1-3). The most important difference between the shells from Sceaux-d’Anjou and those from Renauleau is that the former have a thickened marginal callus distorting the posterior periphery on the right side when the shell is viewed from the ventral aspect. This character is not seen in any of the

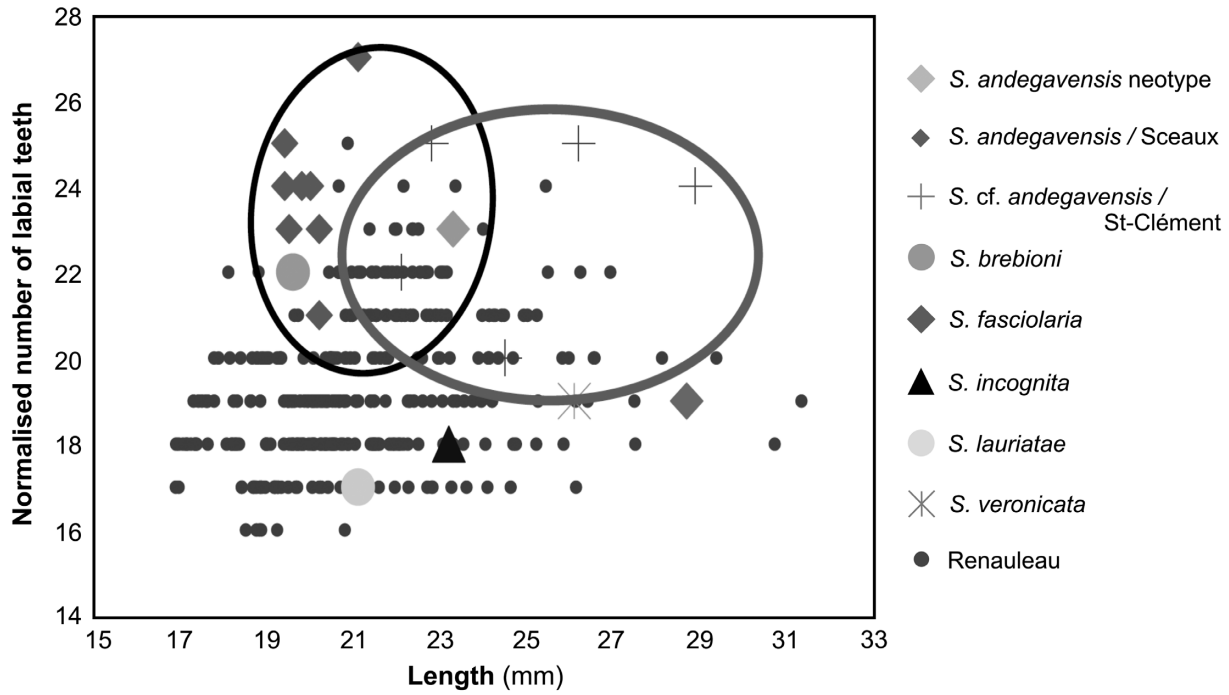


Figure 1. *Schilderia* from Assemblage 1; Normalised number of labial teeth / length.

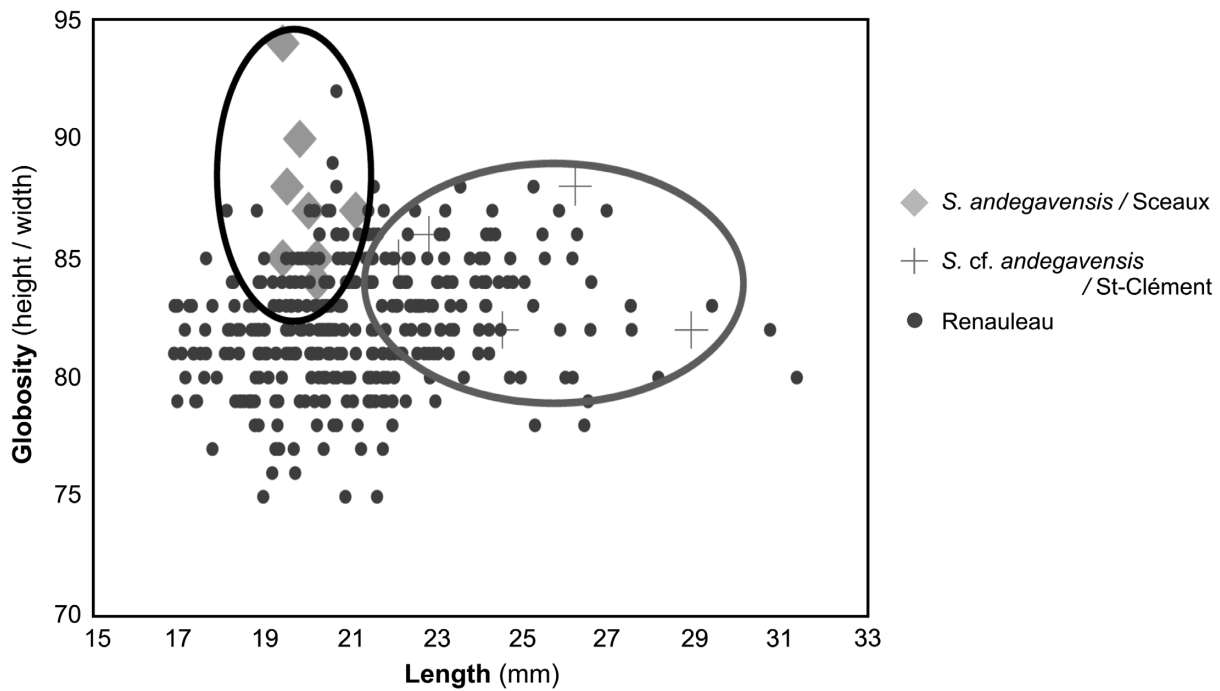


Figure 2. *Schilderia* from Assemblage 1; globosity (height/width)/length.

1000+ specimens from Renauleau.

A smaller number of specimens at hand from St-Clément-de-la-Place have a right posterior marginal callus equal or even more strongly developed than that seen in specimens from Sceaux-d'Anjou. However, we are unsure if these are conspecific with those from Sceaux-d'Anjou, as they differ in being larger and more pyriform (see Figs. 2). This questions whether this callus growth is a specific

or environmental factor.

In summary, we are unsure how many *Schilderia* species occur in the Assemblage I deposits, or which shell characters could be used to separate them. We also find it unlikely that five congeners with such similar shell characters coexisted in one habitat. We provisionally accept the name *S. andegavensis* for the Sceaux-d'Anjou specimens, separated mainly by the presence of a right



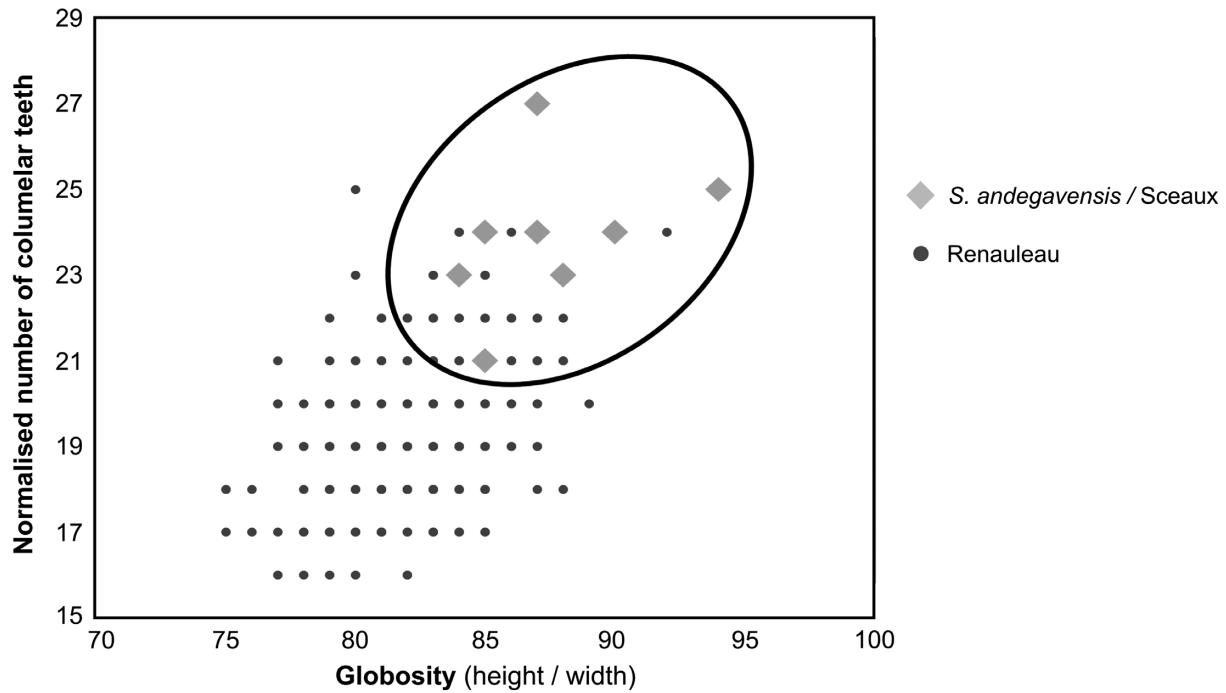


Figure 3. *Schilderia* from Assemblage 1; globosity (height/width)/normalised number columellar teeth.

posterior marginal callus. We consider the St-Clément-de-la-Place specimens to be *S. cf. andegavensis* based on the presence of a right posterior marginal callus, but highlight the difference in size and shape. Thirdly, we cannot reliably separate the Renauleau specimens into five species as suggested by Dolin & Lozouet (2004) and provisionally consider them to be a single species for which, as first revisers we chose the name *S. brebioni* Dolin & Lozouet, 2004 (ICZN, 1999, Art. 24.2.1).

***Schilderia andegavensis* (Defrance, 1826)**  
Plate 150, figs 1-2

- \*1826 *Cypraea andegavensis* Defrance, p. 37.
- 1938 *Cypraea (Ajusta) andegavensis* Defrance – Peyrot, p. 167, pl. 3, figs 25, 26.
- 1964 *Schilderia andegavensis* Defrance, 1826 – Brébion (*partim*), p. 332, pl. 7, fig. 27.
- 2004 *Schilderia andegavensis* (Defrance, 1826) – Dolin & Lozouet, p. 44, pl. 19, figs 3, 4.

*Material and dimensions* – Maximum length 26.8 mm, width 18.3. **Sceaux-d’Anjou:** NHMW 2016/0103/1638-1639 (2), NHMW 2016/0103/1640 (12), RGM.1348059 (4 + 6 fragments), RGM.1348064 (26), RGM.1348087 (5), RGM.1348198 (2), LC (3), FVD (20).

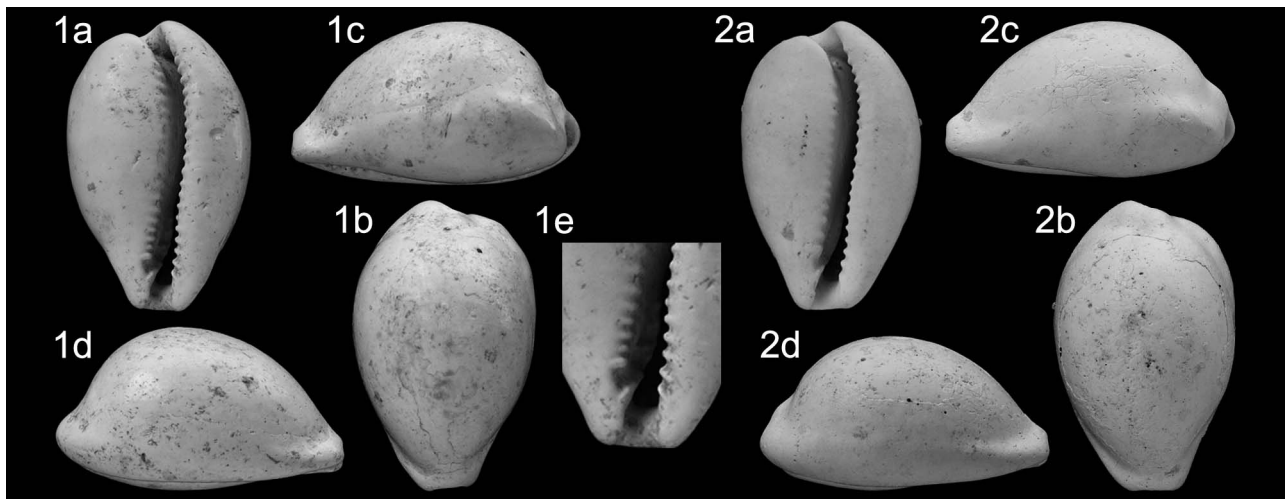


Plate 150. *Schilderia andegavensis* (Defrance, 1826); 1. NHMW 2016/0103/1638, height 20.0 mm, width 12.7 mm, height 11.1 mm; 2. NHMW 2016/0103/1639, height 20.2 mm, width 12.7 mm, height 10.7 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Discussion* – *Schilderia andegavensis* (Defrance, 1826) is characterised by its small lozenge-shaped shell (length 19.4–21.1 mm; average 20.0 mm), its numerous small labial teeth (normalised tooth count 21–27; average 23.8) restricted to the inside edge of the outer lip and in having the columellar teeth developed along the entire length in all but one of the specimens at hand (normalised number columellar teeth 15–20; average 18). The fossula is poorly delimited and almost flat to shallow spoon-shaped, with an inner edge that is almost smooth to bearing up to five subobsolete denticles. The most consistent feature in this species is the well developed marginal callus on the right posterior margin when viewed in ventral aspect (Pl. 150, figs 1c, 2c). For further discussion see generic note above.

Although Millet (1854, p. 158) and Brébion (1964, p. 333) recorded this species from numerous Assemblage I localities, we here restrict the distribution to Sceaux-d'Anjou.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Peyrot, 1938; Brébion, 1964; Dolin & Lozouet, 2004).

***Schilderia cf. andegavensis* (Defrance, 1826)**

Plate 151, fig. 1

*Material and dimensions* – Maximum length 28.9 mm, width 18.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1641 (1), NHMW 2016/0103/1642 (5), RGM.1348633 (2), LC (5), FVD (10).

*Discussion* – *Schilderia cf. andegavensis* (Defrance, 1826) is characterised by its comparatively larger pyriform shell (length 22.1–26.2 mm; average 24.9 mm), its numerous small labial teeth (normalised tooth count 20–25; average 23.2) restricted to the inside edge of the outer lip and in having the columellar teeth developed along the entire length (normalised number columellar teeth 15–19; average 17.8). The fossula is similar to that described from the specimens from Sceaux-d'Anjou (above), but five coarse denticles are developed at the inner edge in all specimens at hand, coarser than those

seen in the Sceaux-d'Anjou shells. The right posterior marginal callus pad described in the Sceaux-d'Anjou specimens is even more strongly developed in those from St-Clément-de-la-Place (Pl. 151, figs 1b, 1d). For further discussion see generic note above. We hesitate to say they are conspecific with the Sceaux-d'Anjou specimens mainly due to their difference in shell shape and globosity (see Fig. 2). We restrict the distribution of this form to St-Clément-de-la-Place.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Peyrot, 1938; Brébion, 1964; Dolin & Lozouet, 2004).

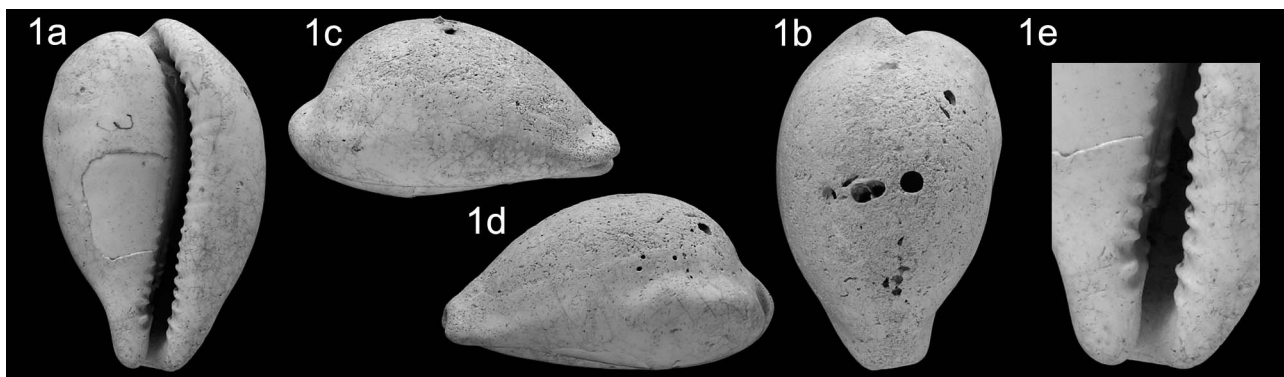
***Schilderia brebioni* Dolin & Lozouet, 2004**

Plate 152, figs 1–6

- \*2004 *Schilderia brebioni* Dolin & Lozouet, p. 41, pl. 20, figs 1, 2.
- 2004 *Schilderia fasciolaria* Dolin & Lozouet, p. 42, pl. 19, figs 5, 6.
- 2004 *Schilderia incognita* Dolin & Lozouet, p. 43, pl. 20, figs 4, 5.
- 2004 *Schilderia lauriatae* Dolin & Lozouet, p. 44, pl. 20, figs 6, 7.
- 2004 *Schilderia veronicata* Dolin & Lozouet, p. 46, pl. 20, fig. 3.

*Material and dimensions* – Maximum height 21.2 mm. **Renauleau**: NHMW 2016/0103/1643–1648 (6), NHMW 2016/0103/1649 (50+), RGM.1348976 (18), LC (50+), FVD (50+). **Beugnon**: RGM.1348400 (3), RGM.1348401 (1 + 4 fragments), LC (2), FVD (1).

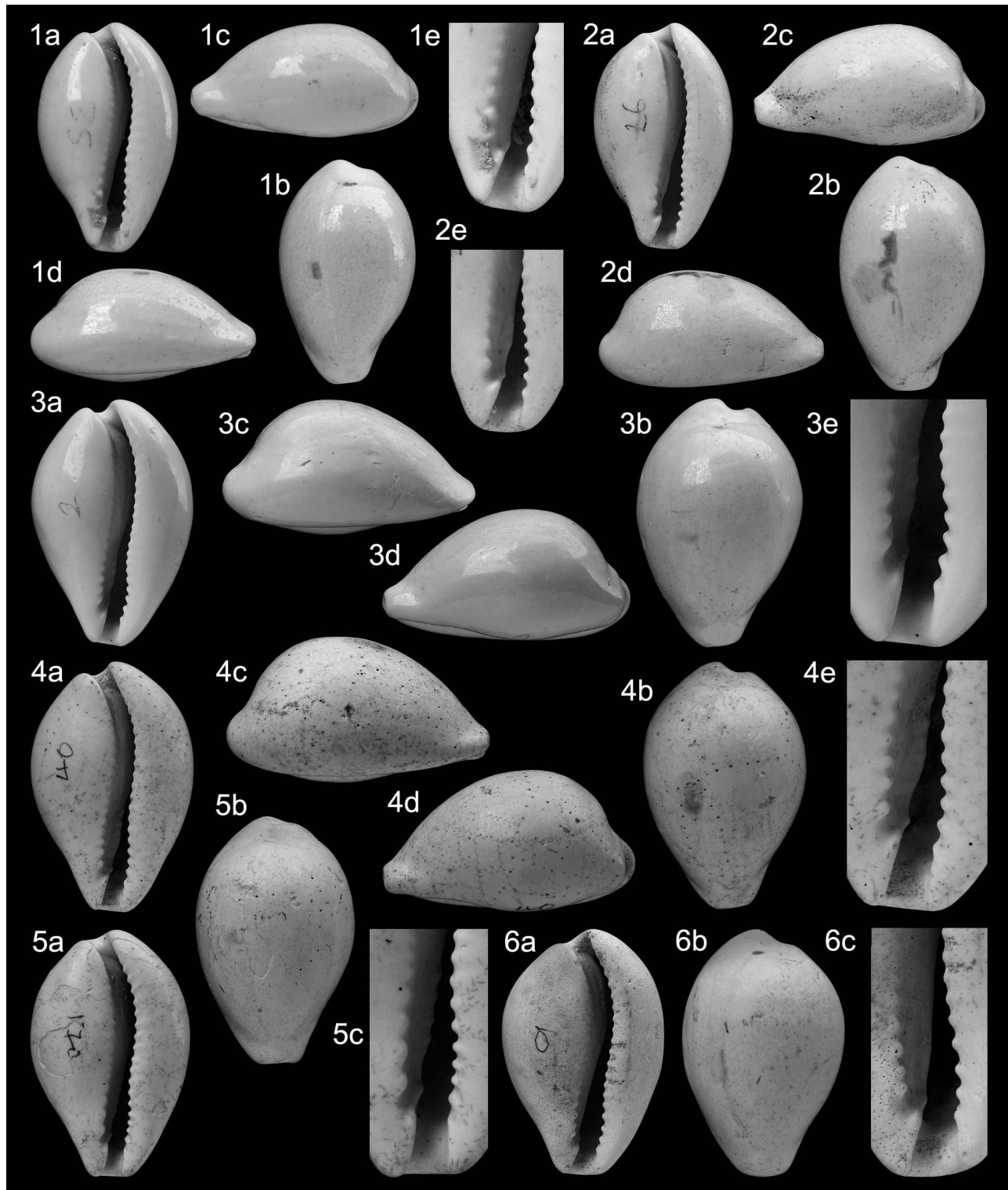
*Discussion* – As discussed in the generic note above, the cypraeids from Renauleau are problematic. Although we can recognise all of the forms described at species level by Dolin & Lozouet (2004) (Pl. 152, figs 1–6), we fail to separate them reliably. More data in the original description reflecting the intraspecific variability in these five species would have been helpful, as none of the shell morphometrics undertaken by us delimit five species groups amongst the Renauleau cypraeids. We



**Plate 151.** *Schilderia cf. andegavensis* (Defrance, 1826); 1. NHMW 2016/0103/1641, height 28.9 mm, width 18.8 mm, height 15.4 mm. Le Grand Chauverau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

therefore provisionally consider them a single species and first revisers we chose the name *S. brebioni* Dolin & Lozouet, 2004. For further discussion see generic note above.

*Distribution* – Upper Miocene, Tortonian, Atlantic, NW France (Dolin & Lozouet, 2004).



**Plate 152.** *Schilderia brebioni* Dolin & Lozouet, 2004; 1. NHMW 2016/0103/1643, height 21.7 mm, width 13.5 mm, height 10.5 mm; 2. NHMW 2016/0103/1644, height 29.6 mm, width 12.6 mm, height 10.7 mm; 3. NHMW 2016/0103/1645, height 31.4 mm, width 20.9 mm, height 16.6 mm; 4. NHMW 2016/0103/1646, height 26.6 mm, width 17.5 mm, height 14.4 mm; 5. NHMW 2016/0103/1647, height 26.5 mm, width 18.3 mm, height 14.4 mm; 6. NHMW 2016/0103/1648, height 26.6 mm, width 17.5 mm, height 14.7 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



Family Eratoidae Gill, 1871  
Genus *Erato* Risso, 1826

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

1826 *Erato* Risso, p. 240.

***Erato andecavica* Schilder, 1933**

Plate 153, figs 1-2

- \*1933b *Erato incrassata andecavica* Schilder, p. 250, 254, 260, 282, 283, fig. 73.
- 2002 *Erato andecavica* Schilder, 1933 – Fehse & Landau, p. 94, figs 10, 11, 14, 30, 33/2.
- 2016 *Erato andecavica* Schilder, 1933 – Van Dingenen *et al.*, p. 125, pl. 4, fig. 8.

*Material and dimensions* – Maximum height 10.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0373 (1), NHMW 2016/0103/0374 (50+), RGM.1347885 (1), RGM.1347909 (3), RGM.1348024 (17), RGM.1348832 (1), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0376 (15), RGM.1347877 (13), RGM.1347881 (50+), RGM.1347891 (50+), RGM.1347896 (49), RGM.1347900 (50+), RGM.1347910 (50+), RGM.1348290 (4), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0375 (47), RGM.1348975 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1348378 (17), RGM.1348381 (1), RGM.1348383 (18), RGM.1348384 (10), RGM.1348388 (10), FVD (1).

*Discussion* – *Erato andecavica* Schilder, 1933 is characterised by its strongly inflated shape, the dimple on the anterior end of the dorsum and the greatly thickened, basally flattened outer lip, with an angular margin and strong denticles. The species is constant in shape, but varies greatly in the character of the denticles on the columella. It is the largest *Erato* species in the upper Miocene and lower Pliocene of northwestern France. *Erato andecavica* is closely similar to the stratigraphically slightly older species *E. gallica* Schilder, 1933 from the middle Miocene of the Loire Basin, but differs in having an even more inflated shell, with fewer and coarser

denticles on the outer lip. The columellar denticles are strongly developed in the abapical third, but obsolete adapically, forming a callosity along the parietal edge. In *E. gallica* the columellar teeth usually persist further adapically.

*Distribution* – Upper Miocene, Tortonian, Atlantic, NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

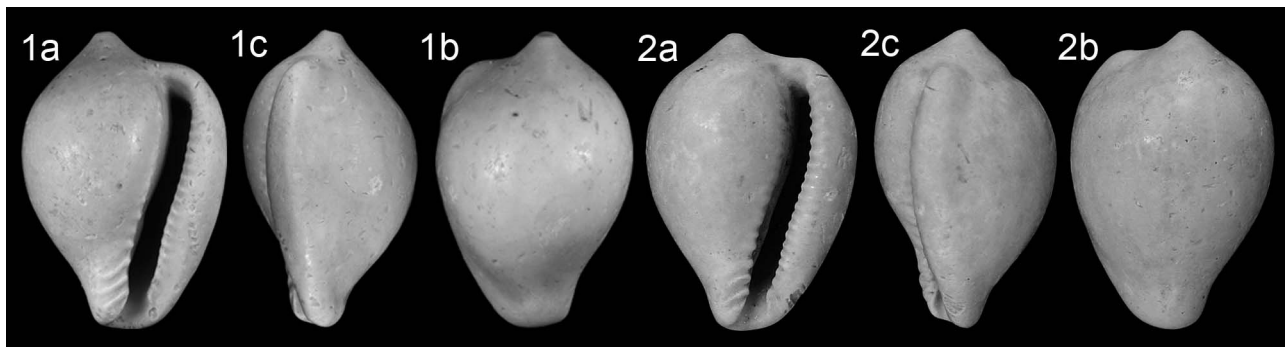
***Erato britannica* Schilder, 1933**

Plate 154, figs 1-2

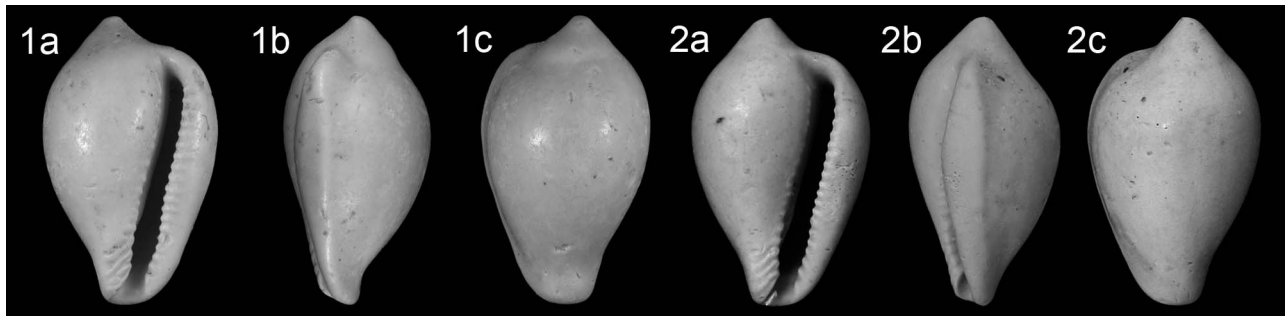
- \*1933a *Erato (Erato) cypraeola britannica* Schilder, p. 7.
- 2002 *Erato britannica* Schilder, 1933 – Fehse & Landau, p. 92, figs 20, 25, 27, 29, 33/1.
- 2016 *Erato britannica* Schilder, 1933 – Van Dingenen *et al.*, p. 125, pl. 4, fig. 9 (*cum syn.*).

*Material and dimensions* – Maximum height 9.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0369 (1), NHMW 2016/0103/0683 (1), NHMW 2016/0103/0370 (50+), RGM.1347886 (8), RGM.1348833 (2), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0372 (50+), RGM.1347878 (29), RGM.1347882 (50+), RGM.1347892 (50+), RGM.1347897 (28), RGM.1347901 (37), RGM.1347911 (50+), RGM.1347993 (50+), RGM.1348945 (4), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0371 (50+), RGM.1348984 (12), LC (50+), FVD (50+). **Beugnon:** RGM.1348379 (4), RGM.1348382 (1), RGM.1348385 (3), RGM.1348389 (17).

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



**Plate 153.** *Erato andecavica* Schilder, 1933; 1. NHMW 2016/0103/0373, height 10.1 mm, width 7.1 mm; 2. NHMW 2016/0103/0684, height 10.7 mm, width 7.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.



**Plate 154.** *Erato britannica* Schilder, 1933; 1. NHMW 2016/0103/0369, height 7.8 mm, width 5.1 mm; 2. NHMW 2016/0103/0683, height 7.7 mm, width 4.9 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

to other similar species see Fehse & Landau (2002, p. 94, table 2).

**Distribution** – Upper Miocene, Atlantic (Tortonian), NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016); NSB, Coralline Crag, England (Wood, 1848; Harmer, 1920), Kattendijk Formation, Belgium (Schilder, 1933a). Upper Pliocene: NSB, Red Crag, England (Wood, 1848; Harmer, 1920); Lillo Formation, Belgium (Glibert, 1958).

***Erato cooperi* Fehse & Landau, 2002**

Plate 155, figs 1-2

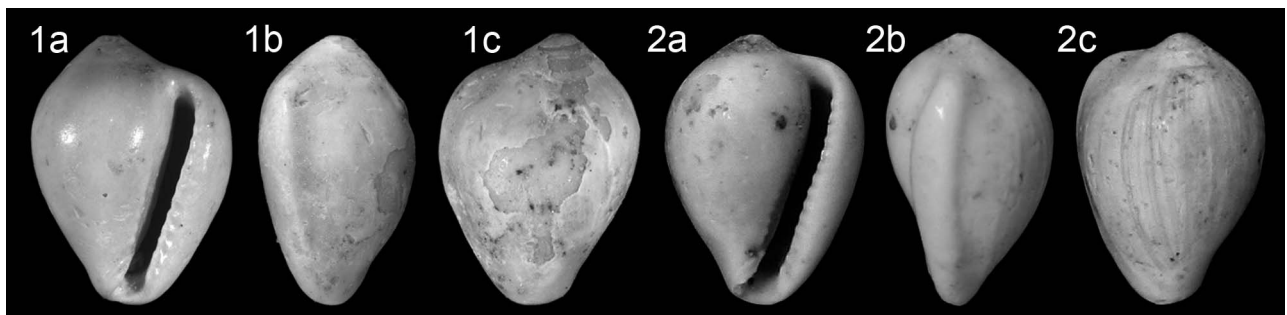
- \*2002 *Erato cooperi* Fehse & Landau, p. 95, figs 18, 23, 24, 31, 33/3.
- 2016 *Erato cooperi* Fehse & Landau, 2002 – Van Dingenen *et al.*, p. 125, pl. 4, fig. 10.

**Material and dimensions** – Maximum height 4.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0377 (1), NHMW 2016/0103/0685 (1), NHMW 2016/0103/0378 (25), RGM.1347887 (8), RGM.1347908 (4). **Sceaux-d’Anjou:** NHMW 2016/0103/0380 (50+), RGM.1347880 (31), RGM.1347883 (50+), RGM.1347893 (50+), RGM.1347899 (43), RGM.1347902 (34), RGM.1347912 (27), RGM.1347994 (50+), RGM.1348932 (11), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0379 (50+), RGM.

1348983 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1348380 (36), RGM.1348386 (50+), RGM.1348390 (50+), LC (5), FVD (4).

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

**Distribution** – Upper Miocene, Tortonian, Atlantic, NW France (Fehse & Landau, 2002). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).



**Plate 155.** *Erato cooperi* Fehse & Landau, 2002; 1. NHMW 2016/0103/0377, height 4.1 mm, width 3.1 mm; 2. NHMW 2016/0103/0685, height 4.2 mm, width 3.1 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Hespererato* Schilder, 1933

*Type species* (by original designation) – *Erato vitellina* Hinds, 1844, present-day, Baja California.

1933b *Hespererato* Schilder, pp. 246, 248.

***Hespererato marqueti* Fehse & Landau, 2002**

Plate 156, figs 1-2

2002 *Hespererato marqueti* Fehse & Landau, p. 97, figs 1, 3, 9a, b, 32, 33/4.

*Material and dimensions* – Maximum height 6.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0679-0680 (2), NHMW 2016/0103/0682 (50+), RGM.1347888 (50+), RGM.1347906 (6), RGM.1347907 (50+), RGM.1348834 (13), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0681 (50+), RGM.1347879 (28), RGM.1347884 (39), RGM.1347894 (50+), RGM.1347898 (37), RGM.1347903 (19), RGM.1347913 (15), RGM.1347995 (50+), LC (50+), FVD (50+). **Renauleau:** LC (?). **Beugnon:** RGM.1348387 (3), RGM.1348391 (3).

*Discussion* – As discussed by Fehse & Landau (2002, p. 99), *Hespererato marqueti* Fehse & Landau, 2002 shows characters of the genus *Hespererato* Schilder, 1933 in having a wide aperture, weak dentition and a poorly developed fossula. The last two characters are a little stronger than usual and the terminal ridge much stronger than normal for the genus, somewhat between *Hespererato* and *Erato* Risso, 1826. However, the general shape and wide aperture place it closer to *Hespererato*.

*Hespererato marqueti* differs from the Mediterranean Pliocene *Hespererato cocconii* Schilder, 1932 in being smaller, with a relatively broader, squatter shell and higher spire, the density of the labial teeth is lower, and the columellar teeth are subobsolete. For further discussion see Fehse & Landau (2002).

*Distribution* – Upper Miocene, Tortonian, Atlantic, NW France (Fehse & Landau, 2002).

Family Ovulidae Fleming, 1822  
Subfamily Simniinae Schilder, 1925  
Genus *Neosimnia* Fischer, 1884

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

1884 *Neosimnia* Fischer, p. 664.

For generic synonymy see Van Dingenen *et al.* (2016, p. 126).

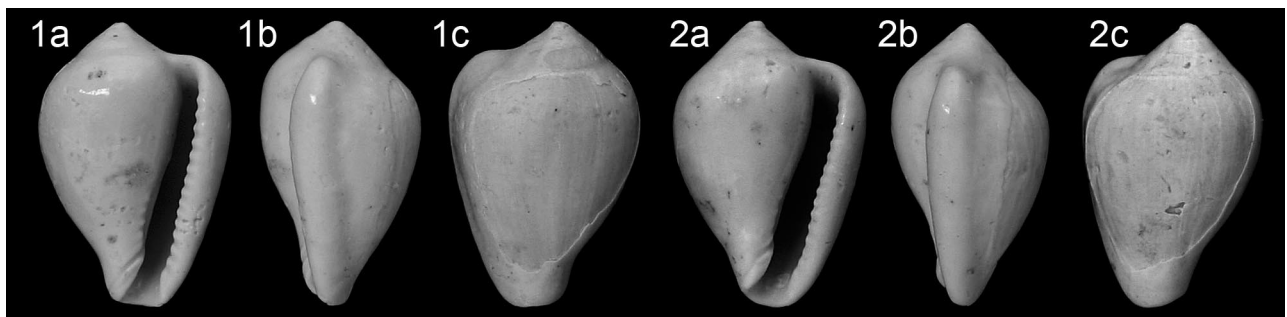
***Neosimnia semen* (Defrance, 1825)**

Plate 157, figs 1-3.

- \*1825 *Ovula semen* Linnaeus, p. 132.
- 1854 *Ovula Striatula* Millet, p. 158 (*non Ovulum striatulum* G.B. Sowerby I, 1828).
- 1865 *Ovula striatula* Millet – Millet, p. 585 (*non Ovulum striatulum* G.B. Sowerby I, 1828).
- 1952a *Simnia* (*Neosimnia*) *semen* Defrance – Glibert, p. 264, pl. 3, fig. 5.
- 1964 *Simnia* (*Neosimnia*) *semen* Defrance, 1825 – Brébion, p. 336.

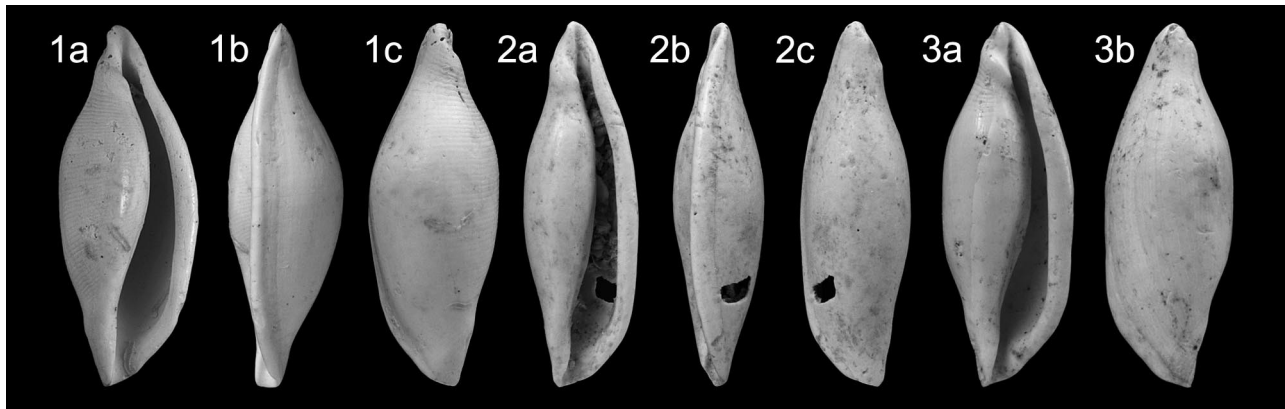
*Material and dimensions* – Maximum height 13.0 mm. **Sceaux-d’Anjou:** NHMW 2016/0103/0381-0382 (2), NHMW 2016/0103/1650 (1), NHMW 2016/0103/1651 (1), RGM.1347981 (4 juveniles), RGM.1347992 (2 fragments), RGM.1348886 (2 subadults), LC (4), FVD (2).

*Discussion* – Van Dingenen *et al.* (2016, p. 127) highlighted the difficulties concerning the identification of fossil ovulid shells due to the lack of morphological shell characters. It does not help that in some cases shells of distinct species seem identical until the animal and radula are examined (Landau & Fehse, 2004), and conversely, some species that could be distinguished based on shell character and mantle colour are conspecific based on genetic analysis (Reijnen *et al.*, 2010). Not only is this group problematic at species level, but in some groups there is also no consensus at genus level. The genus *Neosimnia* Fischer, 1884 was synonymised with *Simnia* Risso, 1826 by Gofas *et al.* (2001), whilst Lorenz



**Plate 156.** *Hespererato marqueti* Fehse & Landau, 2002; 1. NHMW 2016/0103/0679, height 6.3 mm, width 4.5 mm; 2. NHMW 2016/0103/0680, height 6.4 mm, width 4.5 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.





**Plate 157.** *Neosimnia semen* (DeFrance, 1825); 1. NHMW 2016/0103/0381, height 13.0 mm, width 5.3 mm; 2. NHMW 2016/0103/0382, height 13.0 mm, width 4.0 mm; 3. NHMW 2016/0103/1650, height 10.9 mm, width 4.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

& Fehse (2009, pl. 122-132) considered the two distinct. Van Dingenen *et al.* (2016) provisionally accepted the genus *Neosimnia* for thicker-shelled species with a thickened labial varix.

The shells from the upper Miocene Assemblage I localities are here ascribed to *Neosimnia semen* (DeFrance 1825), originally described from the middle Miocene of the Loire Basin of France. This species is characterised by being relatively thin-shelled, in lacking a flattened area on the venter of the last whorl between the ventral keel and the cardinal ridge, and in having spiral sculpture along the entire length of the last whorl. This last character is often abraded on the dorsum (Glibert, 1952a, p. 265), but can be seen on the venter in one of the figured specimens (Pl. 157, fig. 1a). The series illustrated from Sceaux-d'Anjou shows some variability in the degree of inflation mid-whorl.

Van Dingenen *et al.* (2016, p. 127) recorded the living Mediterranean species *N. spelta* (Linnaeus, 1758) from the upper Pliocene Assemblage III locality of Le Pigeon Blanc. *Neosimnia spelta* differs from *N. semen* in being thicker-shelled, in having spiral sculpture restricted to the terminals, and in having a flattened area on the venter of the last whorl between the ventral keel and the cardinal ridge. Although we provisionally consider these forms distinct, in view of the unexpected molecular data of Reijnen *et al.* (2010), all the Neogene and present-day European forms could represent a single species. We await further genetic data on present-day ovulids to see if the findings by Reijnen *et al.* (2010) are isolated to the genus *Cyphoma* or widespread amongst ovulids. For further discussion and comparison see Van Dingenen *et al.* (2016, p. 127).

Brébion (1964, p. 336) recorded this species from Assemblage I localities (Thorigné, Sceaux-d'Anjou, St-Clément-de-la-Place). Millet (1854, p. 158) also recorded it from Renauleau.

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

#### Family Triviidae Troschel, 1863

**Note** – The Triviidae are an important component of the Assemblage I fauna. Not only are they abundant, but varied in form. However, we have found it difficult to delimit clear boundaries between species, based on shell characters. Although most shells can be relatively satisfactorily placed within one of the groups discussed below, there are a number of specimens that are difficult to place. The presence/absence of the dorsal sulcus, which bisects the dorsal ribs, has usually been accepted a valid generic criterion separating the genera *Trivia* Gray, 1837 and *Niveria* Joussemae, 1884. In the Assemblage I groups this distinction is clear in some species such as *Trivia acuminata* Schilder, 1932 and *Niveria dimidiatoaffinis* (Sacco, 1894). However, in some shells the dorsal sulcus does not bisect all the ribs, or forms a narrow groove into which the ribs dip, but are not bisected. These intermediate forms throw into question the validity of the dorsal sulcus as a generic character and we await genetic studies to elucidate the value of this shell feature.

Despite the difficulties is classification, we can state with relative certainty that whilst the Triviinae form an important component of both the upper Miocene Assemblage I and lower Pliocene Assemblage III faunas (Van Dingenen *et al.*, 2016) of north western France, with the exception of the very rare occurrence of *Trivia pisolina* (Lamarck, 1811) in Assemblage III, the species present in the upper Miocene are not the same as those found in the lower Pliocene.

#### Genus *Trivia* Gray, 1837

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

1837 *Trivia* Gray, p. 256.

1840 *Trivea* Swainson, pp. 135, 325. Incorrect subsequent spelling.

- 1847 *Coccinella* Herrmannsen, p. 254. '*Coccinella* Leach' listed by Herrmannsen, and considered equal to *Trivia*. Not treated as valid by Herrmannsen and therefore not available; if available, it would be a junior homonym of *Coccinella* Linnaeus, 1758 [Coleoptera].

***Trivia acuminata* Schilder, 1932**

Plate 158, figs 1-2

- 1894 *Trivia europaea* var. *cocineloides* (Sow.) – Sacco, p. 46, pl. 3, fig. 27 [non *Trivia cocineloides* (J. de C. Sowerby, 1823)].
- 1911 *Cypraea europaea* var. *pediculoides* Cerulli-Irelli (*partim*), p. 273, pl. 26, figs 15, 16.
- \*1932a *Trivia acuminata* Schilder, p. 257, text fig. 2.
- 1932c *Trivia acuminata* Schil. – Schilder, p. 108.
- 1941 *Trivia (Trivia) acuminata* Schilder 1932 – Schilder, p. 73.
- 1970 *Trivia (Trivia) acuminata* Schilder, 1932 – Pavia & Demagistris, p. 131, pl. 1, fig. 1.
- 1971 *Trivia (Trivia) acuminata acuminata* Schilder, 1932 – Schilder & Schilder, p. 17.
- 1984 *Trivia europaea* var. *cocineloides* (Sowerby, 1823) – Ferrero Mortara *et al.*, p. 153, pl. 26, fig. 8a-c [non *Trivia cocineloides* (J. de C. Sowerby, 1823)].
- 2003 *Trivia acuminata* Schilder, 1932 – Fehse & Landau, p. 91, figs 1/3a-c, 6/5a-c.

*Material and dimensions* – Maximum height 6.9 mm. **Sceaux-d'Anjou:** NHMW 2016/0103/0614 (1), NHMW 2016/0103/0654 (1), NHMW 2016/0103/0615 (16), RGM.

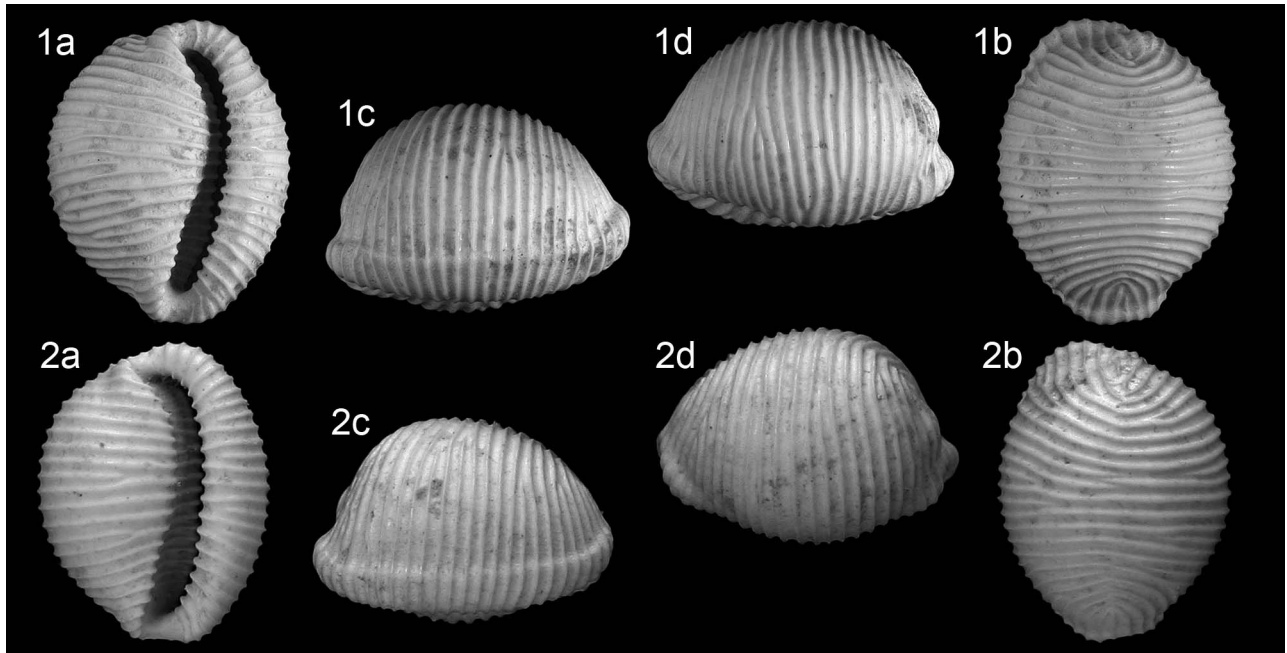
1348266 (3), RGM.1348284 (6), RGM.1348356 (3), RGM.1348653 (1), RGM.1348776 (2).

*Discussion* – *Trivia acuminata* Schilder, 1932 is characterised by its slightly elongated shape, evenly rounded dorsum, relatively high number of ribs and the slightly protruding fossula.

The specimens from Sceaux-d'Anjou are comparable in size and shape to those described by Fehse & Landau (2003, p. 91) from the lower Piacenzian, upper Pliocene Estepona Basin of southern Spain. They are not quite as elongate, nor do they have as many ribs as the holotype (Fehse & Landau, 2003, pl. 6, fig. 5), but otherwise fit well within the species concept.

Both *T. cocineloides* (J. de C. Sowerby, 1823) and *T. candidula* (Gaskoin, 1836) have more rounded shells, with a dorsal hump, fewer ribs, and have the fossula not protruding. In both, the siphonal and anal canals are indented, whereas in *T. acuminata* the canals follow the shell contour. *Trivia candidula* has a similarly callused outer margin of the lip, but may be distinguished by the more centrally placed aperture, with the carinal ridge covered by the apertural lip when seen in ventral view; *T. cocineloides* has a non-callused lip margin (Fehse & Landau, 2003, p. 92). This is the first Miocene record of *T. acuminata*.

*Distribution* – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Upper Pliocene: western Mediterranean, Estepona Basin (Fehse & Landau, 2003); central Mediterranean, Italy (Sacco, 1894; Pavia & Demagistris, 1970; Ferrero Mortara *et al.*, 1984; Fehse & Landau, 2003). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911).



**Plate 158.** *Trivia acuminata* Schilder, 1932; 1. NHMW 2016/0103/0614, length 6.3 mm, height 4.4 mm, width 4.9 mm; 2. NHMW 2016/0103/0654, length 5.8 mm, height 4.1 mm, width 4.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*Trivia sceauxensis* nov. sp.

Plate 159, figs 1-6

*Type material* – Holotype MNHN.F.A57897, length 5.7 mm, width 4.3 mm, height 3.9 mm; paratype 1 MNHN.F.A57898, length 5.6 mm, width 4.5 mm, height 3.8 mm; paratype 2 NHMW 2016/0103/0655, length 5.5 mm, width 4.3 mm, height 3.6 mm; paratype 3 NHMW 2016/0103/0656, length 4.9 mm, width 4.0 mm, height 3.6 mm; paratype 4 NHMW 2016/0103/0657, length 4.9 mm, width 3.9 mm, height 3.2 mm; paratype 5 NHMW 2016/0103/0658, length 4.9 mm, width 3.8 mm, height 3.5 mm; paratype 6 RGM.1348267, height 5.4 mm, width 4.4 mm; paratype 7 RGM.1348268, height 5.2 mm, width 4.2 mm; paratype 8 RGM.1348269, height 5.5 mm, width 4.1 mm; paratype 9 RGM.1348270, height 5.5 mm, width 4.2 mm.

*Other material* – Maximum length 5.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0660 (21), RGM.1348527 (2), RGM.1348678 (3). **Sceaux-d'Anjou:** NHMW 2016/0103/0659 (25), RGM.1348271 (39), RGM.1348285 (13), RGM.1348357 (7), RGM.1348649 (5), RGM.1348681 (9), RGM.1348774 (7). **Renaleau:** NHMW 2016/0103/0661 (30).

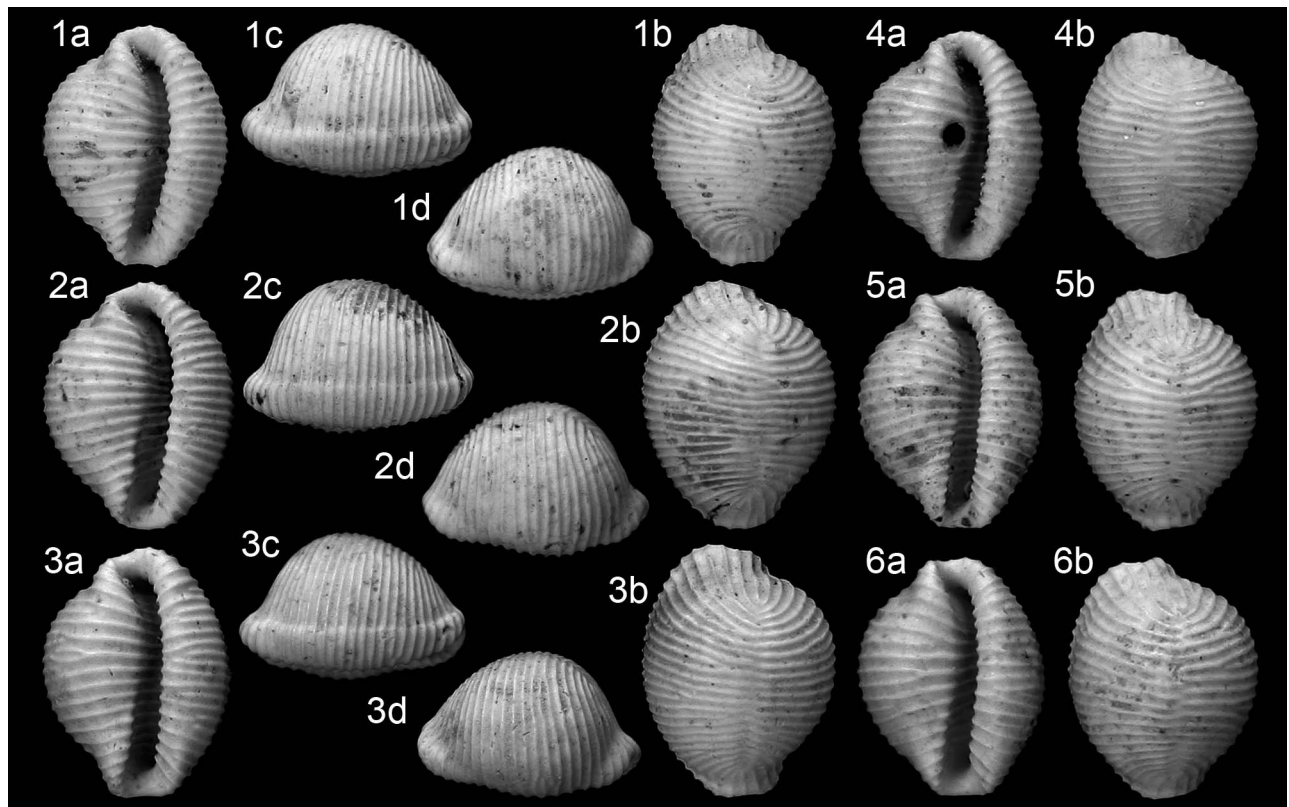
*Etymology* – Named after the type locality of Sceaux-d'Anjou, Maine-et-Loire, North West France. *Trivia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Trivia* species of small size, with strongly globose last whorl, strongly produced terminals, 18-20 dorsal ribs, uninterrupted mid-dorsum, irregular weak to subobsolete dorsal sulcus or depression that bisects ribs towards extremities, thickened outer lip with 16-21 denticles, and 14-16 columellar denticles (for measurements see Table 7).

*Description* – Shell small, strongly globose, with strongly produced terminals. Spire covered by callus. Last whorl globose, about 75% of total height. Terminals produced, rounded. Dorsum strongly and evenly rounded, completely covered by 18-20 ribs, slightly narrower than their interspaces. Ribs uninterrupted mid-dorsum in most specimens. Irregular dorsal sulcus or depression present, at least subobsoletely in most specimens, irregularly bisecting ribs at extremities, although all ribs bisected in exceptional specimens. Base and terminals evenly convex. Aperture weakly curved, hardly wider anteriorly. Outer lip broad, thickened by labial varix, evenly rounded, widest in mid-portion, narrowing towards terminals bearing 16-21 narrow, equal denticles. Siphonal and anal



**Plate 159.** *Trivia sceauxensis* nov. sp.; 1. **Holotype** MNHN.F.A57897, length 5.7 mm, width 4.3 mm, height 3.9 mm; 2. **Paratype 1** MNHN.F.A57898, length 5.6 mm, width 4.5 mm, height 3.8 mm; 3. **Paratype 2** NHMW 2016/0103/0655, length 5.5 mm, width 4.3 mm, height 3.6 mm; 4. **Paratype 3** NHMW 2016/0103/0656, length 4.9 mm, width 4.0 mm, height 3.6 mm; 5. **Paratype 4** NHMW 2016/0103/0657, length 4.9 mm, width 3.9 mm, height 3.2 mm; 6. **Paratype 5** NHMW 2016/0103/0658, length 4.9 mm, width 3.8 mm, height 3.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.



Specimens from St-Clément-de-la-Place N = 10	
Length (H)	max = 5.7 mm; min = 4.4 mm
Width (D)	max = 4.5 mm; min = 3.6 mm
Dorso-ventral height (d)	max = 3.9 mm; min = 3.2 mm
d/D index	87.3 (range 82-92)
d/H index	69.1 (range 66-73)
Number of denticles outer lip	18.3 (range 16-21)
Number of denticles inner lip	14.8 (range 14-16)

**Table 7.** *Trivia sceauxensis* nov. sp.; morphometrics of specimens from St-Clément-de-la-Place. Abbreviations follow Glibert (1949): H = length, D = width, d = dorso-ventral height.

canals relatively wide, weakly indented. Columella concave, bordered internally by very weak carinal ridge, bearing 14-15 ribs, which run unaltered onto carinal ridge. Carinal ridge expanded in fossular region. Fossula concave, poorly delimited.

**Discussion** – We have placed this species in the genus *Trivia* Gray, 1837, as the ribs are uninterrupted at the mid-dorsum in most specimens. However, placement in *Niveria* Jousseume, 1884 is also possible on account of the poorly developed dorsal sulcus, which in some specimens is represented by a subobsolete depression, whilst in others there is an irregular sulcus bisecting the ribs at the extremities. The dorsal sulcus in *Trivia sceauxensis* nov. sp. is not as regular as it is in the *Niveria* species discussed below. *Trivia sceauxensis* is the smallest triviid found in the Assemblage I deposits. It differs from *Trivia acuminata* Schilder, 1932 and other congeners such as the Pliocene to present-day Mediterranean and Amphiatlantic species *Trivia candidula* (Gaskoin, 1836) in being smaller, more globose and in having more produced extremities, especially the posterior terminal. In having the ribs interrupted at the extremities it can be compared with *Niveria pseudoavellana* (Sacco, 1894) (see below), but this is a much larger species, less globose, with less

produced terminals, and the dorsal sulcus is better-developed and bisects or distorts the ribs more extensively.

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

***Trivia pisolina* (Lamarck, 1811)**

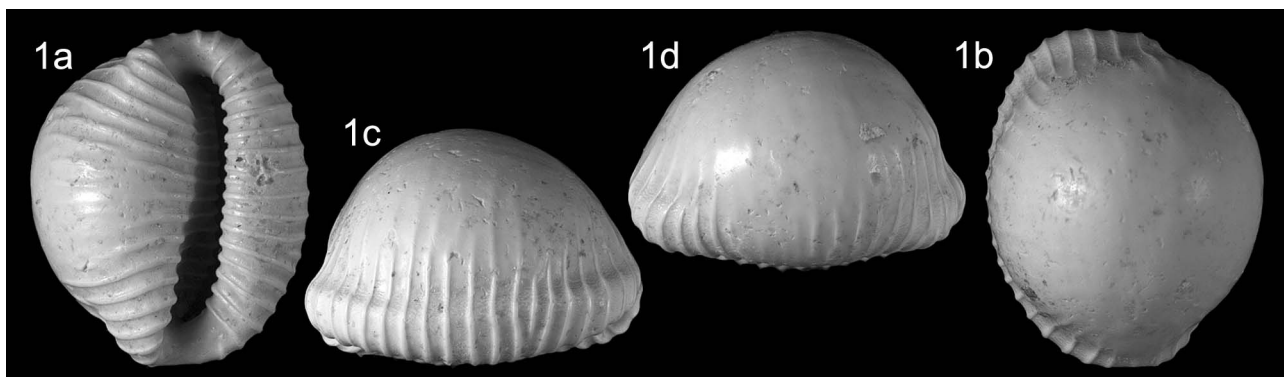
Plate 160, fig. 1

- \*1811 *Cypraea pisolina* Lamarck, p. 108.
- 1854 *Cypraea Pisolina* Lmk. – Millet, p. 158.
- ?1914 *Trivia pisolina* (Lamarck) – Harmer, p. 50, pl. 2, fig. 17.
- non 1924 *Trivia* cf. *pisolina* Lamarck – Cossmann & Peyrot, p. 388, pl. 11, figs 2, 3.
- 1938 *Trivia pisolina* Lamarck – Peyrot, p. 170, pl. 4, figs 2, 8, 9.
- 1964 *Trivia pisolina* Lamarck, 1810 [*sic*] – Brébion, p. 322, pl. 7, figs 31-33.
- 2016 *Trivia pisolina* (Lamarck, 1811) – Van Dingenen *et al.*, p. 124, pl. 4, fig. 6.

**Material and dimensions** – Maximum length 15.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0515 (1), NHMW 2016/0103/0516 (50+), RGM.1347842 (2), RGM.1347845 (18), RGM.1347847 (6), RGM.1348302 (1), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0517 (23), RGM.1347841 (37), RGM.1347843 (44), RGM.1347844 (50+), RGM.1347846 (14), RGM.1348265 (46), RGM.1348358 (5), RGM.1348652 (1), RGM.1348687 (29), LC (50+), FVD (50+). **Renaleau:** NHMW 2016/0103/0613 (50+), RGM.1348977 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1348452 (9), RGM.1348453 (3), RGM.1348454 (18), RGM.1348461 (12), FVD (3).

**Discussion** – *Trivia pisolina* (Lamarck, 1811) is a very distinctive species, characterised by its smooth dorsum, devoid of ribs and the coarse apertural dentition. Few European Neogene triviids have a smooth dorsum. *Trivia perobsoleta* Sacco, 1894, from the Mediterranean Pliocene also lacks ribs, but differs in being larger and having finer apertural dentition.

The shell figured by Harmer (1914, pl. 2, fig. 17) from



**Plate 160.** *Trivia pisolina* (Lamarck, 1811); 1. NHMW 2016/0103/0515, length 8.1 mm, height 5.8 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the English Crag seems to be an internal mould. We are uncertain if it is *T. pisolina* and exclude it from the distribution. The shell identified as *Trivia* cf. *pisolina* by Cossmann & Peyrot (1924, pl. 11, figs 2, 3) from the lower Miocene Aquitaine Basin is not this species. It is probably a subadult specimen of another triviid.

Millet (1854, p. 158) recorded this species from Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place). Brébion (1964, p. 324) added Les Pierres Blanches and Beaulieu, and Assemblage II (Apigné, Carcé). Van Dingenen *et al.* (2016, p. 124) added Assemblage III (Le Pigeon Blanc).

*Distribution* – Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Peyrot, 1938; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al.*, 2016).

Genus *Niveria* Jousseume, 1884

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

1884b *Niveria* Jousseume, p. 415.

For generic synonymy see Van Dingenen *et al.* (2016, p. 124).

***Niveria cylindriclementi* nov. sp.**

Plate 161, figs 1-3

*Type material* – Holotype MNHN.F.A57912, length

6.4 mm, width 4.6 mm, height 3.8 mm; paratype 1 MNHN.F.A57913, length 6.4 mm, width 4.5 mm, height 3.7 mm; paratype 2 NHMW 2016/0103/0621, length 6.3 mm, width 4.3 mm, height 3.6 mm; paratype 3 NHMW 2016/0103/0622, length 6.1 mm, width 4.3 mm, height 3.6 mm; paratype 4 NHMW 2016/0103/0623, length 6.4 mm, width 4.5 mm, height 3.7 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1348277, height 6.3 mm, width 4.4 mm; paratype 6 RGM.1348278, height 6.1 mm, width 4.2 mm; paratype 7 RGM.1348279, height 4.9 mm, width 3.6 mm; paratype 8 RGM.1348280, height 6.2 mm, width 4.3 mm, **Sceaux-d'Anjou**.

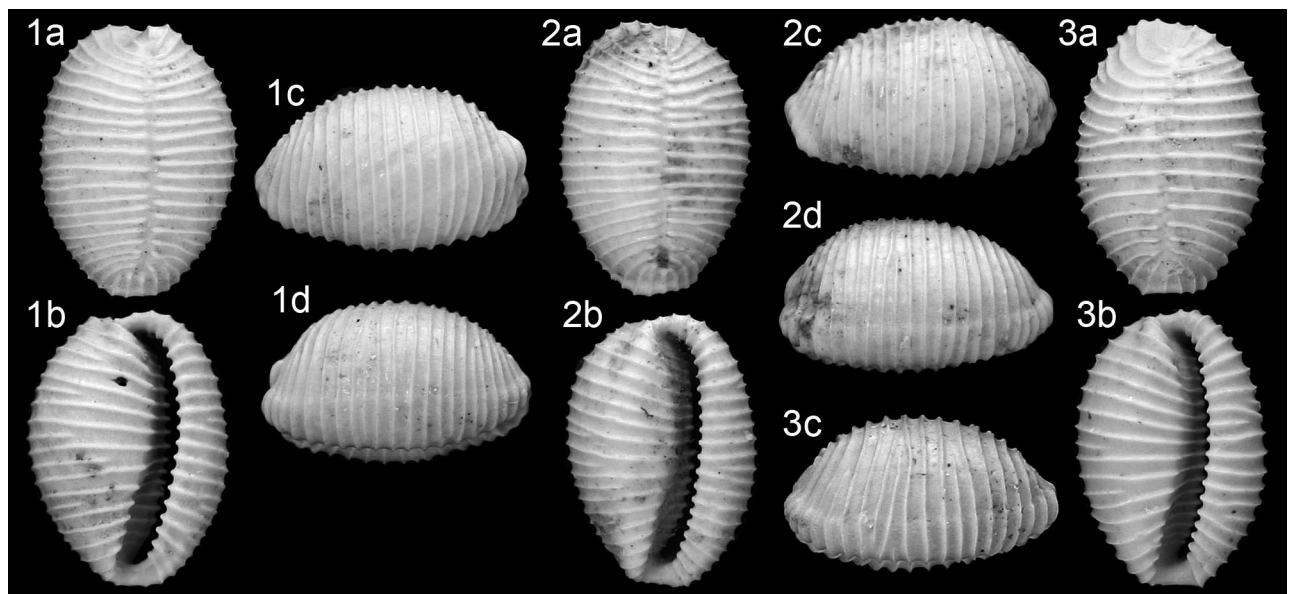
*Other material* – Maximum length 6.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0624 (50+), RGM.1348526 (7), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0625 (50+), RGM.1348281 (39), RGM.1348283 (50+), RGM.1348359 (50+), RGM.1348647 (41), RGM.1348679 (45), RGM.1348772 (28), RGM.1348882 (38), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0666 (4).

*Etymology* – Compound name formed from the cylindrical shell shape and the type locality of St-Clément-de-la-Place. *Niveria* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Niveria* species of small size, cylindrical somewhat dorsally depressed shape, with terminals hardly produced, straight, narrow dorsal sulcus that is not depressed, but bisects all ribs, ribs minimally thickened ad-



**Plate 161.** *Niveria cylindriclementi* nov. sp.; 1. **Holotype** MNHN.F.A57912, length 6.4 mm, width 4.6 mm, height 3.8 mm; 2. **Paratype 1** MNHN.F.A57913, length 6.4 mm, width 4.5 mm, height 3.7 mm; 3. **Paratype 2** NHMW 2016/0103/0621, length 6.3 mm, width 4.3 mm, height 3.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Specimens from St-Clément-de-la-Place N = 10	
Length (H)	max = 6.4 mm; min = 5.4 mm
Width (D)	max = 4.6 mm; min = 3.8 mm
Dorso-ventral height (d)	max = 3.8 mm; min = 3.2 mm
d/D index	82.7 (range 81-84)
d/H index	58.1 (range 57-59)
Number of denticles outer lip	19.9 (range 18-23)
Number of denticles inner lip	16.1 (range 14-17) 90% specimens with 16-17

**Table 8.** *Niveria cylindriclementi* nov. sp.; morphometrics of specimens from St-Clément-de-la-Place. Abbreviations follow Glibert (1952a): H = length, D = width, d = dorso-ventral height.

adjacent to sulcus, moderately thickened and varicose outer lip, bearing 18-23 strong, equal denticles, well-developed fossula, and 16-17 equal columellar denticles.

**Description** – Shell small for genus, cylindrical oval, somewhat dorsally depressed (for measurements see Table 8). Spire covered by callus. Last whorl narrow cylindrical and rounded, 100% of total height. Terminals hardly produced. Dorsum rounded, completely covered by 15-19 narrow ribs, half to one-third width of their interspaces. Dorsal sulcus straight, narrow, not depressed, extending longitudinally across centre of dorsum bisecting all ribs. Ribs minimally thickened adjacent to the sulcus. Base slightly convex, with short terminals recurved. Aperture of moderate width, curved adapically, slightly wider anteriorly. Outer lip somewhat broadened by moderate labial varix, convex, widest in mid-portion, narrowing towards terminals, regularly rounded. Outer lip bearing 18-23 strong, equal denticles. Siphonal and anal canals hardly protruding. Fossula broadly concave, delimited from the rest of the columella. Columella convex, tapering steeply inwards, bordered internally by a weak carinal ridge. Columella bearing 16-17 equal denticles,

which continue onto carinal ridge. Columellar angulation present, but not sharp.

**Discussion** – *Niveria cylindriclementi* nov. sp. differs from *N. dimidiatoaffinis* (Sacco, 1894) in being smaller, more evenly cylindrical and less globose, in having less produced terminals and in having fewer columellar denticles. In both species the dorsal sulcus is straight, not depressed and neatly bisects all ribs. The ribs in *N. cylindriclementi* are slightly narrower than in *N. dimidiatoaffinis* and even less swollen adjacent to the dorsal sulcus. The characters of the fossula, columella and columellar angulation are similar in both species, but as *N. cylindriclementi* has fewer columellar denticles, fewer ribs cross the fossula and they are more widely spaced than in *N. dimidiatoaffinis* along the entire venter.

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

#### *Niveria dimidiatoaffinis* (Sacco, 1894)

Plate 162, figs 1-3

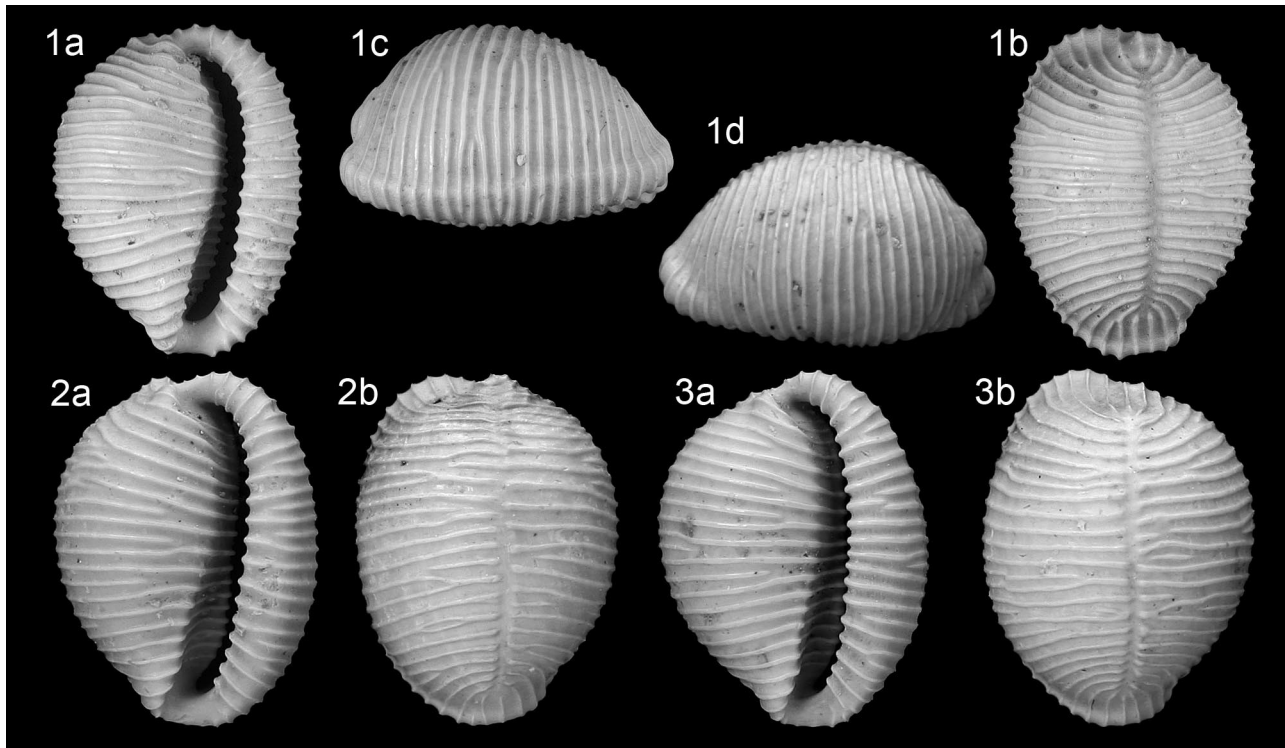
- 1837 *Cypraea affinis* Dujardin, p. 304, pl. 19, fig. 12 (non Gmelin, 1791).  
 1852 *Trivia affinis* Duj. – Hörnes, p. 72, pl. 8, fig. 14.  
 \*1894 *Trivia affinis* var. *dimidiatoaffinis* Sacco, p. 51 (nom. nov. pro *Cypraea affinis* Dujardin, 1837, non Gmelin, 1791).  
 1952a *Trivia dimidiatoaffinis* Sacco, 1894 – Glibert, p. 270, pl. 3, fig. 9.  
 1964 *Trivia dimidiatoaffinis* Sacco, 1894 – Brébion, p. 324.  
 2013 *Niveria dimidiatoaffinis* (Sacco, 1894) – Landau et al., p. 112, pl. 12, fig. 8 (cum syn.).

**Material and dimensions** – Maximum length 12.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0616-0618 (3), NHMW 2016/0103/0619 (25), RGM.1348319 (2), RGM.1348528 (3), RGM.1348677 (1), FVD (11). **Sceaux-d'Anjou:** NHMW 2016/0103/0620 (8), RGM.1348282 (9), RGM.1348287 (7), RGM.1348360 (12), RGM.1348651

	Specimens from St-Clément-de-la-Place N = 10	From Glibert (1952a) N = 100
Length (H)	max = 12.5 mm; min = 7.4 mm	max = 14.2 mm; min = 9.0 mm
Width (D)	max = 9.6 mm; min = 5.7 mm	max = 10.5 mm; min = 6.5 mm
Dorso-ventral height (d)	max = 8.2 mm; min = 4.9 mm	max = 8.6 mm; min = 5.6 mm
d/D index	84.3 (range 79-87)	82.6 (range 81.9-83.3)
d/H index	63.4 (range 58-67)	62.4 (range 61.4-63.4)
Number of denticles outer lip	20 (range 17-24)	18-20 in 2/3 specimens (range 15-24)
Number of denticles inner lip	19.2 (range 17-22)	Not given

**Table 9.** *Niveria dimidiatoaffinis* (Sacco, 1894); morphometrics of specimens from St-Clément-de-la-Place compared to those given by Glibert (1952a, p. 271) for specimens from the middle Miocene Loire Basin. Abbreviations follow Glibert (1952a): H = length, D = width, d = dorso-ventral height.





**Plate 162.** *Niveria dimidiatoaffinis* (Sacco, 1894); 1. NHMW 2016/0103/0616, length 8.6 mm, height 3.4 mm; 2. NHMW 2016/0103/0617, length 9.4 mm, height 5.9 mm; 3. NHMW 2016/0103/0618, length 9.0 mm, height 5.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(11), RGM.1348682 (9), RGM.1348775 (17), FVD (8).  
**Renauleau:** NHMW 2016/0103/0662 (20), FVD (27).  
**Beugnon:** RGM.1348451 (1), RGM.1348455 (5), RGM.1348458 (4), FVD (1).

*Discussion* – *Niveria dimidiatoaffinis* (Sacco, 1894) is characterised by its elongate shape, rather narrow ribs, about half the width of their interspaces, which are hardly swollen at their termination, sharply cut by the straight dorsal sulcus (for measurements see Table 9). The rib terminations at the sulcus tend to be alternating in position. The Assemblage I specimens are usually slightly less elongate than those from the middle Miocene Loire Basin, but the morphometrics between the two populations overlap. We note with a little scepticism the narrow ranges for d/D and d/H recorded by Glibert compared to those found in the specimens from St-Clément-de-la-Place.

*Distribution* – Middle Miocene: Atlantic, Aquitaine Basin (Serravallian), France (Cossmann & Peyrot, 1924), Loire Basin (Langhian), France (Peyrot, 1938; Glibert, 1952a); Paratethys (Langhian-Serravallian), Poland (Friedberg, 1912, 1951; Bałuk, 1995), Austria (Hörnes, 1852), Hungary (Csepregy-Meznerics, 1954, 1956, 1969; Strausz, 1962, 1966), Bulgaria (Kojumdzieva & Strachimirov, 1960), Ukraine (Zelinskaya *et al.*, 1968); Protoediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic, NW France (Brébion, 1964).

#### *Niveria excoccinella* (Sacco, 1894)

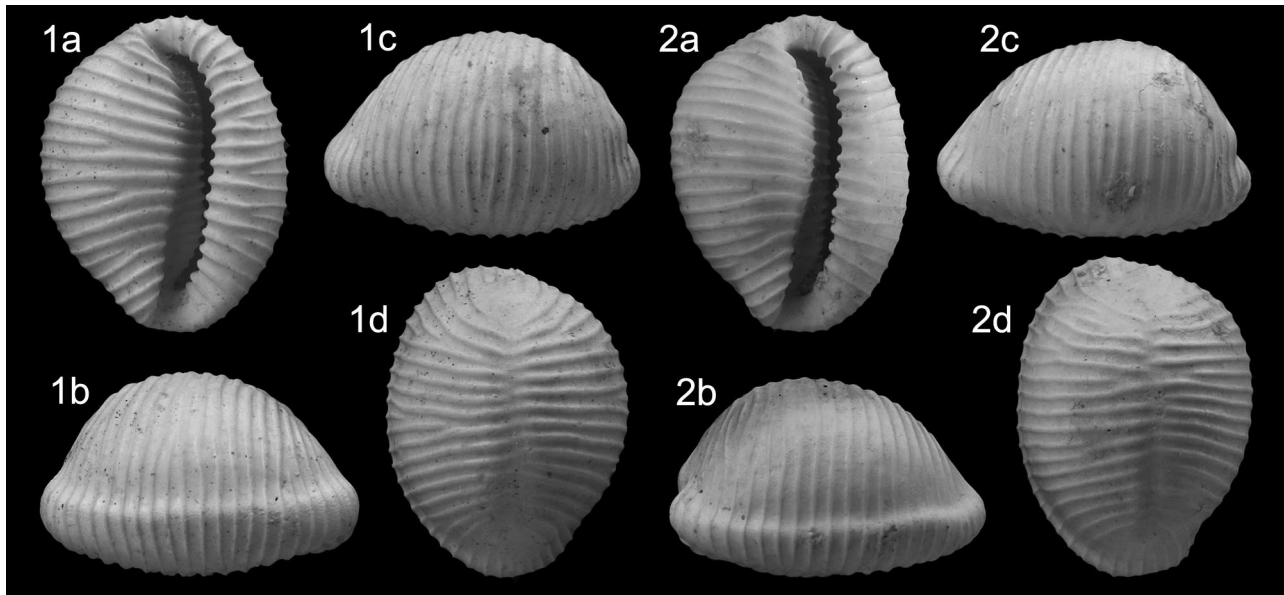
Plate 163, figs 1-2

- 1845 *Cypraea coccinella* Lam. – Grateloup, pl.41, fig. 31 (*non* Lamarck, 1811).  
 \*1894 *Trivia affinis* var. *excoccinella* Sacco, p. 50 (*nom. nov. pro Cypraea coccinella* Grateloup, 1845, *non* Lamarck, 1811).  
 1924 *Trivia burdigalensis* var. *excoccinella* Sacco – Cossmann & Peyrot, p. 384, pl. 10, figs 31-32.  
 1938 *Trivia sphaericulata* var. *minor* Montr. – Peyrot, p. 169, pl. 4, figs 70, 78 (on plate caption as *T. arctica* var. *minor*) (*non* Monterosato, 1878).  
 1952a *Trivia dimidiatoaffinis excoccinella* Sacco, 1894 – Glibert, p. 267, pl. 3, fig. 7.  
 1964 *Trivia dimidiatoaffinis* var. *excoccinella* Sacco, 1894 – Brébion, p. 325.

*Material and dimensions* – Maximum length 13.3 mm.

**Renauleau:** NHMW 2016/0103/1601-1602 (2), 2016/0103/1603 (18). **Beugnon:** RGM.1348378457 (6), RGM.1348459 (2).

*Discussion* – *Niveria excoccinella* (Sacco, 1894) is characterised by having a rather gibbose shell, broad and widely spaced ribs (14-18 in Renauleau specimens) that are not always bisected by the dorsal sulcus and a broad marginal callus. This is the largest *Niveria* species in the Assemblage I fauna. We have found it only at Renauleau. It differs from *N. dimidiatoaffinis* (Sacco, 1894), with



**Plate 163.** *Niveria excoccinella* (Sacco, 1894); 1. NHMW 2016/0103/1601, length 11.6 mm, height 7.6 mm; 2. NHMW 2016/0103/0617, length 13.0 mm, height 8.2 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

which it co-occurs (see above), in being larger, in having fewer and broader axials that are not as neatly bisected by the dorsal sulcus as they are in *N. dimidiatoaffinis*, and in having a wider marginal callus. *Niveria cylindriclementi* nov. sp. is much smaller, more cylindrical and again with neatly bisected axials along the dorsum. *Niveria pseudoavellana* (Sacco, 1894) is more globose with more numerous finer axials, which are not bisected by the dorsal sulcus mid-dorsum.

Brébion (1964, p. 326) recorded this species from Assemblages I-IV. However, we only confirm the Assemblage I locality of Renauleau. The rest of the records most probably pertain to other *Niveria* species.

**Distribution** – Lower Miocene: Atlantic, Aquitaine Basin (Burdigalian), France (Cossmann & Peyrot, 1924). Middle Miocene: Atlantic, Loire Basin (Langhian), France (Peyrot, 1938; Glibert, 1952a); Upper Miocene: Atlantic, NW France (Brébion, 1964).

#### *Niveria pseudoavellana* (Sacco, 1894)

Plate 164, figs 1-3

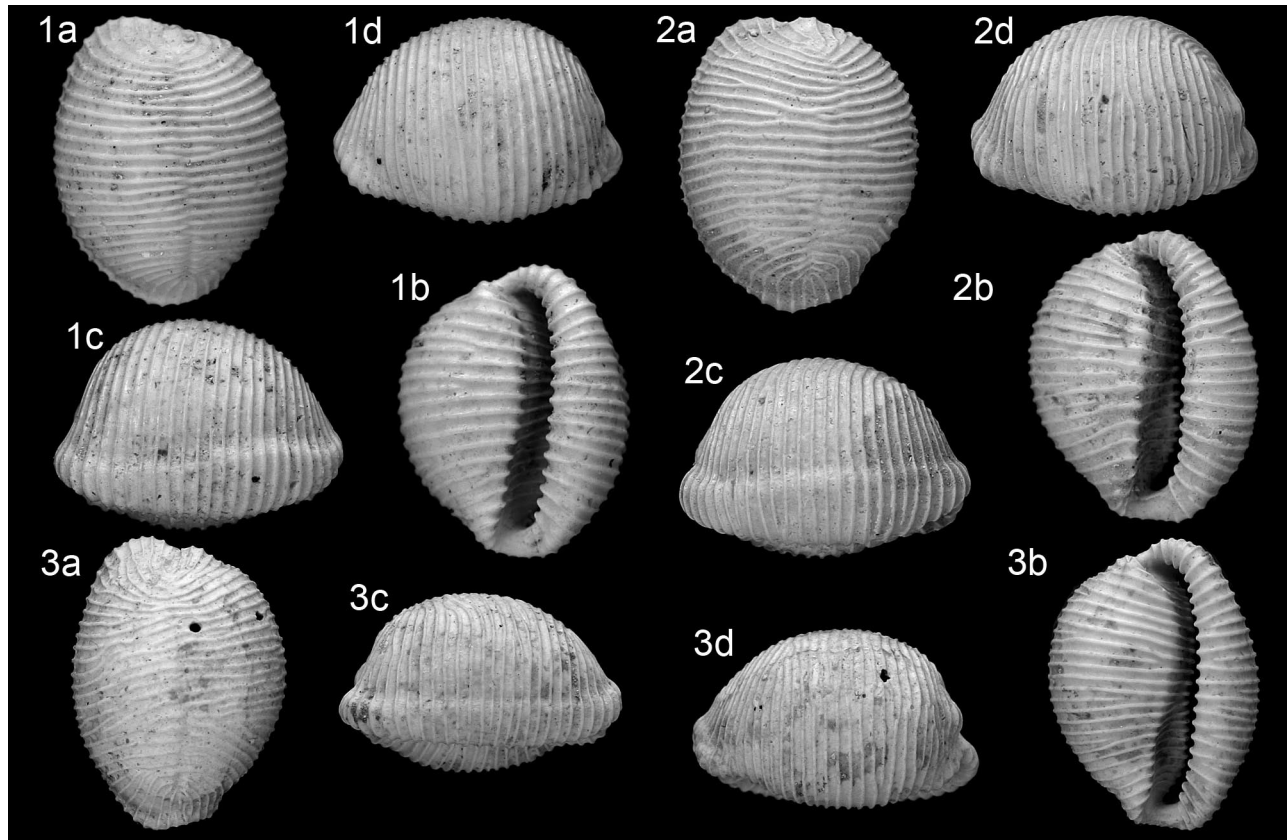
- \*1894 *Trivia sphaericulata* var. *pseudoavellana* Sacco, p. 49, pl. 3, fig. 34.
- 1938 *Trivia affinis* var. *pseudoavellana* Peyr. (*lapsus?*) – Peyrot, p. 172, pl. 4, fig. 74.
- 1984 *Trivia sphaericulata* var. *pseudoavellana* Sacco, 1894 – Ferrero Mortara *et al.*, p. 154, pl. 27, fig. 2.

**Material and dimensions** – Maximum length 10.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0646-0648 (3), NHMW 2016/0103/0649 (17), RGM.1348529 (1), RGM.1348676 (2). **Sceaux-d’Anjou:** RGM.1348288 (3), RGM.1348361 (15), RGM.1348650 (6), RGM.1348683 (4),

RGM.1348777 (1). **Renauleau:** NHMW 2016/0103/0663 (5).

**Revised description** – Shell medium-sized for genus, globose, oval (for measurements see Table 10). Spire covered by callus. Last whorl globose, rounded, 90% of total height. Terminals moderately produced. Dorsum rounded, completely covered by 22-25 narrow ribs, half the width of their interspaces. Dorsal sulcus marked by narrow, shallow, sinuous depression that bisects ribs only on dorsal quarters towards each extremity. Mid-dorsum, dorsal sulcus narrows, distorts or leaves ribs unaltered. When ribs bisected, minimally thickened adjacent to the sulcus. Base convex, with short terminals recurved. Aperture of moderate width, curved apically, slightly wider anteriorly. Outer lip somewhat broadened by moderate labial varix, convex, widest in mid-portion, narrowing towards terminals, regularly rounded. Outer lip bearing 17-22 strong, equal denticles. Siphonal and anal canals hardly protruding. Fossula broadly concave, poorly delimited from the rest of the columella. Columella convex, tapering steeply inwards, bordered internally by a weak carinal ridge. Carinal ridge expanded in fossular region. Columella bearing 16-17 equal denticles, which continue onto carinal ridge. Columellar angulation present, but not sharp.

**Discussion** – *Niveria pseudoavellana* (Sacco, 1894) is characterised by its medium-sized shell, globose ovate shape, with terminals weakly produced, a sinuous, narrow, shallow dorsal sulcus that bisects ribs only towards the extremities; ribs mid-dorsum narrowed, distorted or unaltered by the sulcus, ribs when bisected minimally thickened adjacent to the sulcus, a moderately thickened and varicose outer lip, bearing 17-22 strong, equal denticles, a broad, poorly delimited fossula and 16-17 equal



**Plate 164.** *Niveria pseudoavellana* (Sacco, 1894); 1. NHMW 2016/0103/0646, length 9.4 mm, width 7.6 mm, height 6.6 mm; 2. NHMW 2016/0103/0647, length 10.0 mm, width 8.2 mm, height 7.0 mm; 3. NHMW 2016/0103/0648, length 10.9 mm, width 8.1 mm, height 6.9 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

columellar denticles. It is closely similar in shape and size to *N. dimidiatoaffinis* (Sacco, 1894), with which it co-occurs, but is immediately separated by its dorsal sculpture. In *N. dimidiatoaffinis* the dorsal sulcus is straight, narrow, not depressed and cleanly bisects all the dorsal ribs, whereas in *N. pseudoavellana* the dorsal sulcus is slightly sinuous, depressed and only bisects the ribs towards the extremities. The sculpture mid-dorsum

is highly variable in that the ribs can be narrowed, discontinuous and overlapping, distorted or unaltered by the dorsal sulcus. *Niveria cylindriclementi* nov. sp. (see above) has similar dorsal sculpture to *N. dimidiatoaffinis*, with the sulcus bisecting all the dorsal ribs, but differs from both of the above species in having a smaller, more cylindrical and narrow shell. Two further species illustrated by Glibert (1952a) from the middle Miocene of the Loire Basin of France should be compared; *N. antiquosphaera* (Sacco, 1894) is probably the most similar to *N. pseudoavellana*, and has the same number of dorsal ribs, but in that species the dorsal sulcus, which is also marked by a narrow sinuous depression seems to either bisect, distort or narrow the ribs in a more irregular fashion and not bisect them at the extremities and modify or leave them unaltered mid-dorsum as in *N. pseudoavellana*. Moreover, according to Glibert's figure (1952a, pl. 3, fig 6d) the ribs are closer-set and equal to or wider than their interspaces, whereas in *N. pseudoavellana* the ribs are about half the width of their interspaces. The second species, *N. excocinella* (Sacco, 1894) also has a similar dorsal sulcus, but has wider ribs separated by narrow interspaces. The number of labial and columellar denticles cannot be used to separate any of these *Niveria* species reliably, although *N. dimidiatoaffinis* tends to have more columellar denticles than the other congeners discussed here.

Specimens from St-Clément-de-la-Place  
N = 10

Length (H)	max = 10.9 mm; min = 7.3 mm
Width (D)	max = 8.1 mm; min = 5.6 mm
Dorso-ventral height (d)	max = 6.9 mm; min = 4.8 mm
d/D index	84.5 (range 81-87)
d/H index	68.4 (range 63-70)
Number of denticles outer lip	18.4 (range 17-22)
Number of denticles inner lip	16.8 (range 15-22)
	80% specimens with 16-17

**Table 10.** *Niveria pseudoavellana* (Sacco, 1894); morphometrics of specimens from St-Clément-de-la-Place. Abbreviations follow Glibert (1952a): H = length, D = width, d = dorso-ventral height.



*Distribution* – Middle Miocene: Atlantic, Loire Basin (Langhian), France (Peyrot, 1938). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Mediterranean, Italy (Sacco, 1894). Upper Pliocene: Mediterranean, Italy (Sacco, 1894).

***Niveria* sp.**

Plate 165, figs 1-2

*Material and dimensions* – Maximum length 8.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0650 (1), NHMW 2016/0103/0651 (4). **Sceaux-d'Anjou:** NHMW 2016/0103/0652 (1), NHMW 2016/0103/0653 (13), RGM. 1348289 (8), RGM.1348362 (4). **Renauleau:** NHMW 2016/0103/0664 (1), LC (2).

*Discussion* – For measurements see Table 11. *Niveria* sp. is characterised by its strongly gibbose dorsum, bearing 23-27 dorsal ribs. The dorsal sulcus is narrow, not depressed and bisects all ribs, the ribs are narrower than their interspaces, and they are hardly thickened adjacent to the sulcus. The outer lip is strongly thickened mid-lip, with 15-18 denticles. The fossula is broadly concave and poorly delimited from the rest of the columella. The columella is convex, tapering steeply inwards, bordered internally by a weak carinal ridge, bearing 14-18 denticles. The shell size and the character of the dorsal sulcus is similar to that of *N. dimidiatoaffinis* (Sacco, 1894), but *Niveria* sp. differs in having a far more elevated gibbose dorsum and more numerous dorsal ribs. The outer lip is also more strongly inflated in the mid-portion. *Niveria pseudoavellana* (Sacco, 1894), like *Niveria* sp. has a more elevated dorsum than *N. dimidiatoaffinis*, but it is more evenly globose and not gibbose posteriorly as in *Niveria*

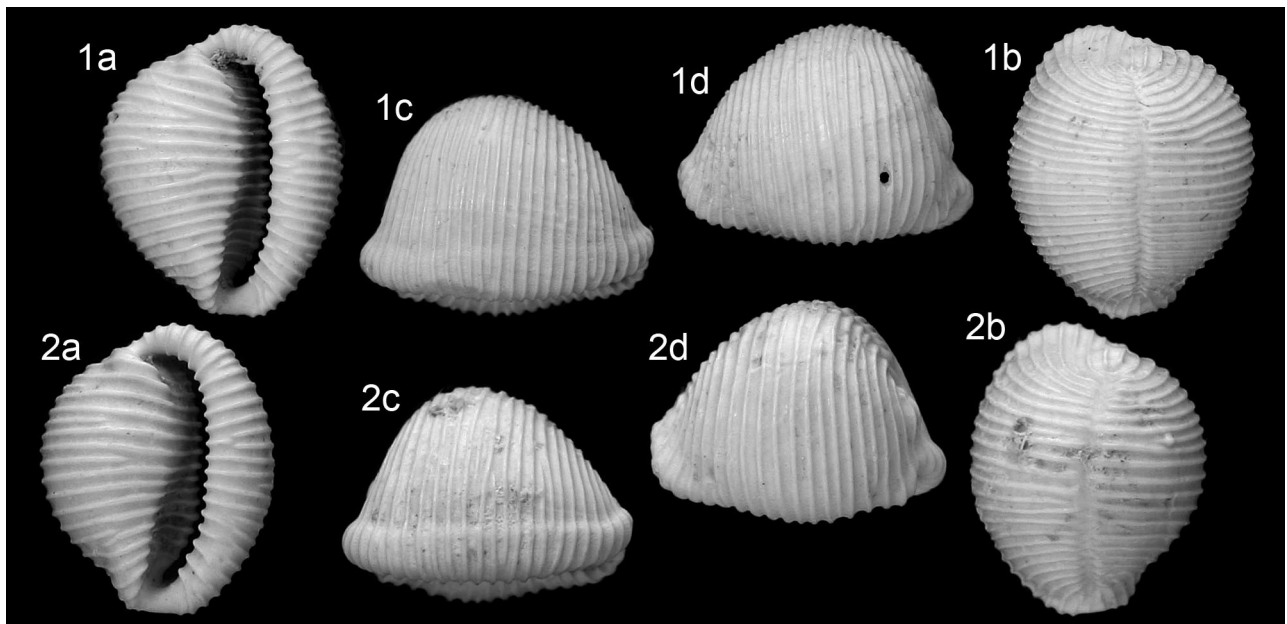
Specimens from St-Clément-de-la-Place  
N = 5

Length (H)	max = 8.1 mm; min = 6.7 mm
Width (D)	max = 5.7 mm; min = 6.7 mm
Dorso-ventral height (d)	max = 5.0 mm; min = 6.0 mm
d/D index	86.6 (range 83-90)
d/H index	72.8 (range 70-74)
Number of denticles outer lip	17.0 (range 15-18)
Number of denticles inner lip	15.6 (range 14-18)

**Table 11.** *Niveria* sp.; morphometrics of specimens from St-Clément-de-la-Place. Abbreviations follow Glibert (1952a): H = length, D = width, d = dorso-ventral height.

sp. The dorsal sulcus in *N. pseudoavellana* does not bisect the ribs mid-dorsum, whereas in *Niveria* sp. all dorsal ribs are bisected by the sulcus. We cannot find any species in the European literature with such a gibbose posterior part to the dorsum, but refrain from formally describing this species as some of the specimens are less gibbose and seem to intergrade with more globose specimens of *N. dimidiatoaffinis*. *Niveria permixta* (de Cristofori & Jan, 1832) from the Mediterranean Pliocene has a superficial dorsal gibbosity mid-dorsum, a callus pad that covers the dorsal ribs, whereas the gibbosity in *Niveria* sp. is due to an unusually elevated posterior dorsum.

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



**Plate 165.** *Niveria* sp.; 1. NHMW 2016/0103/0650, length 8.1 mm, height 6.0 mm, width 6.7 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/0652, length 6.5 mm, height 4.8 mm, width 5.4 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Cleotrivia* Iredale, 1930

*Type species* (by original designation) – *Cypraea pilula* Kiener, 1845, present-day, Hawaii.

1930 *Cleotrivia* Iredale, p. 83.

***Cleotrivia gallica* nov. sp.**

Plate 166, figs 1-5

*Type material* – Holotype MNHN.F.A57910, length 6.0 mm, width 5.0 mm, height 4.4 mm; paratype 1 MNHN.F.A57911, length 6.4 mm, width 5.1 mm, height 4.5 mm; paratype 2 NHMW 2016/0103/0626, length 6.9 mm, width 5.6 mm, height 5.0 mm; paratype 3 NHMW 2016/0103/0627, length 6.2 mm, width 5.1 mm, height 4.7 mm; paratype 4 NHMW 2016/0103/0629, length 6.7 mm, width 5.4 mm, height 4.9 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1348272, height 5.0 mm, width 4.1 mm; paratype 6 RGM.1348273, height 4.9 mm, width 4.3 mm; paratype 7 RGM.1348274, height 5.5 mm, width 4.4 mm; paratype 8 RGM.1348275, height 5.3 mm, width 4.3 mm, **Sceaux-d'Anjou**.

*Other material* – Maximum length 6.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0628 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0630-0631 (2), NHMW 2016/0103/0632 (20), RGM.1348276 (21), RGM.1348286 (29), RGM.1348363 (22), RGM.1348648 (9), RGM.1348680 (26), RGM.1348773 (17). **Renauleau**: NHMW 2016/0103/0665 (50+), RGM.1348883 (11), LC (50+), FVD (50+). **Beugnon**: RGM.1348456 (6), RGM.1348460 (4), RGM.1348462 (9).

*Etymology* – Named after the Roman province of Gaul, Latin: *Gallia*, a region of Western Europe encompassing present-day France. *Cleotrivia* gender feminine.

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

*Stratum typicum* – Tortonian, upper Miocene.

*Diagnosis* – *Cleotrivia* species of small size, globose, of medium thickness, dorsum evenly rounded, completely covered by 14-17 strong, irregular, interrupted ribs, which are usually bisected, narrowed or distorted by well developed dorsal sulcus, although occasionally unaltered, outer lip broad, thickened by labial varix, bearing 14-19 narrow, equal denticles, 14-15 columellar denticles, which run unaltered onto carinal ridge, fossula weakly concave, poorly delimited.

*Description* – Shell small, of medium thickness, globose (for measurements see Table 12). Spire covered by callus, faintly visible beneath three vertical riblets extending upwards from the posterior terminal. Last whorl globose, about 90% of total height. Terminals moderately produced, blunt, flattened. Dorsum evenly rounded,

Specimens from St-Clément-de-la-Place  
N = 10

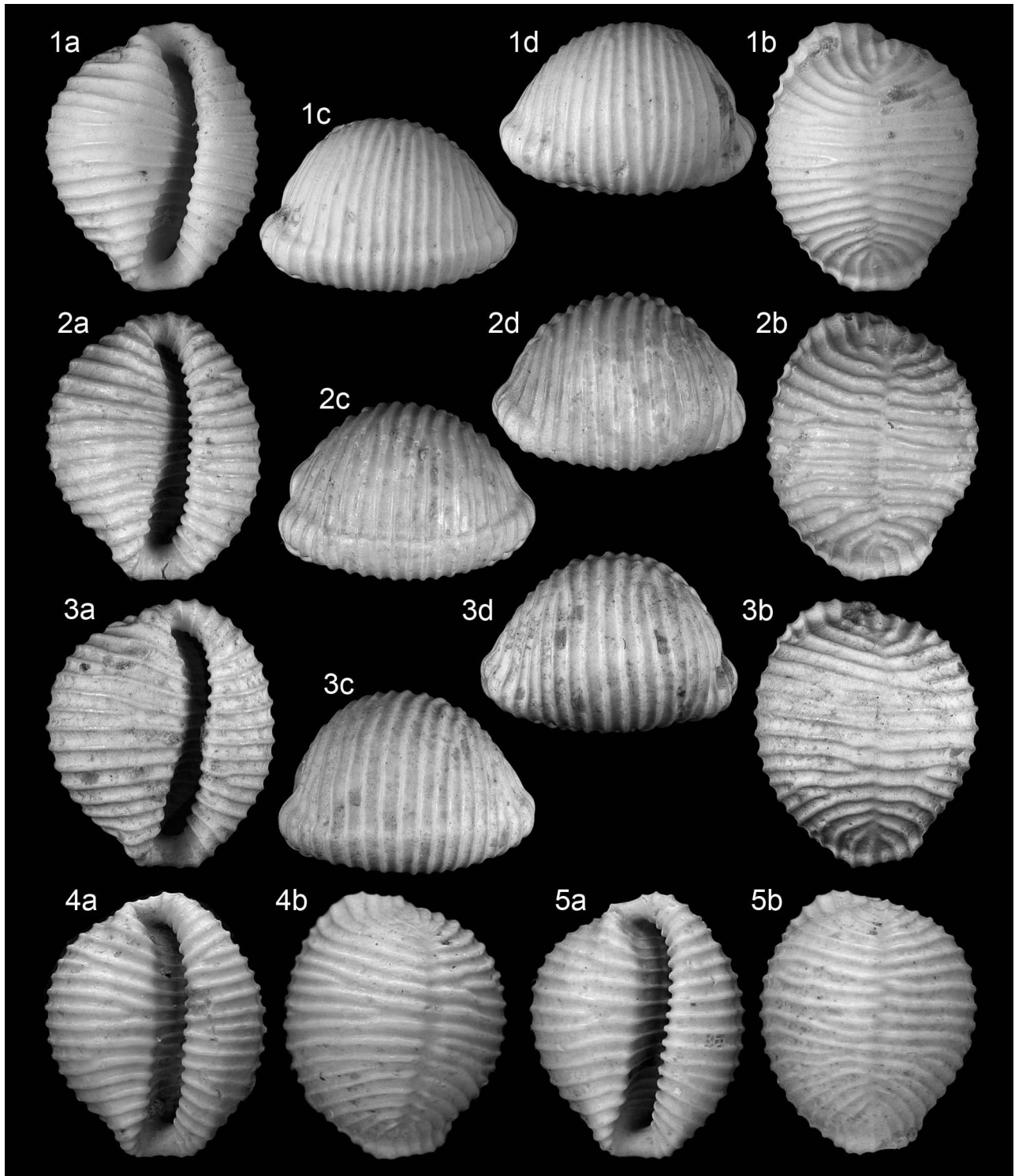
Length (H)	max = 6.9 mm; min = 4.9 mm
Width (D)	max = 5.6 mm; min = 3.9 mm
Dorso-ventral height (d)	max = 5.0 mm; min = 3.2 mm
d/D index	88.9 (range 88-92)
d/H index	72.8 (range 70-76)
Number of denticles outer lip	17.3 (range 14-19)
Number of denticles inner lip	14.5 (range 14-15)

**Table 12.** *Cleotrivia gallica* nov. sp.; morphometrics of specimens from St-Clément-de-la-Place. Abbreviations follow Glibert (1949): H = length, D = width, d = dorso-ventral height.

completely covered by 14-17 strong, irregular ribs, with interruptions. Dorsal sulcus well developed, marked by dorsal depression, bisecting, narrowing or distorting ribs, although occasionally ribs unaltered. Base and terminals evenly convex. Aperture weakly curved, slightly wider anteriorly. Outer lip broad, thickened by labial varix, evenly rounded, widest in mid-portion, narrowing towards terminals bearing 14-19 narrow, equal denticles. Siphonal and anal canals wide, weakly indented. Columella concave, bordered internally by very weak carinal ridge, bearing 14-15 ribs, which run unaltered onto carinal ridge. Carinal ridge expanded in fossular region. Fossula weakly concave, poorly delimited.

*Discussion* – We use the genus *Cleotrivia* Iredale, 1930 for species with a small, globular or subglobular inflated shell, the presence of a dorsal sulcus of variable strength, which influences the dorsal ribbing to a variable degree, and short blunt terminals. Fehse & Landau (2003, p. 104) recognised an Indo-Pacific group in which the shell was strongly globose and the sulcus deeply grooved, extending the whole length of the dorsum, and an Atlantic-Caribbean group with less globose shells, in which the sulcus was most strongly developed mid-dorsally, but shorter, not extending all the way between the terminals, only slightly depressing the dorsal ribbing. *Cleotrivia esteponica* Fehse & Landau, 2003 from the lower Piacenzian upper Pliocene of the Estepona Basin, southern Spain, was the first European fossil member of the genus recognised. It is characterised by its inflated shell, elevated dorsum and weak dorsal sulcus typical of the Atlantic-Caribbean group and was considered most similar, and possibly ancestral to *C. wernerii* (Fehse, 1999).

*Cleotrivia gallica* nov. sp. has a well-developed depressed dorsal sulcus, which extends across the entire dorsum, but affects the ribs variably; bisecting, narrowing or distorting them, and occasionally the ribs cross the sulcus unaltered. This leads to a wide variability in dorsal rib pattern as can be seen in the series illustrated. The strength of the dorsal sulcus separates this species from all its European and West African congeners and is un-



**Plate 166.** *Cleotrivia gallica* nov. sp.; 1. **Holotype** MNHN.F.A57910, length 6.0 mm, width 5.0 mm, height 4.4 mm; 2. **Paratype 1** MNHN.F.A57911, length 6.4 mm, width 5.1 mm, height 4.5 mm; 3. **Paratype 2** NHMW 2016/0103/0626, length 6.9 mm, width 5.6 mm, height 5.0 mm; 4. **Paratype 3** NHMW 2016/0103/0627, length 6.2 mm, width 5.1 mm, height 4.7 mm; 5. **Paratype 4** NHMW 2016/0103/0629, length 6.7 mm, width 5.4 mm, height 4.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

sual for the Atlantic-Caribbean group. The importance of the dorsal sulcus as a generic character in this and other triviid genera, as well as the biogeographic scenario and circumglobal monophyly suggested by Fehse (1999) for

*Cleotrivia* needs to be tested genetically.

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



Superfamily Vetulinoidea Gray, 1840  
 Family Vetulinidae Gray, 1840  
 Subfamily Lamellariinae d'Orbigny, 1841  
 Genus *Lamellaria* Montagu, 1815

*Type species* (by subsequent designation, Pchelintsev & Korobkov, 1960): *Helix perspicua* Linnaeus, 1758, present-day, Europe.

- 1815 *Lamellaria* Montagu, p. 184.  
 1823 *Marsenia* Oken, pp. 458, 460. *Type species* (by monotypy): *Bulla haliotoidea* Montagu, 1803 [= *Lamellaria perspicua* (Linnaeus, 1758)], present-day, Europe.  
 1853 *Cryptocella* H. & A. Adams, p. 202. *Type species* (by subsequent designation, Kobelt, 1878): *Lamellaria tentaculata* Montagu, 1815 [= *Lamellaria latens* (Müller, 1776)], present-day, Europe.

***Lamellaria falunica* de Morgan, 1920**

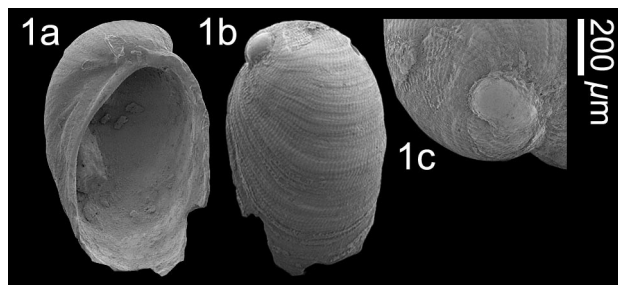
Plate 167, fig. 1

- \*1920 *Lamellaria falunica* de Morgan, p. 334, fig. 41.

*Material and dimensions* – Maximum height 2.2 mm, width 1.4 mm. **Renauleau:** NHMW 2016/0103/0686 (1), NHMW 2016/0103/1442 (2).

*Discussion* – *Lamellaria falunica* de Morgan, 1920 is exceedingly uncommon in the Assemblage I deposits. The few shells available agree with the description and figure given by de Morgan (1920, p. 334), which shows a very small shell, rather more flattened than the present-day European species *L. latens* (Müller, 1776) and *L. perspicua* (Linnaeus, 1758), which are both markedly larger than the French Miocene species. The apical whorl is abraded in the material at hand, but it seems to have a paucispiral protoconch (Pl. 167, fig. 1c). The elongate oval contour and the narrow venter of the last whorl are similar to one of the shells illustrated by de Morgan (1920, fig. 41 a, b).

*Distribution* – Middle Miocene: Atlantic, Loire Basin, France (de Morgan, 1920). Upper Miocene: Atlantic (Tortonian), NW France (this paper).



**Plate 167.** *Lamellaria falunica* de Morgan, 1920; 1. NHMW 2016/0103/0686, height 1.9 mm, width 1.2 mm (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

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

- 1798 *Ficus* Röding, p. 148.

For generic synonymy see Van Dingenen *et al.* (2016, p. 154).

***Ficus geometra* (Borson, 1825)**

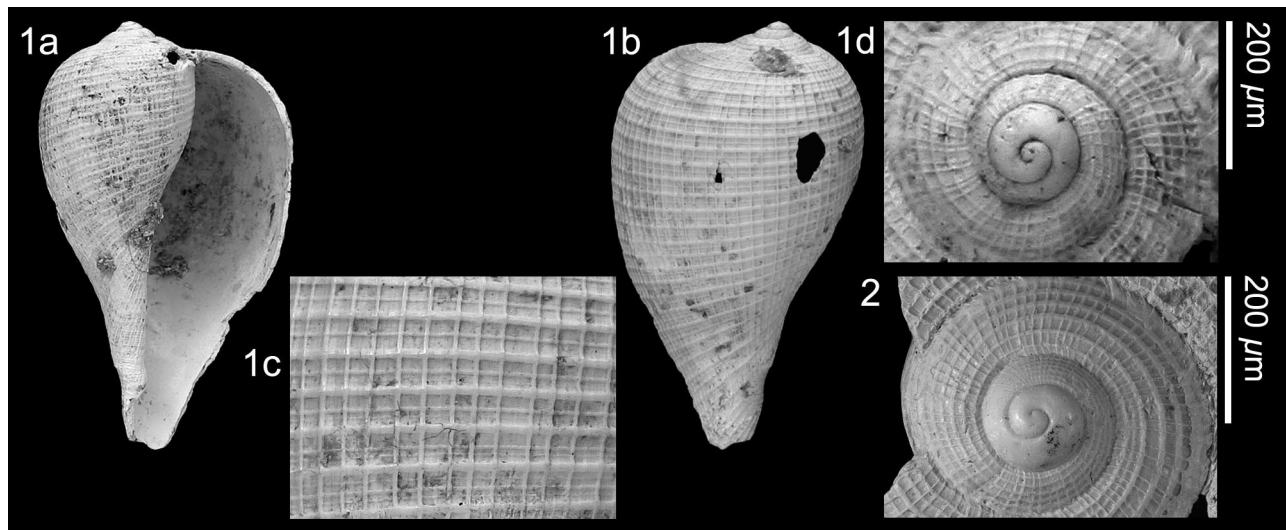
Plate 168, figs 1-2

- \*1825 *Pyrula geometra* Borson, p. 311.  
 1854 *Pyrula Subclathrata* d'Orb – Millet, p. 162 (*non* d'Orbigny, 1852).  
 1964 *Ficus geometra* var. *berilla* de Gregorio, 1885 – Brébion, p. 360, pl. 8, fig. 22-24.  
 1964 *Ficus geometra* var. *bifida* Brébion, p. 360, pl. 8, fig. 25.  
 2004b *Ficus geometra* (Borson, 1825) – Landau *et al.*, p. 79, pl. 8, fig. 3 (*cum syn.*).  
 2016 *Ficus geometra* (Borson, 1825) – Van Dingenen *et al.*, p. 154, pl. 13, figs 5, 6 (*cum syn.*).

*Material and dimensions* – Maximum height 30.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0563 (fragments), RGM.1348248 (2 fragments). **Sceaux d'Anjou:** NHMW 2016/0103/0562 (fragments), RGM.1347954 (1 juveniles + 4 fragments), RGM.1347975 (2), RGM.1347979 (3 fragments), RGM.1348023 (22 fragments), RGM.1348572 (1 fragment), RGM.1348878 (1 fragment), FVD (1). **Renauleau:** NHMW 2016/0103/1407 (1), LC (5), FVD (2). **Beugnon:** RGM.1348392 (1 adult fragment + 1 juvenile).

*Discussion* – Landau *et al.* (2004b) discussed the Mediterranean Pliocene species of *Ficus*, drawing attention to the importance of the protoconch characters, and concluded that three species occurred: *Ficus subintermedia* (d'Orbigny, 1852), *F. geometra* (Borson, 1825) and *F. ficoides* (Brocchi, 1814). The numerous Pliocene records for *F. condita* (Brongniart, 1823) are incorrect and refer to *F. subintermedia*.

*Ficus geometra* differs from *F. subintermedia* in having the squares formed by the reticulate pattern flat and without secondary spiral ornament, or at most one secondary spiral thread, whereas in *F. subintermedia* they are concave, with 1-3 spiral threads in the interspaces. The number of primary spiral cords in *F. subintermedia* is always greater than in *F. geometra* (20-25 vs. 30+). According to Caprotti (1973) the number of spiral cords on the first two teleoconch whorls is the most reliable distinguishing character; three spiral cords are present in *F. subintermedia*, 5-6 in *F. geometra*. The specimens from Assemblage I have a single thread running along



**Plate 168.** *Ficus geometra* (Borson, 1825); 1. NHMW 2016/0103/0562, height 30.0 mm, width 17.2 mm; 1c, detail of teleoconch sculpture; 1d, detail of protoconch. La Presselière, Sceaux-d'Anjou; 2. NHMW 2016/0103/0563, detail of protoconch. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the centre of the squares and six spiral cords on the early teleoconch whorls; typical for *F. geometra*.

The three Pliocene species can also be distinguished by their protoconchs. Both *Ficus ficoides* and *F. geometra* have relatively large protoconchs with a small nucleus, whereas *F. subintermedia* has a protoconch of only 1.5 whorls with a smaller diameter, but a larger nucleus than in *F. geometra* and *F. ficoides*. The protoconch of the specimens at hand consists of 2.2 whorls, slightly less than the 2.4-2.75 recorded by Landau *et al.* (2004b, p. 79) for *F. geometra* and consequently slightly smaller in diameter, but with a similar nuclear and first protoconch whorl diameter ( $dp = 180 \mu\text{m}$ ,  $dn = 25 \mu\text{m}$ ,  $dp1 = 60 \mu\text{m}$ ). *Ficus ficoides* is easily distinguished from the other two Pliocene species by the character of the spiral sculpture, which forms 15-18 prominent, subacute carinae with strongly concave interspaces. For further discussion see Van Dingenen *et al.* (2016, p. 155).

Brébion (1964, p. 360) recorded this species, as *F. geometra* var. *berilla*, from Assemblage I localities (Renauleau, Thorigné, Sceaux-d'Anjou, St-Michel, Contigné) and as *F. geometra* var. *bifida* (1964, p. 361) from Assemblage III localities (Le Pigeon Blanc, Les Cléons, La Dixmerie) and Assemblage IV (Gourbesville), which were said to be a little different. We have not seen these specimens, and provisionally exclude them from the distribution.

**Distribution** – Middle Miocene: ?North Sea basin, Jutland, Denmark (Sorgenfrei, 1958); Proto-Mediterranean, Italy (Sacco, 1890b); Paratethys Austria, (Hörnes, 1856; Hoernes & Auinger, 1890), Poland (Friedberg, 1912; Baluk, 1995), Hungary (Csepregy-Meznerics, 1969; Strausz, 1966). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1890b). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al.*, 2016); western Mediterranean, northeastern Spain, (Martinell, 1979;

Solsona, 1998, 1999); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1973, 1974; Pavia, 1975; Cavallo & Repetto, 1992; Chirli, 2008; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona, S. Spain (Landau *et al.*, 2004b), France (Chirli & Richard, 2008); central Mediterranean, Italy (Sacco, 1890b; Caprotti, 1973).

Superfamily Stromboidea Rafinesque, 1815

Family Aporrhaidae Gray, 1850

Subfamily Aporrhainae Gray, 1850

Genus *Aporrhais* Da Costa, 1778

**Type species** (by monotypy) – *Strombus pespelecani* Linnaeus, 1758, present-day, Europe.

1778 *Aporrhais* Da Costa, p. 138.

1836 *Chenopus* Philippi, p. 214. Type species (by subsequent designation, Cossmann, 1904): *Strombus pespelecani* Linnaeus, 1758, present-day, Europe. Junior objective synonym of *Aporrhais*, with the same type species.

#### ***Aporrhais uttingeriana* (Risso, 1826)**

\*1826 *Rostellaria uttingerianus* Risso, p. 225.

1964 *Aporrhais uttingerianus* Risso, 1826 – Brébion, p. 101, pl. 7, fig. 29.

2004a *Aporrhais* (*Aporrhais*) *uttingeriana* (Risso, 1826) – Landau *et al.*, p. 67, pl. 14, fig. 8.

2008 *Aporrhais uttingerianus* (Risso, 1826) – Chirli & Richard, p. 25, pl. 3, fig. 9.

2008 *Aporrhais uttingerianus* (Risso, 1826) – Chirli, p. 11, pl. 3, figs 10-16.

2010 *Aporrhais uttingeriana* (Risso, 1826) – Sosso &

Dell'Angelo, p. 23, unnumbered fig. p. 33, 3<sup>rd</sup> row right.

2014 *Aporrhais uttingeriana* (Risso, 1826) – Brunetti, p. 31, unnumbered figs.

**Material and dimensions** – Maximum height 22.0 mm, width 14.5 mm. **St-Clément-de-la-Place**: 2 specimens; musée d'Angers (*vide* Brébion, 1964, p. 319).

**Discussion** – Brébion (1964, p. 319) recorded two specimens from the Assemblage I locality of St-Clément-de-la-Place. Despite consulting extensive collections from this locality, we have not seen a single fragment of aporrhaid from any Assemblage I locality. This is unexpected, as in the authors' experience, in deposits in which *Aporrhais* occur, they are usually plentiful. The specimen figured by Brébion is typical of the species *A. uttingeriana* (Risso, 1826), characterised by having a relatively short, broad spire, a sharp, obsolete nodular carina, extensive, thick columellar callus and labial digitations that are long, almost straight and not expanded. *Aporrhais uttingeriana* is usually found in deposits representing deeper muddy bottoms, which may explain their scarcity in these predominantly very shallow sandy Assemblage I deposits, where one would expect to find *A. pespelicani* (Linnaeus, 1758). Nevertheless, it is impossible to confuse this species with any other, and we therefore accept Brébion's record and include it here in the assemblage.

**Distribution** – Middle Miocene: Paratethys, Poland (Friedberg, 1911), Vienna (Venzo & Pelosio, 1963). Upper Miocene: Atlantic, NW France (Brébion, 1964), Morocco (Lecointre, 1952); Proto-Mediterranean, Po valley, Italy (Sacco, 1893). Lower Pliocene: western Mediterranean, northeastern Spain, (Martinell, 1979), Roussillon, France (Fontannes, 1879; Martinell & Domènech, 1986); central Mediterranean, Italy (Sacco, 1893; Palla, 1967; Caprotti, 1974; Chirli, 2008; Brunetti, 2014), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Morocco (Lecointre, 1952); western Mediterranean, Estepona, Spain, (Landau *et al.*, 2004a), France (Chirli & Richard, 2008); central Mediterranean, Italy (Malatesta, 1974; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1912; Brambilla *et al.*, 1988), Sicily (Glibert, 1963).

Superfamily Xenophoroidea Troschel, 1852 (1840)

Family Xenophoridae Troschel, 1852 (1840)

Genus *Xenophora* Fischer von Waldheim, 1807

**Type species** (by subsequent designation, Gray, 1847b) – *Xenophora laevigata* Fischer von Waldheim, 1807 (= *Trochus conchyliophorus* Born, 1780), present-day, Caribbean.

1807 *Xenophora* Fischer von Waldheim, p. 213.

1810 *Phorus* de Montfort, p. 158. Type species (by original designation): *Trochus agglutinans* Lamarck, 1804, Eocene, France.

### *Xenophora deshayesi* (Michelotti, 1847)

Plate 169, figs 1-2

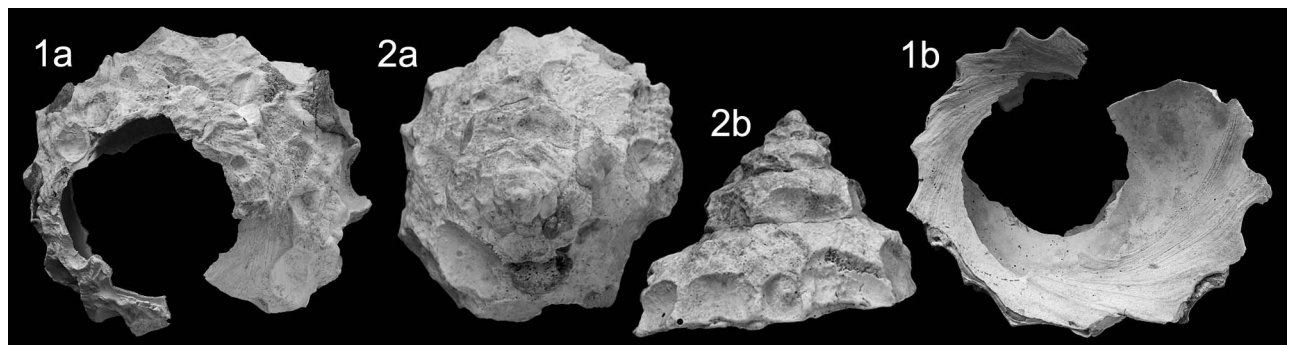
\*1847 *Phorus Deshayesii* Michelotti, p. 173.

2013 *Xenophora deshayesi* (Michelotti, 1847) – Landau *et al.*, p. 97, fig. 19/2, pl. 9, figs 11, 12 (*cum syn.*).

**Material and dimensions** – Height 24.1 mm; width 29.4 mm (fragment). **Sceaux-d'Anjou**: RGM.1348199 (1 fragment), LC (1 fragment), FVD (1). **Renauleau**: NHMW 2016/0103/1473 (1), LC (3 fragments), FVD (1 + 1 fragment).

**Discussion** – This species was fully discussed in Landau *et al.* (2013, p. 97). The Assemblage I material is fragmentary, but the strongly stepped spire and the coarse rugose sculpture is characteristic of the species. For comparison with European Neogene congeners see Landau *et al.* (2013). Stratigraphically this is the youngest record for the species.

**Distribution** – Lower Miocene: Atlantic (Aquitainian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1919; Lozouet *et al.*, 2001; Min-Da, 1984); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Denmark (Sorgenfrei, 1958); Netherlands (Nordsieck, 1972; Janssen, 1984), Belgium (Glibert, 1952b), Germany (Kautsky, 1925; Anderson, 1964; Wienrich, 2001). Middle Miocene: northeastern



**Plate 169.** *Xenophora deshayesi* (Michelotti, 1847); 1. FVD collection, height 38.3 mm, width 80.8 mm; 2. NHMW 2016/0103/1473, height 24.1 mm; width 29.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.



Atlantic (Langhian): Aquitaine Basin, (Min-Da, 1984); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1928; Bafuk, 2001), Vienna Basin, Austria (Hörnes, 1856; Schultz, 1998), Bulgaria (Kojumdzieva & Strachimirov, 1960), Hungary (Strausz, 1962, 1966), Ukraine (Zelinskaya *et al.*, 1968); Proto-Mediterranean Sea (Langhian): Kasaba Basin, Turkey (İslamoğlu, 2004), (Serravallian): Karaman Basin, Turkey (Fischer, 1866; Landau *et al.*, 2013). Upper Miocene: Atlantic, NW France (this paper).

## Discussion

In this paper we record 174 caenogastropod species (of which 20 are left in open nomenclature), representing 78 genera. This is almost three times the number of species reported by Brébion (1964) from the Assemblage I localities of NW France. Sixty-five are described as new: *Bittium crassum* nov. sp., *Bittium gallicum* nov. sp., *Bittium pingue* nov. sp., *Bittium renauleauense* nov. sp., *Semibittium brebioni* nov. sp., *Archimediella sancticlementensis* nov. sp., *Oligodia chauvereauensis* nov. sp., *Crassitonella lozoueti* nov. sp., *Acirsa sceauxensis* nov. sp., *Papuliscala redoniensis* nov. sp., *Papuliscala presselierensis* nov. sp., *Payraudeautia obelixa* nov. sp., *Inella alia* nov. sp., *Inella rolani* nov. sp., *Monophorus renauleauensis* nov. sp., *Obesula marshalli* nov. sp., *Triphora buscheri* nov. sp., *Triphora chauvereauensis* nov. sp., *Triphora fernandezgarcesi* nov. sp., *Triphora lherbetorum* nov. sp., *Triphora miopygmaea* nov. sp., *Triphora sancticlementensis* nov. sp., *Cerithiopsis cerithiopsoides* nov. sp., *Cerithiopsis esterae* nov. sp., *Cerithiopsis mira* nov. sp., *Dizoniopsis boucheti* nov. sp., *Seila petasa* nov. sp., *Ataxocerithium turbineum* nov. sp., *Alvania armata* nov. sp., *Alvania couffoni* nov. sp., *Alvania fezata* nov. sp., *Alvania globosa* nov. sp., *Alvania insulsa* nov. sp., *Alvania josephineae* nov. sp., *Alvania lachrimula* nov. sp., *Alvania milletispinosa* nov. sp., *Alvania miocalasi* nov. sp., *Alvania miolactea* nov. sp., *Alvania napoleoni* nov. sp., *Alvania parasusieae* nov. sp., *Alvania redoniana* nov. sp., *Alvania renauleauensis* nov. sp., *Alvania subtiliangulosa* nov. sp., *Alvania susieae* nov. sp., *Alvania tenuisculpturata* nov. sp., *Alvania turtaudierei* nov. sp., *Pseudosetia wahreni* nov. sp., *Pseudosetia sergegofasi* nov. sp., *Pseudosetia peyroti* nov. sp., *Pseudosetia ivolasi* nov. sp., *Onoba redoniensis* nov. sp., *Onoba incisa* nov. sp., *Onoba fragilis* nov. sp., *Rissoa decorticata* nov. sp., *Rissoa torquata* nov. sp., *Powellisetia europaea* nov. sp., *Pusillina dollfusi* nov. sp., *Pusillina gallica* nov. sp., *Discopsis pseudocanui* nov. sp., *Tornus superlatus* nov. sp., *Teinostoma obesum* nov. sp., *Macromphalina morgani* nov. sp., *Trivia sceauxensis* nov. sp., *Niveria cylindriclementi* nov. sp. and *Cleotrivia gallica* nov. sp.

Of the 174 caenogastropod species recorded here, 112 (64%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. Stratigraphically (see Fig. 4), 43 (25%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1949). Forty-four species

(26%) are also present in the Assemblage III (sensu Van Dingenen *et al.*, 2015) of northwestern France. Twenty-one species (12%) are also found in the North Sea Basin Pliocene. Forty-four species (25%) are relatively cosmopolitan in the European Pliocene, found in the Atlantic and Mediterranean. Twenty-three (13%) are still living in European Atlantic and/or Mediterranean waters.

We were able to identify or interpret most of the species recorded by Brébion (1964) with a few exceptions:

*Nerita (Theliostyla) funata* Dujardin, 1837 (1964, p. 138, not figured) is represented by a single specimen from St-Michel. This record is probably reliable, but we cannot confirm it.

*Protoma quadriplicata* de Basterot, 1825 (1964, p. 5, fig. 11) is represented by a single fragment from Sceaux-d'Anjou. This species was synonymised with *P. cathedralis* (Brongniart, 1823) (Lozouet *et al.*, 2001, p. 28). The figured fragment does not seem to represent that species. The genus *Protoma* is typical of the lower Miocene and we are not aware of its presence of in the European upper Miocene.

*Melanopsis praemorsa* (Linnaeus, 1758) (1964, pl. 5, fig. 18). Five specimens recorded from St-Michel. This is a freshwater species that we have not found in any of the collections consulted.

*Potamides (Ptychopotamides) papaveraceus* de Basterot, 1825 (1964, p. 220, not figured). Brébion referred to a record by Dollfus (1907) from Beaulieu. This species was synonymised with *Tympanotonos cinctus* (Bruguière, 1792) (Lozouet *et al.*, 2001, p. 26). Like Brébion, we have not found it in any of the collections consulted.

*Thyca (Cyclothyca) sulcosa* (Brocchi, 1814) (1964, p. 312, not figured). Brébion referred to species lists given by Couffon (1907) from St-Clément-de-la-Place and Les Pierres Blanches. Like Brébion, we have not found it in any of the Assemblage I collections consulted. It is possible that this is a misidentification and the record refers to *Clathrella chlathrata* (Philippi, 1844), a pyramidellid with a superficially similar shell that is abundant in those deposits.

*Neverita olla* (de Serres, 1829) (1964, p. 338, not figured) Brébion recorded this species widely in the Assemblage I deposits; from Renauleau, Sceaux-d'Anjou, St-Clément-de-la-Place and Les Pierres Blanches, and yet, inexplicably, there is not a single specimen in any of the collections consulted. *Neverita olla* is widely distributed in both the European Miocene and Pliocene and it is hard to imagine a mis-identification with such a recognizable shell. We await confirmation before listing this species.

The generic composition is not unusual for European Miocene Atlantic assemblages, with a strong presence of small-shelled genera, which are not only prominent in

numbers but also rich in species; for example the genus *Bittium* is represented by seven species and *Alvania* by 25 species. Even groups usually represented by medium-sized species, such as the turritellids, are here represented by small endemic species. The larger-shelled groups, such as the tonnoideans and strombids, are notable for their absence. The dwarfism seen in the fauna, or what Lauriat-Rage (1981) called 'nanisme' was already commented on in part 1 of this series (Landau *et al.*, 2017).

The assemblage is highly endemic with 109 (63%) species occurring exclusively in the northwestern French Assemblage I-III. This concurs with the observation that there is a strong predisposition for non-planktotrophic-type protoconchs, especially amongst the endemic species. Interestingly, the rate of endemism found amongst the Patellogastropoda and Vetigastropoda was also 63% (Landau *et al.*, 2017).

The caenogastropod generic composition is not particularly thermophilic, although it does include a number of taxa that no longer occur at these latitudes today, but do occur along the eastern Atlantic frontage further south, such as *Cochlis*, *Payraudeautia*, *Thylacodes*, *Macromphalus*, *Schilderia* and *Neosimnia*. As mentioned above strombids, which are a caenogastropod marker for fully tropical environments (Monegatti & Raffi, 2001), are absent from Assemblage I-IV.

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

### Acknowledgements

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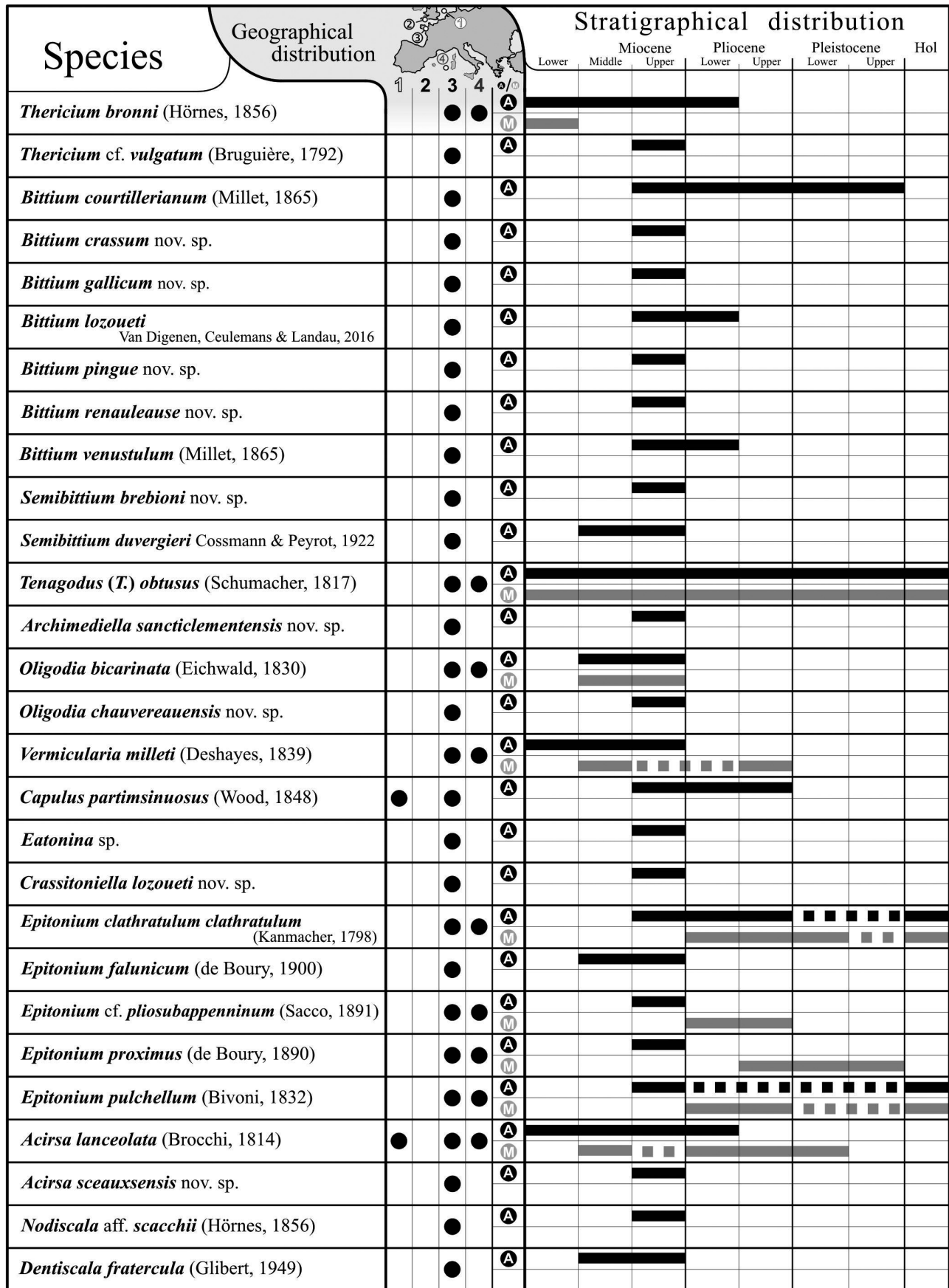


Figure 4. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black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



Species	Geographical distribution					Stratigraphical distribution							
	1	2	3	4	A/M	Miocene Lower	Miocene Middle	Miocene Upper	Pliocene Lower	Pliocene Upper	Pleistocene Lower	Pleistocene Upper	Hol
<i>Cirsotrema bourgeoisi</i> de Boury in Cossmann, 1912			●		A		■	■					
<i>Cirsotrema funiculus</i> (Wood, 1872)	●		●		A			■	■	■	■	■	■
<i>Papuliscala redoniensis</i> nov. sp.			●		A			■					
<i>Papuliscala presselierensis</i> nov. sp.			●		A			■					
<i>Cheilea equestris</i> (Linnaeus, 1758)			●	●	A M	■	■	■	■				
<i>Littorinopsis prevostina</i> (de Basterot, 1825)			●		A	■							
<i>Melarhaphé gibbosa</i> (Etheridge & Bell, 1893)	●	●	●		A			■	■	■	■	■	■
<i>Cochlis neglecta</i> (Mayer, 1858)	●		●	●	A	■	■	■					
<i>Cochlis</i> sp.			●		A			■					
<i>Tectonatica prietoi</i> (Hidalgo, 1873)			●	●	A M			■	■	■	■	■	■
<i>Euspira helicina helicina</i> (Brocchi, 1814)	●		●	●	A	■	■	■	■	■	■	■	■
<i>Euspira varians</i> (Dujardin, 1837)			●		A			■	■	■	■	■	■
<i>Payraudeautia obelixi</i> nov. sp.			●		A			■					
<i>Payraudeautia pigenblancensis</i> Van Dingenen, Ceulemans & Landau, 2016			●		A			■	■				
<i>Polinices redemptus</i> (Michelotti, 1847)			●	●	A M	■	■	■	■	■	■	■	■
<i>Inella alia</i> nov. sp.			●		A			■					
<i>Inella rolani</i> nov. sp.			●		A			■					
<i>Monophorus renauleauensis</i> nov. sp.			●		A			■					
<i>Obesula marshalli</i> nov. sp.			●		A			■					
<i>Triphora buscheri</i> nov. sp.			●		A			■					
<i>Triphora chauvereauensis</i> nov. sp.			●		A			■					
<i>Triphora fernandezgarcesi</i> nov. sp.			●		A			■					
<i>Triphora lherbetorum</i> nov. sp.			●		A			■					
<i>Triphora miopygmaea</i> nov. sp.			●		A			■					
<i>Triphora sancticlementensis</i> nov. sp.			●		A			■					
<i>Metaxia metaxa</i> (Delle Chiaje, 1828)	●	●	●		A M			■	■	■	■	■	■
<i>Cerithiopsis barleei</i> Jeffreys, 1867	●	●	●		A M			■	■	■	■	■	■
<i>Cerithiopsis cerithiopsoides</i> nov. sp.			●		A			■					
<i>Cerithiopsis esterae</i> nov. sp.			●		A			■					
<i>Cerithiopsis minima</i> (Brusina, 1865)			●	●	A M			■	■	■	■	■	■

Species	Geographical distribution					Stratigraphical distribution							
	1	2	3	4	a/o	Lower	Middle	Upper	Lower	Upper	Lower	Upper	Hol
<i>Cerithiopsis mira</i> nov. sp.			●		A			■					
<i>Cerithiopsis</i> sp.			●		A			■					
<i>Cerithiopsidella</i> sp. 1			●		A			■					
<i>Cerithiopsidella</i> sp. 2			●		A			■					
<i>Dizoniopsis bilineata</i> (Hörnes, 1848)			●	●	A M			■	■				
<i>Dizoniopsis boucheti</i> nov. sp.			●		A			■					
<i>Seila</i> cf. <i>carinata</i> (Smith, 1871)			●		A			■					
<i>Seila petasa</i> nov. sp.			●		A			■					
<i>Seila sancticlemanti</i> Marquet, 2001			●		A			■					
<i>Seila trilineata andegavensis</i> Marquet, 2001			●		A		■	■					
<i>Seila</i> sp.			●		A			■					
<i>Ataxocerithium cylindratum</i> (Jeffreys, 1885)			●	●	A M			■	■	■	■	■	■
<i>Ataxocerithium jucundum</i> (Millet, 1865)			●		A			■	■				
<i>Ataxocerithium petitianum</i> (Millet, 1865)			●		A			■	■				
<i>Ataxocerithium turbineum</i> nov. sp.			●		A			■					
<i>Ataxocerithium turgidulum</i> (Millet, 1865)			●		A			■					
<i>Petalocochus intortus</i> (Lamarck, 1818)	●	●	●		A M	■	■	■	■	■	■	■	■
<i>Thylacodes arenarius</i> (Linnaeus, 1758)	●	●	●		A M	■	■	■	■	■	■	■	■
<i>Dendropoma cristatum</i> s.l. (Biondi, 1859)			●	●	A M			■	■	■	■	■	■
<i>Alvania acuticarinata</i> nov. nom.			●		A			■					
<i>Alvania armata</i> nov. sp.			●		A			■					
<i>Alvania couffoni</i> nov. sp.			●		A			■					
<i>Alvania fezata</i> nov. sp.			●		A			■					
<i>Alvania globosa</i> nov. sp.			●		A			■	■				
<i>Alvania insulsa</i> nov. sp.			●		A			■					
<i>Alvania josephineae</i> nov. sp.			●		A			■					
<i>Alvania lachesis</i> (de Basterot, 1825)	●	●	●	●	A M	■	■	■	■	■	■	■	■
<i>Alvania lacrimula</i> nov. sp.			●		A			■					
<i>Alvania</i> cf. <i>milleti</i> nov. nom.			●		A			■					
<i>Alvania milletispinosa</i> nov. sp.			●		A			■					

Species	Geographical distribution					Stratigraphical distribution							
						Lower	Middle	Upper	Lower	Upper	Lower	Upper	Hol
	1	2	3	4	a/b/c								
<i>Alvania miocalasi</i> nov. sp.			●		Ⓐ			■					
<i>Alvania miolactea</i> nov. sp.			●		Ⓐ			■					
<i>Alvania napoleoni</i> nov. sp.			●		Ⓐ			■					
<i>Alvania parasusieae</i> nov. sp.			●		Ⓐ			■					
<i>Alvania redoniana</i> nov. sp.			●		Ⓐ			■					
<i>Alvania renauleauensis</i> nov. sp.			●		Ⓐ			■					
<i>Alvania robusta</i> Calas, 1949			●		Ⓐ			■					
<i>Alvania subtiliangulosa</i> nov. sp.			●		Ⓐ			■					
<i>Alvania susieae</i> nov. sp.			●		Ⓐ			■					
<i>Alvania tenuisculpturata</i> nov. sp.			●		Ⓐ			■					
<i>Alvania tiberiana</i> (Coppi, 1876)			●	●	Ⓐ	■	■	■	■	■	■	■	■
<i>Alvania turtaudierei</i> nov. sp.			●		Ⓐ			■					
<i>Alvania zetlandica</i> (Montagu, 1815)	●		●	●	Ⓐ			■	■	■	■	■	■
<i>Alvania ziziphina</i> Calas, 1949			●		Ⓐ			■					
<i>Manzonina crassa</i> (Kanmacher, 1798)	●		●	●	Ⓐ	■	■	■	■	■	■	■	■
<i>Pseudosetia wareni</i> nov. sp.			●		Ⓐ			■					
<i>Pseudosetia sergegofusi</i> nov. sp.			●		Ⓐ			■					
<i>Pseudosetia peyroti</i> nov. sp.			●		Ⓐ			■					
<i>Pseudosetia ivolasi</i> nov. sp.			●		Ⓐ			■					
<i>Onoba galaica</i> Rolán, 2008			●		Ⓐ			■	■	■	■	■	■
<i>Onoba redoniensis</i> nov. sp.			●		Ⓐ			■					
<i>Onoba incisa</i> nov. sp.			●		Ⓐ			■					
<i>Onoba fragilis</i> nov. sp.			●		Ⓐ			■					
<i>Rissoa decorticata</i> nov. sp.			●		Ⓐ			■					
<i>Rissoa obeliscoides</i> nov. nom.			●		Ⓐ			■					
<i>Rissoa torquata</i> nov. sp.			●		Ⓐ			■					
<i>Powellisetia europea</i> nov. sp.			●		Ⓐ			■					
<i>Pusillina dollfusi</i> nov. sp.			●		Ⓐ			■					
<i>Pusillina gallica</i> nov. sp.			●		Ⓐ			■					
<i>Pusillina</i> sp.			●		Ⓐ			■					



Species	Geographical distribution					Stratigraphical distribution							
	1	2	3	4	o/d	Lower	Middle	Upper	Lower	Upper	Lower	Upper	Hol
<i>Setia</i> sp.			●		A			■					
<i>Rissoina exdecussata</i> Sacco, 1895			●		A		■	■					
<i>Rissoina rissoides</i> (Millet, 1865)			●		A			■					
<i>Zebinella decussata</i> s.l. (Montagu, 1803)			●	●	A		■	■	■	■	■	■	■
<i>Zebinella obsoleta</i> (Hörnes, 1856)			●	●	A		■	■					
<i>Caecum aartseni</i> Van Dingenen, Ceulemans & Landau, 2016			●		A			■	■				
<i>Caecum glabrum</i> (Montagu, 1803)	●	●	●		A	■	■	■	■	■	■	■	■
<i>Parastrophia asturiana</i> de Folin, 1870			●	●	A			■	■	■	■	■	■
<i>Pseudocirsope delphinuloides</i> (Millet, 1865)			●	●	A		■	■					
<i>Hydrobia tournoueri</i> Sandberger, 1875			●		A		■	■					
<i>Peringia fontannesii</i> (Dollfus & Dautzenberg, 1886)			●		A		■	■					
<i>Ceratia ligeriana</i> (Peyrot, 1938)			●		A		■	■					
<i>Pseudonoba</i> aff. <i>striata</i> (Hörnes, 1856)			●		A			■	■				
<i>Bouryia cylindrica</i> (Cossmann & Peyrot, 1918)			●		A		■	■					
<i>Discopsis pseudocanui</i> nov. sp.			●		A			■	■				
<i>Tornus pedemontanus</i> Pavia, 1980			●	●	A			■	■				
<i>Tornus subcarinatus</i> (Montagu, 1803)	●	●	●		A	■	■	■	■	■	■	■	■
<i>Tornus superlatus</i> nov. sp.			●		A			■	■				
<i>Teinostoma obesum</i> nov. sp.			●		A			■	■				
<i>Circulus planorbillus</i> (Dujardin, 1837)			●		A		■	■					
<i>Circulus striatus</i> (Philippi, 1836)	●	●	●		A			■	■	■	■	■	■
<i>Macromphalus bourgeoisi</i> (de Morgan, 1915)			●		A		■	■					
<i>Macromphalina morgani</i> nov. sp.			●		A			■	■				
<i>Aclis ascaris</i> (Turton, 1819)	●	●	●		A	■	■	■	■	■	■	■	■
<i>Eulima taurinensis</i> (Sacco, 1892)			●	●	A		■	■					
<i>Eulima</i> (s.l.) sp.			●		A			■	■				
<i>Vitreolina</i> cf. <i>subbrevis</i> (d'Orbigny, 1852)			●		A		■	■					
<i>Vitreolina</i> sp.			●		A			■	■				
<i>Melanella alba</i> (Da Costa, 1778)	●	●	●		A	■	■	■	■	■	■	■	■
<i>Melanella</i> sp. 1			●		A			■	■				

Species	Geographical distribution					Stratigraphical distribution							
	1	2	3	4	5/6	Lower	Middle	Upper	Lower	Upper	Lower	Upper	Hol
<i>Melanella</i> sp. 2			●		A			■					
<i>Melanella</i> sp. 3			●		A			■					
<i>Calyptrea chinensis</i> (Linnaeus, 1758)	●		●	●	A	■	■	■	■	■	■	■	■
<i>Crepidula gibbosa</i> Defrance, 1818			●	●	A	■	■	■	■	■	■	■	■
<i>Crepidula unguiformis</i> Lamarck, 1822			●	●	A	■	■	■	■	■	■	■	■
<i>Schilderia andevagensis</i> (Defrance, 1826)			●		A			■					
<i>Schilderia brebioni</i> Dolin & Lozouet, 2004			●		A			■					
<i>Erato andecavica</i> Schilder, 1933			●		A			■	■				
<i>Erato britannica</i> Schilder, 1933	●		●		A			■	■	■			
<i>Erato cooperi</i> Fehse & Landau, 2002			●		A			■	■				
<i>Hespererato marqueti</i> Fehse & Landau, 2002			●		A			■					
<i>Neosimnia semen</i> (Defrance, 1825)			●		A		■	■					
<i>Trivia acuminata</i> Schilder, 1932			●	●	A			■					
<i>Trivia sceauxensis</i> nov. sp.			●		A			■					
<i>Trivia pisolina</i> (Lamarck, 1811)			●		A			■	■				
<i>Niveria cylindriclemeti</i> nov. sp.			●		A			■					
<i>Niveria dimidiatoaffinis</i> (Sacco, 1894)			●	●	A	■	■	■					
<i>Niveria excoccinella</i> (Sacco, 1894)			●		A	■	■	■					
<i>Niveria pseudoavellana</i> (Sacco, 1894)			●	●	A	■	■	■	■				
<i>Niveria</i> sp.			●		A			■					
<i>Cleotrivia gallica</i> nov. sp.			●		A			■					
<i>Lamellaria falunica</i> de Morgan, 1920			●		A		■	■					
<i>Ficus geometra</i> (Borson, 1825)	●		●	●	A	■	■	■	■	■	■	■	■
<i>Aporrhais uttigeriana</i> (Risso, 1826)			●	●	A			■	■	■	■	■	■
<i>Xenophora deshayesi</i> (Michelotti, 1847)			●	●	A	■	■	■					

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