

The upper Miocene gastropods of northwestern France, 7. Pyramidelloidea

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In this paper we review the Pyramidelloidea of the Tortonian upper Miocene (Assemblage I of Van Dingenen *et al.*, 2015) of northwestern France. Seventy-eight species are recorded, of which 27 are new: *Auristomia insulsa* nov. sp., *Megastomia pseudopolysarcula* nov. sp., *Menestho bertieae* nov. sp., *Odostomia fortistriata* nov. sp., *Odostomia robustissima* nov. sp., *Pseudoscilla breitenbergeri* nov. sp., *Ividella tuberculata* nov. sp., *Parthenina brebioni* nov. sp., *Parthenina chauvereauiensis* nov. sp., *Parthenina clementiensis* nov. sp., *Parthenina lamellata* nov. sp., *Parthenina ligeriana* nov. sp., *Parthenina milleti* nov. sp., *Parthenina pouweri* nov. sp., *Parthenina redoniana* nov. sp., *Parthenina sceauxensis* nov. sp., *Parthenina tenuicostata* nov. sp., *Parthenina wesselinghi* nov. sp., *Pyrgulina cancellatissima* nov. sp.; *Pyrgulina presselienensis* nov. sp., *Spiralinella pagoda* nov. sp., *Careliopsis gallica* nov. sp., *Chemnitzia miogallica* nov. sp., *Chemnitzia robusticostata* nov. sp., *Eulimella redoniana* nov. sp., *Eulimella semilaeve* nov. sp., and *Clathrella semilaeve* nov. sp.

Odontostomia rissoides var. *pupa* Gougerot, 1969 non A. Adams, 1860 is replaced by *Odostomia miopupa* nom. nov.

Parthenia (*Pyrgisculus*) *longula* Boettger, 1902 is considered a junior subjective synonym, and *Chrysallida interita* Van der Linden & Eikenboom, 1992 is considered a junior objective synonym of *Pyrgulina parvula* (Nyst, 1845).

The assemblage is strongly endemic, with 69% of the species restricted to the Neogene deposits of western France. This figure is consistent with that found in other parts of this series on the Assemblage I fauna, although with this group of very small species it is likely that they have been understudied in the European Neogene possibly contributing to their apparent endemism.

KEY WORDS: northwestern France, upper Miocene, Gastropoda, Pyramidelloidea, new taxa

Introduction

For introduction to this series see Landau *et al.* (2017, p. 75).

In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded only ten pyramidellid species from Assemblage I deposits, none of which were described as new.

Geological setting and material and methods

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

Authors working with pyramidellids have tended to use the genera as relatively wide concepts (*e.g.* Peñas &

Rolán, 1997, 1998, 1999b, 2010; Chirli & Micali, 2011). Based on molecular data, Schander *et al.* (2003) showed that the usage of *Brachystomia* Monterosato, 1884 and *Megastomia* Monterosato, 1884 as subgenera of *Odostomia* Fleming, 1823 is not supported, and shall be used as valid genera herein, and that *Turbonilla*, as interpreted by most authors, is polyphyletic. The work by Schander included few species and we await further molecular phylogenetic works on the family. More recently there have been attempts to expand on this data and to recognise smaller monophyletic groups within the Pyramidelloidea (Giannuzzi-Savelli *et al.*, 2014; Landau & LaFollette, 2015; Peñas & Rolán, 2017). In this paper we continue to adopt this stricter generic concept in order to identify monophyletic groups and give a detailed stratigraphical and geographical distribution to each species, which is essential in elucidating the palaeobiogeography of the region.

In order to provide the most complete distribution possi-

ble, species that have been listed in relatively recent publications, and the identifications deemed reliable, have been added to the distribution data, but in keeping with the rest of the series have not been added to the chresonymy unless the species was illustrated.

The protoconch terminology

The protoconch shape is a key diagnostic character in pyramidellids, widely used for specific separation. We consider it necessary to discuss here the criteria proposed by previous authors (e.g. Van Aartsen, 1981, 1987; Van der Linden & Eikenboom, 1992; Schander, 1994; Peñas & Rolán, 2010, Giannuzzi-Savelli *et al.*, 2014), as their interpretations have not always been congruent. One must also consider that protoconch form within a species can be variable: in present-day material this can be related to geographical area and environment influences and habitats (*i.e.* littoral vs deep-water, sandy vs muddy, etc.). In the fossil material, when comparing specimens from

different ages, there could also be change in protoconch shape over time (Micali, 1994). Even the way the shell is viewed may lead to differences in calculation of the protoconch angle, for assignment between types B and C. Therefore we advise caution when giving importance to the difference between a “type B tending to C” and a “type C” protoconch.

The method proposed by Van der Linden & Eikenboom (1992, p. 5), adopted by Schander (1994) and Giannuzzi-Savelli *et al.* (2014) defines the type A protoconch as having the axis forming an angle “from 90° to a good 120°”, while for Peñas & Rolán (2010, p. 19) the angle of type A is “approximately 90° or less”. This means that a protoconch between 90° and 120° (e.g. 100°) falls within type A1, according to first criteria, but in type B according to the second criteria. Previously Peñas & Rolán (1997, p. 68), when dealing with *T. rufa*, stated that “aunque mencionan erroneamente que tiene protoconcha del tipo A, cuando realmente es del tipo B” and in a following work (Peñas & Rolán, 2010, p. 310) clearly adopt this criterion describing as type B the protoconch of *Turbonilla cesai*

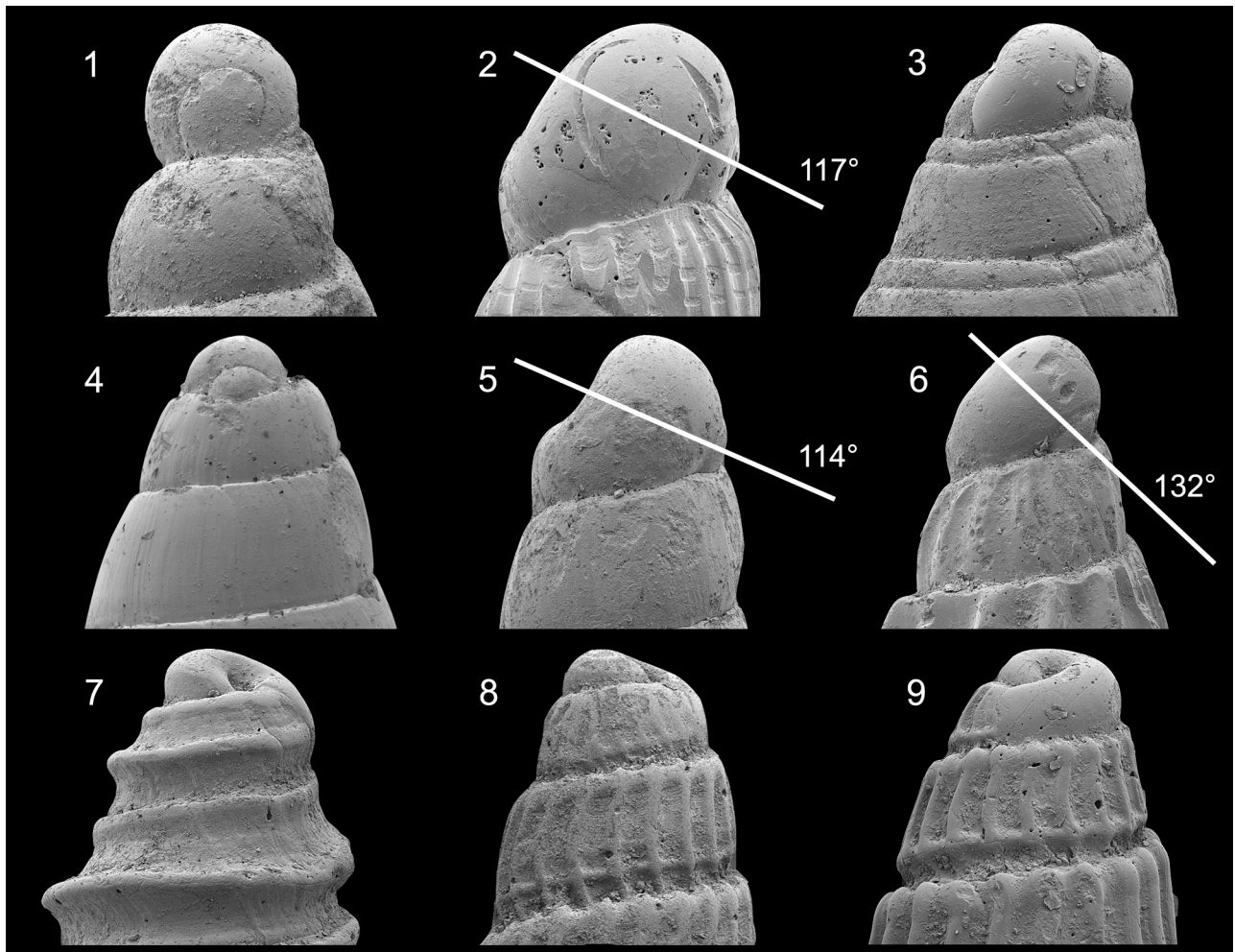


Plate 1. Pyramidellid protoconchs: **Type A1 protoconch:** 1. *Mormula catherinae* (Glibert, 1949); 2. *Pyrgiscus rufus* (Philippi, 1836). **Type A2 protoconch:** 3. *Marginodostomia aturensis* (Cossmann & Peyrot, 1917); 4. *Megastomia conoidea* (Brocchi, 1814). **Type A1 tending to B protoconch:** 5. *Eulimella cf. perspicua* (Cossmann & Peyrot, 1917). **Type B protoconch:** 6. *Sulcoturbonilla costellata* (Dujardin, 1837). 7. *Pyramistoma inaequilirata* (Gougerot, 1969). **Type B tending to C protoconch:** 8. *Parthenina wesselinghi* nov. sp. **Type C protoconch:** 9. *Spiralinella incerta* (Milaschewitch, 1916).

Peñas & Rolán, 2010, whose protoconch forms an angle of “about 100° with respect to teleoconch”. Following this criterion, more forms fall in type B as opposed to of A1 or “A1 tending to A2”.

In the present work we prefer to use the criteria defined by Van der Linden & Eikenboom (1992, p. 5), because type A1, even when the angle is more than 90°, is always clearly different from type B, in having a button-like form, with fully visible nucleus (e.g. *Mormula catherinae* (Glibert, 1949) (Pl. 1, fig. 1) and *Pyrgiscus rufus* (Philippi, 1836) (Pl. 1, fig. 2).

For clarity, the criteria used herein are summarised below:

Type A with the nucleus fully exposed, and the protoconch axis forming an angle from 90° to a good 120° to the main shell axis, with two types: A1 and A2. Type A1 is planispiral, with all protoconch whorls mainly in one plane [e.g. *Mormula catherinae* (Glibert, 1949) (Pl. 1, fig. 1), *Pyrgiscus rufus* (Philippi, 1836) (Pl. 1, fig. 2)], while type A2 is helicoid, with a clearly protruding nucleus [e.g. *Marginodostomia aturensis* (Cossmann & Peyrot, 1917) (Pl. 1, fig. 3)].

In some species the type A2 protoconch, even if maintaining the angle of about 90°, is partially immersed in the first teleoconch whorl, and the topwhorl is partially covered [e.g. *Megastomia conoidea* (Brocchi, 1814) (Pl. 1, fig. 4)], or the angle is about 100°, with the nucleus fully exposed, but only a slightly protruding [e.g. *Macrodostomia wrigleyi* (Glibert, 1949) (Pl. 5, fig. 1c)].

Type B with the protoconch axis forming an angle roughly from 130° to 160°. The topwhorl is partially or completely hidden in the first teleoconch whorl [e.g. *Sulcoturbonilla costellata* (Dujardin, 1837) (Pl. 1, fig. 6) and *Pyramistoma inaequilirata* (Gougerot, 1969) (Pl. 1, fig. 7)]. When the angle is close to 160° will be defined as “B tending to C” [e.g. *Parthenina wesselinghi* nov. sp. (Pl. 1, fig. 8)].

Type C was defined by Van der Linden & Eikenboom (1992) and Schander (1994) with the protoconch axis forming “an angle almost 180°”. This type of protoconch was indicated by Van der Linden & Eikenboom (1992) and Schander (1994) for species with a protoconch angle of between 160° and 180° (e.g. *Chrysallida interita* Van der Linden & Eikenboom, 1992 and *Odostomia (Auristomia) pyxidata* Schander, 1994), therefore type C will be used herein in the wider sense above indicated. Really the angle of exactly 180° is present in very few species. A species having type C protoconch is *Spiralinella incerta* (Milaschewitch, 1916) (Pl. 1, fig. 9).

The columellar terminology

Most Pyramidellidae have a fold on the columellar lip, running obliquely along the entire spire height. This fold may be more or less protruding and/or acute. The fold normally ends a little before the aperture, so that in speci-

mens having a partially broken external lips it seems to be much stronger than in specimens with intact outer lip. Indeed, the generic names *Odostomia* Fleming, 1813 and *Odontostomia* Jeffreys, 1839 originate from the combination of two Greek words meaning ‘tooth’ and ‘mouth’.

The well-developed and acute fold seen in the genus *Megastomia* coincides with a notch in the operculum (Peñas & Rolán, 1999b; Høisæter, 2014). The notch is shallower in species with a depressed or lower fold, as in the genus *Brachystomia*, or even absent in *Parthenina interstincta* (J. Adams, 1797) and other genera (e.g. *Ondina* de Folin, 1870) (Høisæter, 2014). In the literature both terms ‘tooth’ and ‘fold’ have been extensively used, the first to indicate an acute and prominent fold (e.g. in *Megastomia*), the second for a weaker fold (e.g. *Odostomia*, *Brachystomia*, *Syrnola* A. Adams, 1860). The description of the ‘tooth, diente (Spanish)’ and ‘fold, pliegue (Spanish)’ is normally accompanied by an adjective describing how acute, prominent, oblique, etc., the fold is.

In our opinion, these terms have been used rather uncritically and subjectively. Moreover, a ‘tooth’ is a structure of limited length. What has been called a ‘tooth’ in pyramidellids is the appearance at the aperture of a fold that runs along the entire columella, when that fold is prominent. When an acute or prominent fold is seen in cross-section at the aperture it looks like a tooth. Therefore, we follow Giannuzzi-Savelli *et al.* (2014, p. 52) and use only the term ‘fold’, with necessary additional information on its shape.

Abbreviations:

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

Systematics

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

Superorder Pylopulmonata Teasdale, 2017
 Superfamily Pyramidelloidea Gray, 1840
 Family Pyramidellidae Gray, 1840
 Tribe Pyramidellini Gray, 1840
 Genus *Longchaeus* Mörch, 1875

Type species (by subsequent designation, Dall & Bartsch, 1904, p. 4, as *Pyramidella punctata* Chemnitz; invalid, ICZN, 1944, 1954) – *Pyramidella punctata* Férussac, 1821, Holocene, Polynesia and Indian Ocean. *Pyramidel-*

la acus (Gmelin, 1791) is a senior synonym.

1875 *Longchaeus* Mörch, p. 158.

For generic discussion and synonymy see Landau & LaFollette (2015, p. 15).

***Longchaeus plicosus* (Bronn, 1838)**

Plate 2, figs 1, 2

- *1838 *Pyramidella plicosa* Bronn, p. 1026, pl. 40, fig. 24.
- 1854 *Pyramidella Terebellata* Gratt. [sic] – Millet, p. 155 (non Lamarck, 1804).
- 1964 *Pyramidella plicosa* Bronn, 1838 – Brébion, p. 303.
- 2013 *Pyramidella plicosa* Bronn, 1838 – Landau *et al.*, 304, pl. 52, fig. 5 (cum syn.).
- 2018 *Pyramidella plicosa* Bronn, 1838 – Brunetti & Cresti, p. 104, fig. 445.

Material and dimensions – Maximum height 9.5 mm, width 2.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1080-1081 (1), NHMW 2016/0103/1082 (20), RGM.1348329 (13), RGM.1352726 (24), FVD (18). **Sceaux-d’Anjou:** NHMW 2016/0103/1083 (4), RGM. 718053 (34), RGM.1347949 (3), RGM.1348763 (1), RGM. 1352547 (1). **Renauleau:** NHMW 2016/0103/2113 (5), LC (9), FVD (6). **Beugnon:** RGM.1348483 (2), RGM.1352734 (2).

Discussion – As discussed by Landau & LaFollette (2015, p. 16) the defining characters of *Longchaeus* are a turriform shell, relatively flat sided, smooth, polished, not umbilicate columella with three plications, helicoid protoconch strongly tilted and partially submerged in the first teleoconch whorl. By comparison, *Pyramidella* Lamarck, 1799 (type species *Trochus dolabratus* Linnaeus, 1758, by monotypy) is umbilicate, the apical angle broader, the whorls more inflated, aperture proportionately higher, about one-third the height of the shell (com-

pared to one-quarter in *Longchaeus*). A peripheral sulcus may or may not be present, but is not a generic character, as suggested by Landau *et al.* (2013, p. 306).

Longchaeus plicosus (Bronn, 1838) is very variable in shell height, angle of the spire, angulation of the base, and strength of the three columellar folds. The protoconch is of type B, forming an angle of 135-140°, with the nucleus completely immersed or only just visible.

Millet (1854, p. 155) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d’Anjou, St-Clément-de-la-Place and St-Michel, to which Brébion (1964, p. 304) added Renauleau and we add Beugnon. Brébion also recorded it from the Assemblage II locality of Apigné and the Assemblage IV locality of Gourbesville.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1892a). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Belgium (Glibert, 1952b), Bulgaria (Kojumdgieva & Strachimirov, 1960), Denmark (Ravn, 1907; Sorgenfrei, 1958), Germany (von Koenen, 1882; Anderson, 1964; Wienrich, 2007; Moths, 1989; Moths *et al.*, 2010), Netherlands (Van Voorthuysen, 1944; Nordsieck, 1972a; A.W. Janssen, 1984). Middle Miocene: northeastern Atlantic (Langhian): Aquitaine Basin, France (Cossmann & Peyrot, 1917), (Langhian): Loire Basin, France (Glibert, 1949a); Paratethys (Langhian-Serravallian): Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1954, 1962, 1966), Poland (Friedberg, 1928), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: North Sea Basin (Tortonian): Denmark (Schnetler, 2005; Moths & Tüxen, 2008); Atlantic (Tortonian and Messinian), NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1892a). Lower Pliocene: North Sea Basin, England (Wood, 1842, 1848; Harmer, 1920), Belgium (Nyst, 1878, 1882; Glibert, 1958; Marquet, 1997, 1998); western Mediterranean, northeastern Spain, (Almera & Bofill, 1898; Martinell, 1982; Martinell & Domènech, 1982), Roussillon Basin, France (Chirli & Richard, 2008);

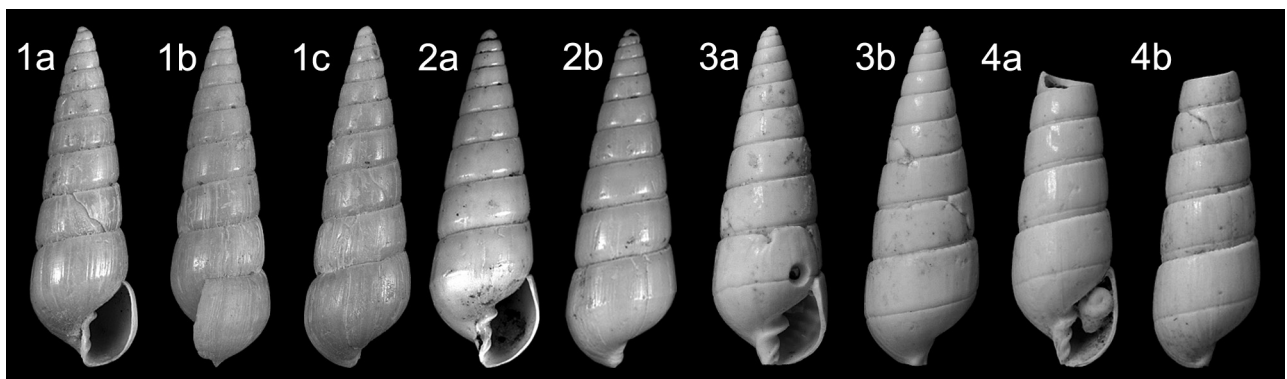


Plate 2. *Longchaeus* species: *Longchaeus plicosus* (Bronn, 1838); 1. NHMW 2016/0103/1080, height 6.7 mm, width 1.1 mm; 2. NHMW 2016/0103/1081, height 6.3 mm, width 1.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place. *Longchaeus unisulcatus* (Dujardin, 1837); 3. NHMW 2016/0103/1084, height 9.0 mm, width 2.8 mm; 4. NHMW 2016/0103/1085, height 5.9 mm, width 2.5 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

central Mediterranean, Italy (Forli *et al.*, 1999; Guioli *et al.*, 2009; Chirli & Micali, 2011; Brunetti & Cresti, 2018), Tunisia (Fekih, 1969). Upper Pliocene: northeastern Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a; Malatesta, 1974; Caprotti & Vescovi, 1973; Caprotti, 1976; Cavallo & Repetto, 1992). Upper Pliocene: North Sea Basin, England (Harmer, 1920), ?Belgium (Marquet, 1997, 1998). Upper Pliocene-Pleistocene: Atlantic, north-west France (Brébion, 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914).

***Longchaeus unisulcatus* (Dujardin, 1837)**

Plate 2, figs 3, 4

- *1837 *Pyramidella unisulcata* Dujardin, p. 282.
- 1854 *Pyramidella Unisulcata* Dujard. – Millet, p. 155.
- 1964 *Pyramidella unisulcata* Dujardin, 1837 – Brébion, p. 304.
- 2003 *Pyramidella unisulcata* Dujardin, 1837 – Moreno *et al.*, p. 137, 153, fig. 61.
- 2013 *Longchaeus unisulcatus* (Dujardin, 1837) – Landau *et al.*, 306, pl. 52, fig. 6 (*cum syn.*).

Material and dimensions – Maximum height 9.0 mm, width 2.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1099 (2). **Sceaux-d’Anjou**: NHMW 2016/0103/1084-1805 (2), NHMW 2016/0103/1086 (2), RGM.734949 (11), RGM.1352539 (1), FVD (1), LC (2). **Renauleau**: NHMW 2016/0103/1116 (11), LC (20 + 15 fragments), FVD (14). **Beugnon**: NHMW 2016/0103/2123 (1), RGM.1352709 (1).

Discussion – *Longchaeus unisulcatus* (Dujardin, 1837) differs from *Longchaeus plicatus* (Bronn, 1838) in having a peripheral sulcus on the last whorl. Unlike *L. plicatus* that has a widespread European distribution until the end of the early Pleistocene, we are not aware of any record of *L. unisulcatus* in the Pliocene or Pleistocene of Europe. For further discussion see Landau *et al.* (2013, p. 306).

Millet (1854, p. 155) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d’Anjou, St-Clément-de-la-Place and St-Michel, to which Brébion (1964, p. 304) added Beaulieu and we add Renauleau. Brébion also recorded it from the Assemblage II localities of Apigné, Le Temple du Cerisier, Carcé and Vieux Chartres.

Distribution – Lower Miocene: Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1892a). Lower-middle Miocene: North Sea Basin (late Burdigalian-Langhian): Netherlands (Van Voorthuysen, 1944; Nordsieck, 1972a; A.W. Janssen, 1984). Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1918), (Langhian): Loire Basin (France (Glibert, 1949a); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856), Poland (Friedberg, 1928), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea: NE

Spain (Moreno *et al.*, 2003), Karaman Basin (Serravallian), Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Brébion, 1964); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1892a).

Subfamily Odostomiinae Pelseneer, 1928

Tribe Odostomiini Pelseneer, 1928

Gougerot (1981) reviewed the genus *Odontostomia* [*sic*] (*Odontostomia* Jeffreys, 1839 is an unjustified emendation for *Odostomia*) in the middle Miocene Loire Basin. This paper is difficult to interpret, as the illustrations are all hand sketched and could apply to several species, and secondly Gougerot considered that a single species [*i.e.* *O. ovulina* (d’Orbigny, 1852), Gougerot, 1981, p. 36] could have different types of protoconch. Following the important works by Van Aartsen (1981, 1984, *inter alia*) we consider the protoconch type to be a species specific character.

Genus *Auristomia* Monterosato, 1884

Type species (by subsequent designation, Crosse, 1885, p. 141) – *Odostomia erjaveciana* Brusina, 1869, present-day, Adriatic.

1884 *Auristomia* Monterosato, p. 95.

Note – *Auristomia* species were characterised by Monterosato as “*Ci avviciniamo alla Auriculinae per la forma discendente degli anfratti ma di una sostanza più solida e senza scultura spirale, nè fessura ombelicale. Apertura proporzionalmente larga, auricolata. Pièga appena visibile* [Similar to *Auriculinae* in having an oblique suture, but more solid, lacking spiral sculpture and umbilical chink. Aperture large, auriculate. Columellar fold barely detectable]” (Monterosato, 1884, p. 95).

***Auristomia degrangei* (Cossmann & Peyrot, 1917)**

Plate 3, figs 1-4

- *1917 *Odontostomia (Auristomia) Degrangei* Cossmann & Peyrot, p. 330, pl. 10, figs 50, 51.

Material and dimensions – Maximum height 2.4 mm, width 1.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1129 (1), NHMW 2016/0103/2140 (1), NHMW 2016/0103/2210 (14), FVD (3). **Sceaux-d’Anjou**: NHMW 2016/0103/2159 (1), NHMW 2016/0103/2179 (1).

Discussion – This species is characterised by its small shell, type B protoconch, teleoconch of 3-4 whorls with a short spire and relatively large inflated last whorl. The aperture is wide, ovate and the columellar fold poorly developed. Microsculpture consisting of very fine spirals and prosocline growth lines. These shells are considered

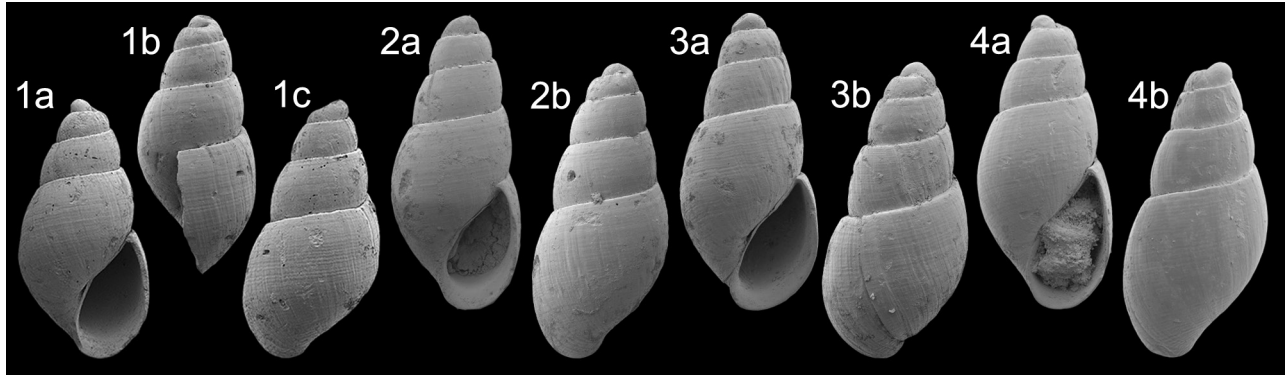


Plate 3. *Auristomia degrangei* Cossmann & Peyrot, 1917; 1. NHMW 2016/0103/1129, height 1.3 mm, width 1.0 mm; 2. NHMW 2016/0103/2140, height 2.4 mm, width 1.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/2159, height 2.4 mm, width 1.1 mm; 4. NHMW 2016/0103/2179, height 2.2 mm, width 1.0 mm (all SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

conspecific with *Odontostomia (Auristomia) degrangei* Cossmann & Peyrot, 1917, described from the lower and middle Miocene Atlantic Aquitaine Basin of France. The shell shape is similar to the specimen illustrated from the Burdigalian of Cestas, France (Cossmann & Peyrot, 1917, pl. 10, figs 50, 51), and the original description comments on subobsolete spiral sculpture present on the last whorl. In shell profile it is similar to the present-day Mediterranean type species *A. erjaveciana* (Brusina, 1869), but that species is larger, more fusiform, with a more intorted type C protoconch.

In Assemblage I *Auristomia degrangei* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Lower Miocene: Atlantic (Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Middle Miocene: Atlantic (Serravallian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

***Auristomia insulsa* nov. sp.**

Plate 4, figs 1-2

Type material – Holotype NHMW 2016/0103/2141, height 2.2 mm, width 700 μm ; paratype 1 NHMW 2016/0103/2151, height 2.0 mm, width 640 μm .

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2211 (17).

Etymology – Latin, ‘*insulsus*, -a, -um’, adjective meaning boring, reflecting the rather non-descript character of this shell. *Auristomia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Auristomia* species of small size, subcylindrical

shape, tall spire, type B tending to C protoconch, 4.5 convex whorls, deeply impressed suture, small aperture, weak columellar fold.

Description – Shell small, slender, subcylindrical, tall spired, blunt apex. Protoconch type B tending to C. Teleconch of 4.5 convex whorls, with periphery below mid-whorl, separated by oblique, deeply impressed, linear suture at 74° to main shell axis. Surface smooth, except for very faint weakly prosocline growth lines. Last whorl 48% of total height, evenly convex, base not delimited, small umbilical chink. Aperture small, 23% of total height, ovate. Outer lip evenly convex, somewhat inflated abapically. Peristome complete; columella slightly thickened and adherent abapically, closing umbilicus; weak columellar fold placed mid-aperture.

Discussion – We have placed this species in the genus *Auristomia* Monterosato, 1884, although it differs from all its European extant congeners such as *A. barashi* (Bogi & Galil, 2000), *A. fusulus* (Monterosato, 1878), *A. nofronii* (Buzzurro, 2002), *A. rutor* (Nofroni & Schander,

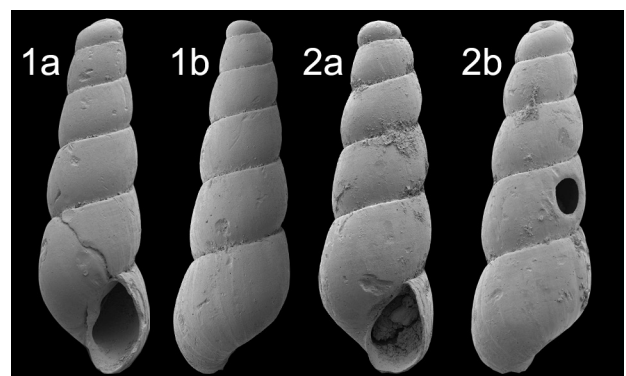


Plate 4. *Auristomia insulsa* nov. sp.; 1. **Holotype** NHMW 2016/0103/2141, height 2.2 mm, width 700 μm ; 2. **Paratype 1** NHMW 2016/0103/2151, height 2.0 mm, width 640 μm (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1994), and the type *A. erjaveciana* (Brusina, 1869) in being far more slender subcylindrical in profile and having a smaller aperture. The holotype (Pl. 4, fig. 1) seems to have a small umbilical chink, but appearance is due to the incomplete aperture. The aperture in the paratype (Pl. 4, fig. 2) is more complete and shows the base to be imperforate.

In shell profile *Auristomia insulsa* nov. sp. is similar to *Liostomia wareni* Schander, 1994 from Dakar, West Africa, but that species has a less inclined and more elevate type B protoconch, a well-developed umbilical chink, and no columellar fold.

In Assemblage I this species has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

Genus *Macrodomostomia* Sacco, 1892

Type species (by subsequent designation, Cossmann & Peyrot, 1917, p. 314) – *Odontostomia* (*Macrodomostomia*) *bismichaelis* Sacco, 1892 (*nom. nov. pro Odontostomia michaelis* Brugnone, 1876, *non* Brugnone, 1873), Pliocene, Italy.

1892a *Macrodomostomia* Sacco, p. 43.

1921 *Macrodomostomia* Cossmann, p. 233. Unjustified emendation of *Macrodomostomia* Sacco, 1892

Note – *Macrodomostomia* Sacco, 1892 species are characterised by their fusiform to subconical shape, flattened whorls separated by a relatively weakly impressed suture, elongate aperture, weak columellar fold placed below mid-aperture and smooth surface (Cossmann, 1921, p. 233). Species of the genus *Auristomia* Monterosato, 1884 (Type species *Odontostomia erjaveciana* Brusina, 1869, by subsequent designation, Crosse, 1885, present-day, Mediterranean) are similar in having a weak columellar fold, but differ in being smaller, thinner shelled, in having ovoid-conical as opposed to fusiform shells.

Macrodomostomia wrigleyi (Glibert, 1949)

Plate 5, figs 1, 2

*1949a *Odontostomia* (*Syrnola*) *wrigleyi* Glibert, p. 186, pl. 12, fig. 9.

Material and dimensions – Maximum height 4.4 mm, width 1.7 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/2166 (1), 2016/0103/2171 (1). **Renauleau**: NHMW 2016/0103/2118 (4), LC (1).

Discussion – *Macrodomostomia wrigleyi* (Glibert, 1949) is characterised by its slender shell, tall cyrtocoid spire composed of straight-sided whorls separated by a weakly impressed suture, and type A1 tending to B protoconch, with a small protruding nucleus. The aperture is relatively small and the columellar fold weak. The specimens illustrated show some variability in shell width. The more slender specimen (Pl. 5, fig. 2) is remarkably similar to the holotype illustrated by Glibert (1949a, pl. 12, fig. 9) from the middle Miocene Loire Basin of France. *Macrodomostomia bismichaelis* (Sacco, 1892) from the upper Miocene to Pliocene of the Mediterranean differs in being more slender, fusiform in profile, with a deeper, more oblique, V-shaped suture and having a more strongly in-torted type B protoconch (Chirli & Micali, 2011, p. 52). *Macrodomostomia submichaelis* (Sacco, 1892) also from the upper Miocene to Pliocene of the Mediterranean has a lower, more regularly conical spire, with a wider angle, flat whorl profile, and a more strongly angled base. In Assemblage I this species has been found at Sceaux-d'Anjou and Renauleau.

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

Macrodomostomia merignacensis Cossmann & Peyrot, 1917

Plate 6, fig. 1

*1917 *Macrodomostomia merignacensis* Cossmann & Peyrot, p. 316, pl. 9, figs 39-40.

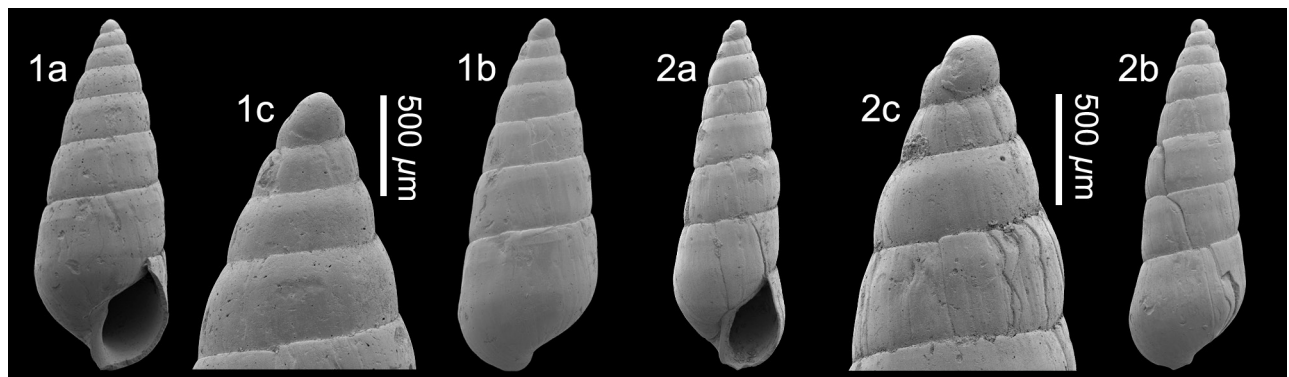


Plate 5. *Macrodomostomia wrigleyi* (Glibert, 1949); 1. NHMW 2016/0103/2166, height 4.4 mm, width 1.7 mm, 1c, detail of protoconch; 2. NHMW 2016/0103/2171, height 5.1 mm, width 1.7 mm, 2c, detail of protoconch (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

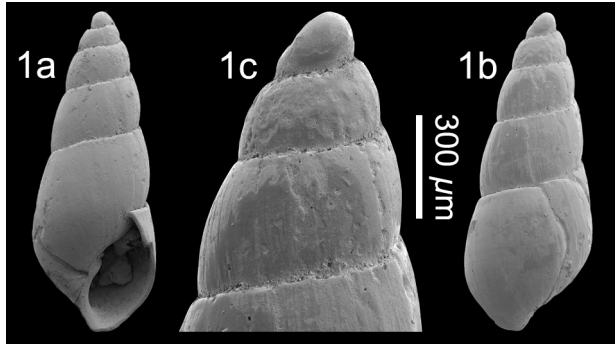


Plate 6. *Macrodomostomia merignacensis* Cossmann & Peyrot, 1917; 1. NHMW 2016/0103/2180, height 2.4 mm, width 915 µm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Material and dimensions – Maximum height 4.4 mm, width 1.7 mm. **Sceaux-d'Anjou:** NHMW 2016/0103/2180 (1).

Discussion – We ascribe this specimen to *Macrodomostomia merignacensis* Cossmann & Peyrot, 1917, which is characterised by its relatively squat shell, the last whorl relatively taller in relation to the total height (about 60%) than in its congeners. The protoconch is small of type B at an angle of about 135° to the main shell axis. It differs from *Macrodomostomia wrigleyi* (Glibert, 1949) in being shorter-spined and in having more convex whorls separated by a more deeply impressed suture. In Assemblage I this species has been found only at Sceaux-d'Anjou.

Distribution – Lower Miocene: Atlantic (Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

Genus *Marginodostomia* Nomura, 1936

Type species (by original designation) – *Odostomia suturamarginata* Nomura, 1936, present-day, Japan.

1936 *Marginodostomia* Nomura, p. 34.

Note – Van Aartsen & Corgan (1999) redescribed and discussed the differences between the odostomid genera *Cyclodostomia* Sacco, 1892 and *Marginodostomia* Nomura, 1936. *Marginodostomia* has a well defined subsutural groove, whereas *Cyclodostomia* has a poorly defined subsutural cord.

***Marginodostomia aturensis* (Cossmann & Peyrot, 1917)**
Plate 7, figs 1-6

*1917 *Odontostomia* (*Cyclodostomia*) *aturensis* Cossmann & Peyrot, p. 328, pl. 9, figs 52-54.

1999 *Marginodostomia aturensis* (Cossmann & Peyrot, 1917) – Van Aartsen & Corgan, p. 66.

Material and dimensions – Maximum height 2.9 mm, width 1.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2232 (20), FVD (4). **Sceaux-d'Anjou:** RGM.719011 (7). **Renauleau:** NHMW 2016/0103/1131 (1), NHMW 2016/0103/2134-2135 (2), NHMW 2016/0103/2136 (7), NHMW 2016/0103/2194 (1); NHMW 2016/0103/2195-2197 (3); LC (3), FVD (1).

Discussion – We have interpreted this species in being highly variable in profile, spire height and inflation of the last whorl. The constant characters are the very robust shell, subrhomboidal aperture and well-developed spiral sulcus placed just below the suture. Although the protoconch in some of the specimens looks like type B (Pl. 7, figs 1, 2), it is incomplete or abraded in all but one of the specimens available. It is of type A2 helicoid (Pl. 7, fig. 6), similar to that described in the type material “...; protoconque courte, obtuse, à nucleus hétérostrophe, reposant sur le sommet de la spire; ...” (Cossmann & Peyrot, 1917, p. 328). The syntype from the lower Miocene Aquitanian of Saint-Paul-lès-Dax, Landes, Aquitaine (MNHN.F.J05606; see <https://science.mnhn.fr/institution/mnhn/collection/f/item/j05606?listIndex=4&listCount=60>) is tall-spined and relatively slender, but similar specimens also occur in Assemblage I (Pl. 7, fig. 5), whereas other specimens are much broader with a markedly inflated last whorl (Pl. 7, fig. 1). We also note that all the specimens from St-Clément-de-la-Place are juvenile shells.

Brachystomia improbabilis Oberling, 1970 is characterised by its low cone shape, type B protoconch, strongly prosocline growth lines, very faint spiral sculpture and one prominent incised spiral groove placed just below the suture on each whorl. The aperture is large and the outer lip expanded abapically. The columella bears a well-developed fold adapically, just above mid-aperture. As illustrated by Peñas *et al.* (1996, figs 125-126) this species is also highly variable in width and inflation of the last whorl. Amati (1987) argued that Oberling's taxon was invalid, as it was proposed conditionally; “...il est probable qu'il s'agit là d'une nouvelle espèce.” (Oberling, 1970, p. 5). Furthermore, the taxon was introduced without illustration and the type was not deposited in a public collection. Nevertheless, Oberling's taxon is valid: as this is the only Mediterranean species with a marked subsutural groove, there are no doubts regarding its interpretation. In Assemblage I this species has been found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

Genus *Megastomia* Monterosato, 1884

Type species (by original designation) – *Odostomia con-*

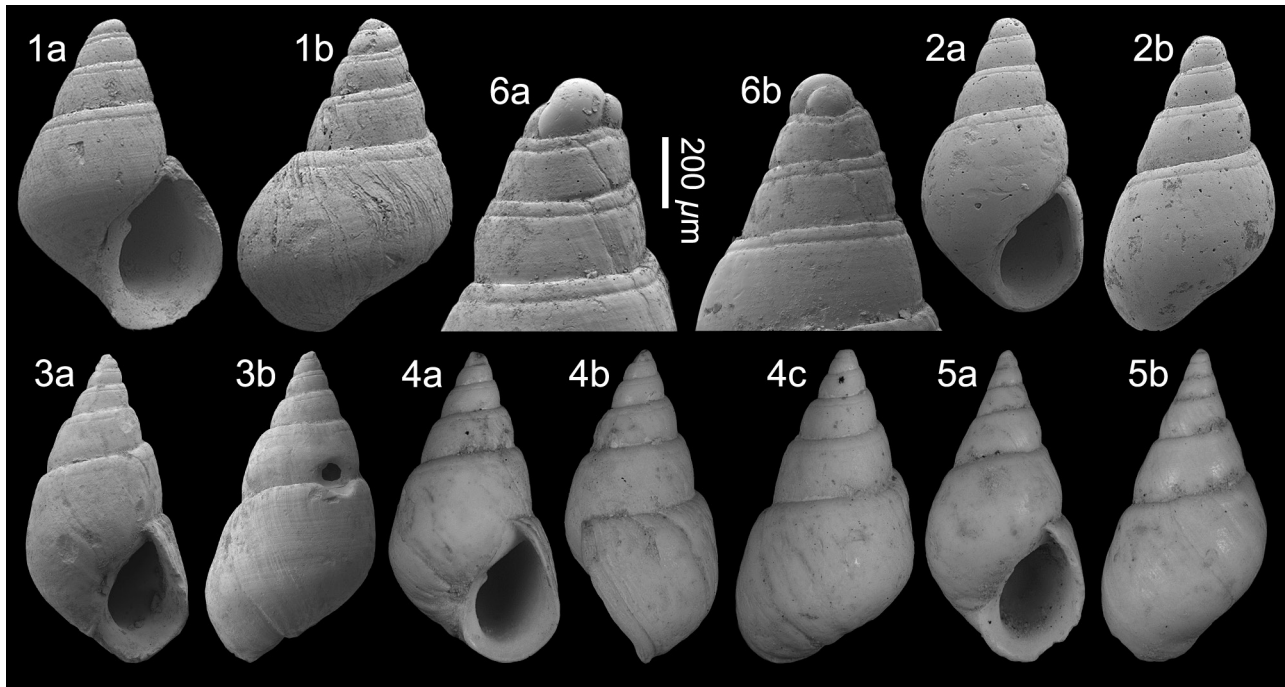


Plate 7. *Marginodostomia aturensis* (Cossmann & Peyrot, 1917); 1. NHMW 2016/0103/2134, height 2.2 mm, width 1.5 mm; 2. NHMW 2016/0103/2135, height 2.5 mm, width 1.5 mm; 3. NHMW 2016/0103/2194, height 2.8 mm, width 1.7 mm (SEM images); 4. NHMW 2016/0103/2196, height 5.8 mm, width 2.9 mm; 5. NHMW 2016/0103/2197, height 5.5 mm, width 2.7 mm (digital images); 6. NHMW 2016/0103/2195 (juvenile) detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

spicua Alder, 1850, present-day, British Isles, Europe.

- 1884 *Megastomia* Monterosato, p. 94.
 1904 *Stomega* Dall & Bartsch, p. 13. Type species (by typification of replaced name): *Odostomia conspicua* Alder, 1850, British Isles, Europe. Established as a *nom. nov. pro Megastomia* Monterosato, 1884, with the same type species, suggesting Dall & Bartsch considered it a junior homonym of *Megastoma* Swainson, 1837 [Aves].
 1921 *Somatomega* Cossmann, p. 241. Unjustified emendation of *Stomega* Dall & Bartsch, 1904. Not available.

Note – *Megastomia* Monterosato, 1884 differs from *Odostomia* Fleming, 1813 in having a series of well-developed, elongated lirae within the outer lip (Schander, 1994; Peñas & Rolán, 1999b). Based on molecular data, Schander *et al.* (2003) showed *Megastomia* not to be monophyletic with *Odostomia*.

***Megastomia alungata* (Nordsieck, 1972)**

Plate 8, fig. 1

- *1972b *Odostomia* (*Megastomia*) *conspicua alungata* Nordsieck, p. 108, PIII, fig. 17.
 1985 *Odostomia* (*Megastomia*) *conspicua alungata* Nordsieck, 1972 – Micali, p. 32, fig. 3.
 2011 *Odostomia conspicua alungata* Nordsieck, 1972 –

- Chirli & Micali, p. 58, pl. 18, figs 11-13, 15 only [fig. 14 = *Megastomia conspicua* (Alder, 1850)].
 2014 *Megastomia alungata* (Nordsieck, 1972) – Giannuzzi-Savelli *et al.*, p. 56, figs 117-118, appendix p. 13, 61.

Material and dimensions – Maximum height 3.2 mm, width 1.3 mm. **Sceaux-d’Anjou:** NHMW 2016/0103/2183 (1), RGM.739205 (3). **Renauleau:** LC (2).

Discussion – *Megastomia alungata* (Nordsieck, 1972) is characterised by its conical shape, type A2 helicoid protoconch, prosocline growth lines (not clearly seen in the

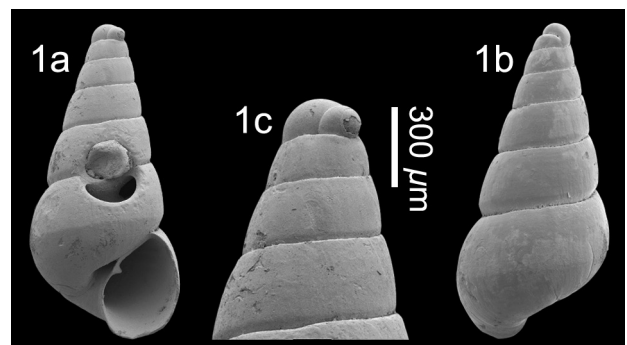


Plate 8. *Megastomia alungata* (Nordsieck, 1972); 1. NHMW 2016/0103/2183, height 2.7 mm, width 1.3 mm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

specimen illustrated), last whorl angular at the base, relatively broad and deep umbilicus, and its sharp, well-developed columellar fold. No lirae are present within the outer lip in the Assemblage I specimen, although they are present in some (but not all) Recent specimens. It differs from *M. conspicua* (Alder, 1850) in being smaller (2.8–3.0 mm vs 4.0–5.0 mm, up to 9.0 mm for *M. conspicua*) and in having a smaller protoconch (diameter ~ 175 µm vs ~ 225 µm) (Giannuzzi-Savelli *et al.*, 2014, p. 13, 61). Chirli & Micali (2011, p. 58) recognised both species in the lower Pliocene Mediterranean deposits of Italy, and *M. alungata* also occurs in the upper Pliocene of the Estepona Basin, southern Spain (Landau & Micali, in prep.). This record for *M. alungata* from NW France suggests a greater geographic range for the species during the late Miocene, as Pliocene to present-day records are restricted to the Mediterranean. In Assemblage I this species has been found at Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli & Micali, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Chirli, in prep.). Present-day: Mediterranean, Ibiza, Corsica (Nordsieck, 1972b; Giannuzzi-Savelli *et al.*, 2014).

Megastomia conoidea (Brocchi, 1814)

Plate 9, figs 1–3

- *1814 *Turbo conoideus* Brocchi, p. 660, pl. 16, fig. 2.
- 1985 *Odostomia conoidea* (Brocchi, 1814) – Micali, p. 31, fig. 4.
- 2011 *Odostomia conoidea* (Brocchi, 1814) – Chirli & Micali, p. 53, pl. 18, figs 1–7 (*cum syn.*).
- 2011 *Odostomia conoidea* (Brocchi, 1814) – Chirli & Linse, p. 201, pl. 77, fig. 2.
- 2013 *Odostomia conoidea* (Brocchi, 1814) – Öztürk *et al.*, p. 143, fig. 6A–D.
- 2013 *Megastomia conoidea* (Brocchi, 1814) – Landau *et al.*, p. 308, pl. 74, fig. 12 (*cum syn.*).
- 2014 ‘*Odostomia*’ *conoidea* (Brocchi, 1814) – Hoisac-

ter, p. 32, figs 45–48.

- 2014 *Megastomia conoidea* (Brocchi, 1814) – Giannuzzi-Savelli *et al.*, p. 56, figs 119–126.
- 2018 *Megastomia conoidea* (Brocchi, 1814) – Ceulemans *et al.*, p. 127, pl. 7, figs 14–17 (*cum syn.*).
- 2018 *Megastomia conoidea* (Brocchi, 1814) – Brunetti & Cresti, p. 110, fig. 480.

Material and dimensions – Maximum height 3.1 mm, width 1.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2137 (10), NHMW 2016/0103/2259–2260 (2). **Renauleau**: NHMW 2016/0103/2209 (7), LC (8), FVD (3).

Discussion – *Megastomia conoidea* (Brocchi, 1814) is characterised by its helicoid protoconch of type A2, in having a relatively broad shell, in having orthocline growth lines and a strongly developed projecting columellar fold. The shell can be extremely variable (Peñas & Rolán, 1999b), and the last whorl may be rounded (in littoral forms) or have a more or less pronounced carina (in deeper-water forms) (Van Aartsen, 1987). For further discussion see Landau *et al.* (2013, p. 309).

The status of *Megastomia ovulina* (d’Orbigny, 1852), described from the Atlantic lower Miocene Aquitanian and Burdigalian of the Aquitaine Basin, France (Cossmann & Peyrot, 1917), and also recorded in the middle Miocene Loire Basin (Peyrot, 1938; Glibert, 1949a; Gougerot, 1981) is problematic. Cossmann & Peyrot (1917, p. 322) considered it to differ from *M. conoidea* in having the last whorl lower, less inflated, less angular at the base. Gougerot (1981, p. 36) discussed the species at length, but his species concept is rejected as he considered this to be one of the pyramidellid species exhibiting dimorphic protoconchs, a concept no longer accepted (see note above under Tribe Odostomiini Pelseneer, 1928). The differences indicated by Cossmann & Peyrot are evident in the specimen from the Cossmann collection (MNHN.F.J05601; <https://science.mnhn.fr/institution/mnhn/collection/f/item/j05601>), however, the protoconch is not preserved. Therefore, it seems that in the middle Miocene at least, there are two species with identical or similar teleoconch characters but with different protoconch types, which are in need of revision. *Megastomia*

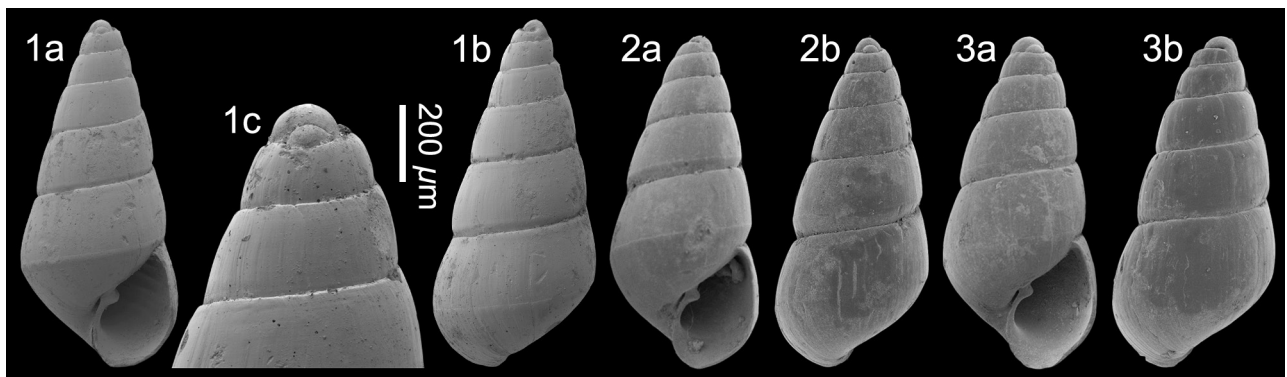


Plate 9. *Megastomia conoidea* (Brocchi, 1814); 1. NHMW 2016/0103/2137, height 3.1 mm, width 1.4 mm, 1c, detail of protoconch; 2. NHMW 2016/0103/2259, height 2.3 mm, width 1.1 mm; 3. NHMW 2016/0103/2260, height 2.8 mm, width 1.0 mm (all SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

aplicangulata (Sacco, 1892) from the Pliocene Mediterranean differs in having a type B protoconch. In Assemblage I *M. conoidea* has been found at St-Clément-de-la-Place and Renauleau.

Distribution – Middle Miocene: Paratethys (Langhian-Serravallian): Bulgaria (Kojumdgieva & Strachimirov, 1960), Poland (Friedberg, 1928); Proto-Mediterranean Sea (Serravallian): Antalya Basin (İslamoğlu & Taner, 2003), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: northeastern Atlantic (Tortonian): NW France (this paper), Algarve Basin, Portugal (Dollfus *et al.*, 1903); Proto-Mediterranean Sea (Tortonian and Messinian): Po Basin, Italy (Sacco, 1892a, 1904; Venzo & Pelosio, 1963), Turkey (early Tortonian): Antalya Basin (İslamoğlu & Taner, 2003). Lower Pliocene: North Sea Basin, British Isles (Harmer, 1920), Belgium (Marquet, 1998); Atlantic, NW France (Ceulemans *et al.*, 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al.*, 1997; Landau *et al.*, 2011); western Mediterranean, northeastern Spain (Martinell, 1982); central Mediterranean, Italy (Sacco, 1892a; Caprotti, 1974; Pavia, 1976; Forli *et al.*, 1999; Guioli *et al.*, 2009; Chirli & Micali, 2011; Brunetti & Cresti, 2018), Tunisia (Fekih, 1969). Upper Pliocene: North Sea Basin, British Isles (Harmer, 1920), Belgium (Marquet, 1993, 1998); Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a, 1904; Cavallo & Repetto, 1992; Ragaini & Bernieri, 2007; Sosso & Dell'Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914; Pelosio, 1960; Greco, 1970; Di Geronimo *et al.*, 1982; Gianolla *et al.*, 2010; Brunetti, 2011); eastern Mediterranean, Rhodes Island (Chirli & Linse, 2011). Lower-upper Pleistocene: North Sea Basin, British Isles (Harmer, 1920), Netherlands (Van Regteren Altena *et al.*, 1964); western Mediterranean, Balearic Islands (Cuerda

Barceló, 1987). Present-day: Atlantic Norway (Høisaeter, 2014) to Angola, Cape Verde Islands, São Tomé and Príncipe archipelagos (Van Aartsen *et al.*, 2000; Rolán, 2005), absent in North Sea (Graham, 1988), Mediterranean (Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean (Öztürk *et al.*, 2013).

***Megastomia pseudopolysarcula* nov. sp.**

Plate 10, figs 1-5

Type material – Holotype NHMW 2016/0103/2132, height 2.6 mm, width 1.3 mm; paratype 1 NHMW 2016/0103/2138, height 2.4 mm, width 1.2 mm, **Renauleau**. Paratype 2 NHMW 2016/0103/2173, height 2.6 mm, width 1.2 mm; paratype 3 NHMW 2016/0103/2174, height 3.0 mm, width 1.4 mm; paratype 4 NHMW 2016/0103/2175, height 3.0 mm, width 1.5 mm, **Sceaux-d'Anjou**.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/2234 (20). **Renauleau**: NHMW 2016/0103/2127 (31), LC (7), FVD (4).

Etymology – Name reflecting the close similarity to *Megastomia polysarcula* (Cossmann & Peyrot, 1917). *Megastomia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Megastomia* species of small size, type B protoconch, low spire, last whorl 60% height, weakly angular at base in most specimens, outer lip lirate within in most specimens, peristome discontinuous, columellar

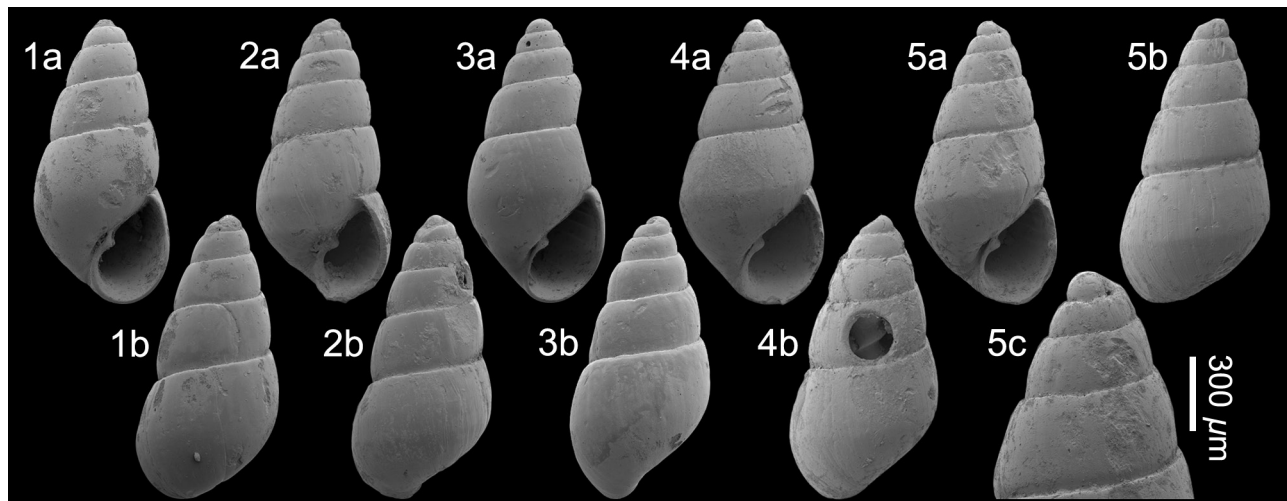


Plate 10. *Megastomia pseudopolysarcula* nov. sp.; 1. **Paratype 2** NHMW 2016/0103/2173, height 2.6 mm, width 1.2 mm; 2. **Paratype 3** NHMW 2016/0103/2174, height 3.0 mm, width 1.4 mm; 3. **Paratype 4** NHMW 2016/0103/2175, height 3.0 mm, width 1.5 mm. La Presselière, Sceaux-d'Anjou. 4. **Paratype 1** NHMW 2016/0103/2132, height 2.6 mm, width 1.3 mm; 5. **Holotype** NHMW 2016/0103/2138, height 2.4 mm, width 1.2 mm, 2c, detail of protoconch (all SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fold well-developed.

Description – Shell small, ovate, low spire. Protoconch type B. Teleoconch composed four weakly convex whorls separated by impressed suture at 81° to main shell axis. Last whorl 60% total height, weakly angular at periphery in most specimens; base convex, non-umbilicate. Aperture 36% total height, pyriform; outer lip rounded, hardly flared abapically, weakly lirate within in most specimens. Peristome discontinuous; columella short, roundly excavated, bearing stout sharp fold at upper end placed just above mid-aperture.

Discussion – This species is characterised by its small size, short spire, type B protoconch and teleoconch composed four weakly convex whorls. The last whorl is weakly angular at the periphery in most, but not all specimens (Pl. 10, fig. 1). The columellar fold is well developed and in most specimens weak lirae are developed within the outer lip, which place this species in the genus *Megastomia* Monterosato, 1884. Not all specimens have lirae (Pl. 10, figs 1, 4) but this is not uncommon for members of the genus, as other species include lirate and smooth-lipped individuals [*e.g.* *Megastomia alungata* (Nordsieck, 1972); see Giannuzzi-Savelli *et al.*, 2014, figs 117-118 for smooth-lipped specimens]. In *Megastomia* the lirae are often associated with size, so that fully grown specimen have lirae, whereas subadults do not. This is indeed the case in the Assemblage I material, in which it is the smaller specimens that do not have lirae.

Megastomia pseudopolysarcula nov. sp. is closely similar to *Odontostomia polysarcula* Cossmann & Peyrot, 1917, described from the middle Miocene Aquitaine Basin of France and also recorded from the Loire Basin (Gougerot, 1981). It differs in having a type B protoconch, whereas *O. polysarcula* has a type A2 protoconch: “...; protoconque hétérostrophe, à nucleus renversé et cachée sur le sommet de la spire; ...” (Cossmann & Peyrot, 1917, p. 320). An A2 protoconch is also suggested by the figure and discussion of the Loire Basin specimens; “L’embryon est à nucleus lateral saillant, ...” (Gougerot, 1981, p. 37). Neither authors describe lirae within the outer lip, plac-

ing Cossmann & Peyrot’s species in the genus *Odostomia* Fleming, 1813. Glibert (1949a, pl. 12, fig. 4) illustrated a specimen as *Odostomia polysarcula*, which he later corrected to *Odostomia ovulina* (d’Orbigny, 1852) (Glibert, 1949b, p. 30). All authors discussing *O. ovulina* describe strong lirae within the outer lip (Cossmann & Peyrot, 1917; Glibert, 1949a; Gougerot, 1981), placing it in the genus *Megastomia*. Apart from the lirate outer lip, it differs from *M. pseudopolysarcula* nov. sp. in being larger, having a more angular base, and possibly in having a type A2 protoconch (Gougerot, 1981, fig. 1), but see note above under *M. conoidea*.

Odostomia (Megastomia) sp. 1 from the middle Miocene North Sea Basin of Germany illustrated by Wienrich (2007, pl. 126, fig. 1) might be conspecific with *M. pseudopolysarcula*, but we hesitate to formally synonymise without direct comparative material.

In Assemblage I *M. pseudopolysarcula* has been found at St-Clément-de-la-Place, Sceaux-d’Anjou and Renauleau.

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

Genus *Menestho* Möller, 1842

Type species (by monotypy) – *Turbo albulus* Fabricius, 1780, present-day, Greenland.

1842 *Menestho* Möller, p. 83.

***Menestho bertieae* nov. sp.**

Plate 11, figs 1-3

Type material – Holotype NHMW 2016/0103/2235, height 1.3 mm, width 535 µm; paratype 1 NHMW 2016/0103/2236, height 1.1 mm, width 475 µm, **St-Clément-de-la-Place**. Paratype 2 NHMW 2016/0103/2158, height 1.3 mm, width 540 µm, **Sceaux-d’Anjou**.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/2237 (8).

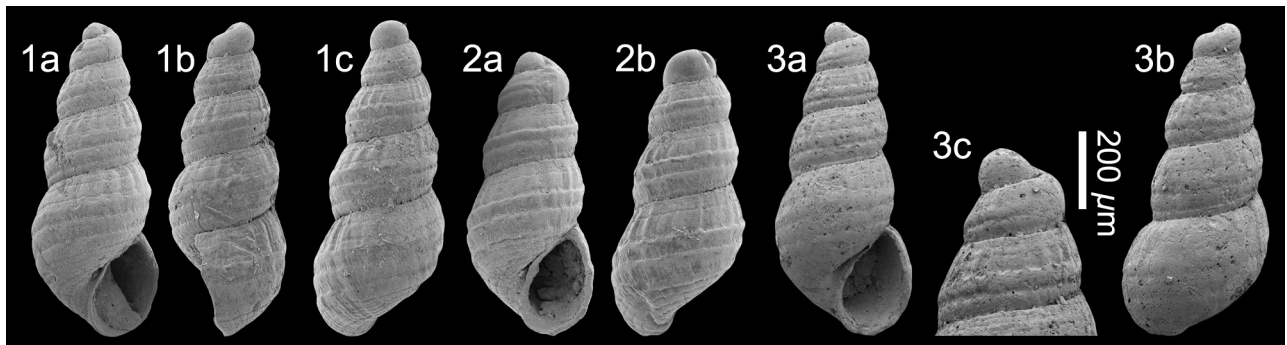


Plate 11. *Menestho bertieae* nov. sp.; 1. **Holotype** NHMW 2016/0103/2235, height 1.3 mm, width 540 µm; 2. **Paratype 1** NHMW 2016/0103/2236, height 1.3 mm, width 535 µm. Le Grand Chauvèreau, St-Clément-de-la-Place. 3. **Paratype 2** NHMW 2016/0103/2158, height 1.1 mm, width 475 µm, 3c, detail of protoconch (all SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Etymology – Name after Bertie Joan van Heuven, laboratory technician at Naturalis Biodiversity Center (Leiden), who's patience and help with all the SEM imagery was much appreciated. *Menestho* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Menestho* species of small size, type B protoconch, strongly convex, weakly shouldered whorls, sculptured with ribs and cords on subsutural ramp, cords only below shoulder, small columellar fold.

Description – Shell small. Protoconch type B. Teleoconch of up to four strongly convex whorls separated by deeply impressed suture. Whorls with broad, convex subsutural ramp, weakly angled at shoulder. Sculpture on subsutural ramp of weak cords and low ribs; ribs predominant. Axial sculpture terminates abruptly at shoulder, below which run three broad cords separated by narrow interspaces. Last whorl 50% total height in adult specimens, shoulder and axial ribs weakening towards aperture, making profile more evenly convex, base not delimited, narrow umbilicus. Aperture about 30% total height, outer lip rounded, weakly flared abapically. Columella oblique, weakly excavated, bearing weak fold mid-aperture.

Discussion – This species might represent a *Menestho* species in the restricted sense discussed by Warén (1991, p. 94). Indeed it is similar to the type species *M. albula* (Fabricius, 1780), but that species is broader, has more numerous spiral cords and lacks the axial sculpture seen on the subsutural ramp in the French species. We can find no present-day species with similar sculpture with which to compare. Today, in European waters, the genus *Menestho* is restricted to the colder North Atlantic and does not occur in warmer Mediterranean waters. It is, therefore, interesting to record it at these northern latitudes where it occurs today, but at a time when waters were tropical/sub-tropical. However, it is also possible that this placement in the genus *Menestho* is incorrect. In Assemblage I *M. bertiae* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

Genus *Odostomia* Fleming, 1813

Type species (by subsequent designation, Gray, 1847b, p. 159) – *Turbo plicatus* Montagu, 1803, present-day, British Isles.

- 1813 *Odostomia* Fleming, p. 76.
1830 *Odontostoma* Turton, 1830, pt. 2, sig. G [1]. Incorrect subsequent spelling of *Odostomia* Fleming, 1813.

- 1839 *Odontostomia* Jeffreys, p. 34. Unjustified emendation of *Odostomia* Fleming, 1813.
1853 *Odontostoma* Philippi, p. 192. Unjustified emendation of *Odostomia* Fleming, 1813.
1886 *Ptychostomon* Locard, p. 228, 571. *Nom. nov. pro Odostomia* Fleming, 1813, rejected by Locard as not properly formed.
1892a *Cyclodostomia* Sacco, p. 46. Type species (by subsequent designation, Verrill & Bush, 1900): *Odontostomia (Cyclodostomia) mutinensis* Sacco, 1892, Miocene, Italy.

Note – *Odostomia* Fleming, 1813 species are characterised by their small, elongate-conical shell, with a smooth surface, lacking any sculpture, type A, B or C protoconch, and well-developed columellar fold (Schander, 1994). Based on molecular data, Schander *et al.* (2003, p. 249) suggested that *Odostomia* in the more restricted sense appeared to be monophyletic.

Odostomia acuta Jeffreys, 1848

Plate 12, fig. 1

- *1848 *Odostomia acuta* Jeffreys, p. 338.
1850 *Odostomia umbilicata* Alder, p. 359.
1892a *Odontostomia acuta* var. *plioastensis* Sacco, p. 37, pl. 1, fig. 78.
1892a *Odontostomia acuta* var. *pedemontana* Sacco, p. 37, pl. 1, fig. 79.
1892a *Odontostomia acuta* var. *inflatorosea* Sacco, p. 37, pl. 1, fig. 80.
1892a *Odontostomia acuta* var. *obliquoides* Sacco, p. 38, pl. 1, fig. 81.
1914 *Odostomia acuta* Jeffr. – Cerulli-Irelli, p. 428, pl. 22, figs 34-37.
1925 *Odostomia acuta* Jeffreys – Harmer, p. 825, pl. 64, fig. 1.
1969 *Odontostomia acuta* Jeffreys – Fekih, p. 14, pl. 2, fig. 3.
1984 *Odontostomia acuta* var. *pedemontana* Sacco, 1892 – Ferrero Mortara *et al.*, p. 72, pl. 10, fig. 10.
1988 *Odostomia acuta* Jeffreys, 1848 – Graham, p. 602, figs 262, 258, 252.1.
1996 *Odostomia acuta* Jeffreys, 1848 – Peñas *et al.*, p. 39, figs 108-109, 111.
1998 *Odostomia acuta* Jeffreys, 1848 – Wilke & Van Aartsen, p. 11, pl. 8, fig. 23.
1999b *Odostomia acuta* Jeffreys, 1848 – Peñas & Rolán, p. 58, figs 131-135, 345.
2004 *Odostomia acuta* Jeffreys, 1848 – Repetto & Lacroce, p. 194, fig. 7.
2011 *Odostomia acuta* Jeffreys, 1848 – Chirli & Micali, p. 49, pl. 16, figs 6-11.
2013 *Odostomia acuta* Jeffreys, 1848 – Öztürk *et al.*, p. 141, figs 2A-B.
2014 *Odostomia acuta* Jeffreys, 1848 – Giannuzzi-Savelli *et al.*, p. 42, fig. 44.
2014 *Odostomia acuta* Jeffreys, 1848 – Høisæter, p. 31, figs 38-42.

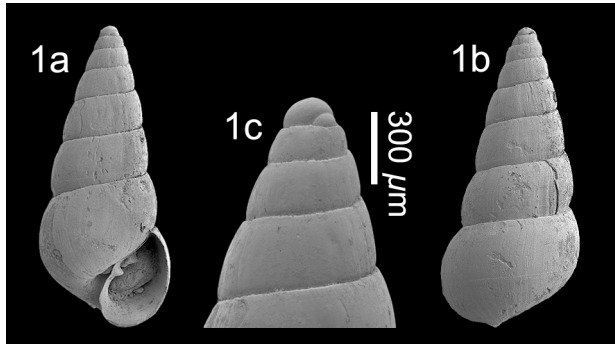


Plate 12. 1. *Odostomia acuta* Jeffreys, 1848; 1. NHMW 2016/0103/1128, height 3.2 mm, width 1.3 mm, 1c, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Material and dimensions – Maximum height 3.2 mm, width 1.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1128 (1). **Sceaux-d’Anjou:** RGM.718034 (50+). **Renauleau:** NHMW 2016/0103/2128 (23), LC (1), FVD (1).

Discussion – *Odostomia acuta* Jeffreys, 1848 is characterised by its tall conical shell, type A2 protoconch, weakly convex whorls, orthocone or very slightly procline axial growth lines, large, rounded last whorl, strongly developed and sharp columellar fold, and well-developed umbilicus. It is similar to the present-day northern European Atlantic *O. umbilicaris* (Malm, 1863), but differs in having a more solid, taller spired shell, less convex whorls, and having the growth lines almost orthocone, about 8–12° as opposed to 25–33° as in *O. umbilicaris* (Graham, 1988, fig. 252). We note that in the molecular work by Schander *et al.* (2003, fig. 2) *O. acuta* was excluded from the *Odostomia* clade and formed a sister group to *Megastomia*. It lacks the internal labial lirae typical of *Megastomia* and we provisionally keep it in *Odostomia* pending further molecular data.

In Assemblage I *O. acuta* has been found at St-Clément-de-la-Place, Sceaux-d’Anjou and Renauleau

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1925); western Mediterranean, Tunisia (Fekih, 1969); central Mediterranean, Italy (Chirli & Micali, 2011). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1925); central Mediterranean, Italy (Sacco, 1892a; Repetto & Lacroce, 2004; Guioli *et al.*, 2009). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1925); central Mediterranean, Italy (Cerulli-Irelli, 1914). Upper Pleistocene: Ireland (Harmer, 1925). Present-day: Eastern Atlantic frontage from Norway to British Isles, south to Canaries, Madeira, Cabo Verde to Angola (Peñas & Rolán, 1999b) into Mediterranean (Graham, 1988; Peñas *et al.*, 1996; Giannuzzi-Savelli *et al.*, 2014; Høisæter, 2014), eastern Mediterranean (Öztürk *et al.*, 2013), Black Sea (Wilke & Van Aartsen, 1998).

***Odostomia bulimoides* (Grateloup, 1838)**

Plate 13, figs 1-4

- *1838 *Actaeon bulimoides* Grateloup, p. 275, pl. 6, figs 44-45.
- 1847 *Actaeon bulimoides* Grat. – Grateloup, pl. 11, figs 44-45.
- 1917 *Odontostomia bulimoides* (Grateloup) – Cossmann & Peyrot, p. 323, pl. 9, figs 43-44.

Material and dimensions – Maximum height 3.7 mm, width 1.2 mm. **St-Clément-de la-Place:** NHMW 2016/0103/2265-2268 (4), NHMW 2016/0103/2269 (2).

Discussion – Identification of this tall, slender odostomiid is tentative. The specimens from Assemblage I are similar to the specimen illustrated on the MNHN (Paris) website (MNHN-F-J05602) as *Odontostomia [sic] bulimoides* (Grateloup, 1838) from Le Pontiac, Merignac, Aquitaine Basin. It is unclear whether the MNHN specimen has a damaged apex or a low type C protoconch. If so, it is slightly more intorted than in the Assemblage I specimens, which have a type B tending to C protoconch.

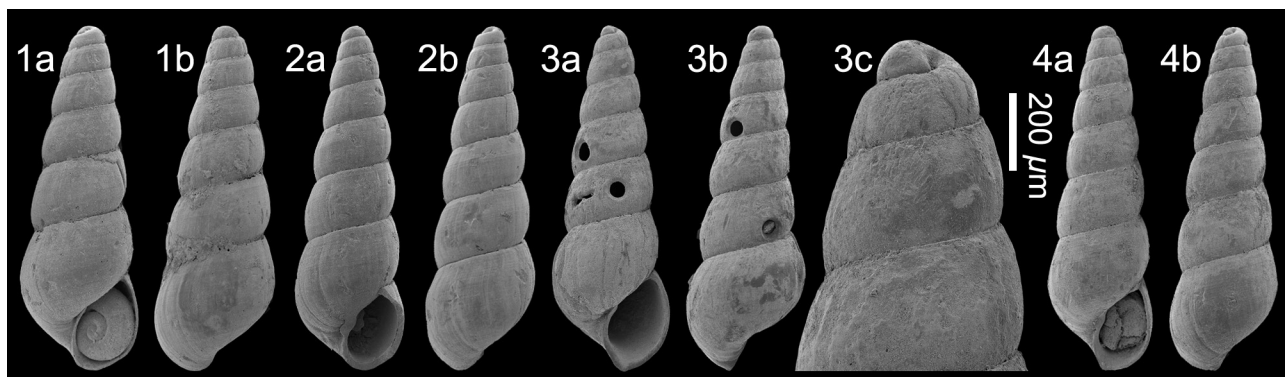


Plate 13. 1. *Odostomia bulimoides* (Grateloup, 1838); 1. NHMW 2016/0103/2265, height 3.1 mm, width 1.1 mm; 2. NHMW 2016/0103/2266, height 3.7 mm, width 1.2 mm; 3. NHMW 2016/0103/2267, height 3.3 mm, width 1.1 mm, 3c, detail of protoconch; 4. NHMW 2016/0103/2268, height 3.6 mm, width 1.1 mm (all SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

In Assemblage I this species has been found only at St-Clément-de-la-Place.

Distribution – Lower Miocene: Atlantic (Aquitainian and Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

***Odostomia cf. dispar* Boettger, 1907**

Plate 14, figs 1-3

- cf. *1907 *Odostomia dispar* Boettger, p. 115.
 cf. 1934 *Odostomia dispar* Boettger – Zilch, p. 239, pl. 12, fig. 23.
 cf. 1981 *Odontostomia cf. dispar* Boettger – Gougerot, p. 38, fig. 8.

Material and dimensions – Maximum height 2.6 mm, width 1.3 mm. **St-Clément-de la-Place:** NHMW 2016/0103/1127 (1), NHMW 2016/0103/2186 (1), NHMW 2016/0103/2208 (50+), FVD (6). **Sceaux-d’Anjou:** NHMW 2016/0103/2133 (1).

Discussion – Like Gougerot (1981, p. 38), we associate this rather non-descript *Odostomia* species to *O. dispar* Boettger, 1907 described from the Paratethian middle Miocene of Romania. It has a type B tending to C protoconch, ovate-fusiform shell shape, teleoconch of four convex whorls separated by an impressed suture. The axial growth lines almost orthocone. The last whorl is rounded at the periphery, the outer lip moderately flared abapically, smooth within, and the peristome discontinuous with a strong fold placed mid-aperture, at the adapical end of the columella. The Assemblage I specimens differ from the holotype figured by Zilch (1934, pl. 12, fig. 23) in having slightly more convex whorls and the last whorl in the Paratethian shell is subobsoletely angular at the periphery. The profile and protoconch type are similar to that figured by Gougerot (1981, fig. 8) for middle Miocene specimens from the Loire Basin, although his drawn figure would suggest a continuous peristome.

Odostomia kromi Van Aartsen, Menkhorst & Gittenber-

ger, 1984, a present-day Mediterranean species, differs in having slightly prosocline growth lines, flatter whorls with less impressed suture, and sub-triangular aperture.

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

***Odostomia fortistriata* nov. sp.**

Plate 15, figs 1, 2

Type material – Holotype NHMW 2016/0103/2182, height 2.2 mm, width 890 μ m; paratype 1 NHMW 2016/0103/2177, height 2.0 mm, width 830 μ m.

Other material – Known from type series only.

Etymology – Name reflecting the conspicuous spiral sculpture seen in this species. *Odostomia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Odostomia* species of small size, type B protoconch, slender conical outline, conspicuous fine spiral sculpture, small aperture, strong columellar fold deep within aperture.

Description – Shell small, tall, slender conical spire. Protoconch type B. Teleoconch composed of 4.5 elevated, weakly convex whorls, separated by impressed suture at 75-80° to main shell axis. Sculpture of close-set spiral threads covers entire teleoconch surface; growth lines orthocone. Last whorl 54% total height, convex at periphery; base convex, non-umbilicate. Aperture small, 28% total height, pyriform. Peristome discontinuous; Strong columellar fold placed deep within aperture, not clearly visible on apertural view when lip complete.

Discussion – This species is represented by one complete specimen and one with the outer lip broken back expos-

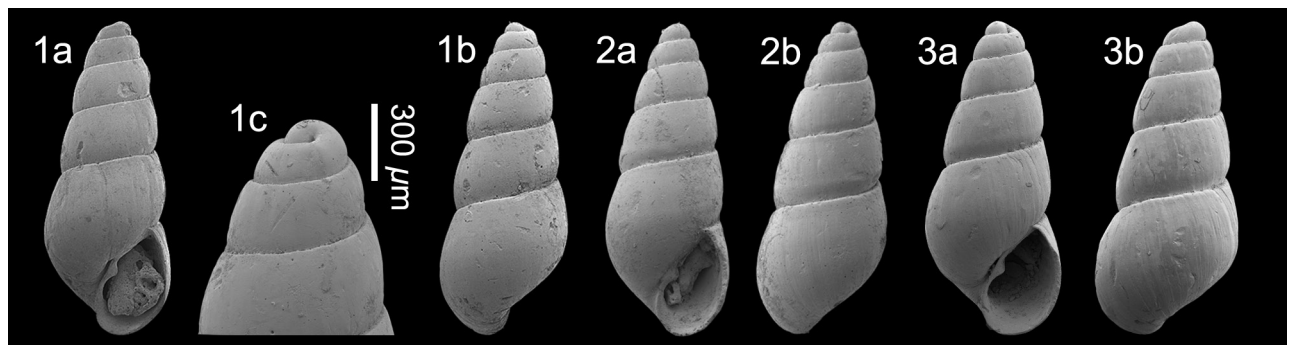


Plate 14. *Odostomia cf. dispar* Boettger, 1907; 1. NHMW 2016/0103/1127, height 3.2 mm, width 1.3 mm, 1c, detail of protoconch; 2. NHMW 2016/0103/2133, height 2.9 mm, width 1.1 mm. Le Grand Chauvereau, St-Clément-de la-Place. 3. NHMW 2016/0103/2186, height 2.7 mm, width 1.2 mm (all SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

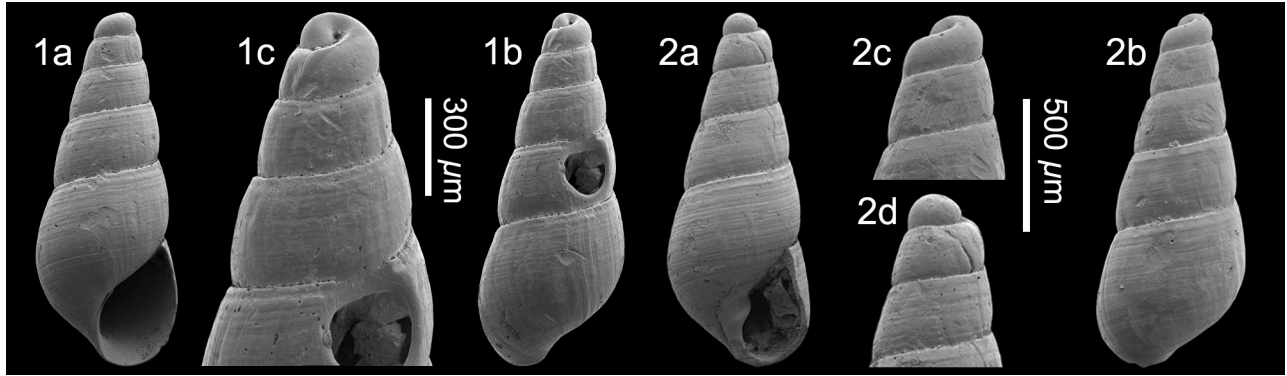


Plate 15. *Odostomia fortistriata* nov. sp.; 1. **Holotype** NHMW 2016/0103/2182, height 2.2 mm, width 890 µm; 2. **Paratype 1** NHMW 2016/0103/2177, height 2.0 mm, width 830 µm, 1c-d, detail of protoconch (SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ing the columella. Most remarkable features are the tall slender conical shape, distinct spiral sculpture for the genus and very stout columellar fold placed deep within the aperture. In profile it is similar to the extant Mediterranean *Auristomia fusulus* (Monterosato, 1878), but the growth lines are orthocone instead of prosocline, whorls are a little more convex, there is a strong spiral sculpture which is absent in *A. fusulus*, and the columellar fold is stouter in the French species. Another European extant species *Odostomia turrata* Hanley, 1844 is also conical in shape and can have subobsolete spiral sculpture (Gianuzzi-Savelli *et al.*, 2014, fig. 80), but the sculpture is not as strong and that species is immediately separated by its A2 type protoconch.

Odostomia fortistriata has so far only been found at Sceaux-d’Anjou.

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

***Odostomia miopupa* nom. nov.**

Plate 16, fig. 1

- *1969 *Odontostomia rissoides* var. *pupa* Gougerot, p. 930, pl. 29, fig. 1 (*non* A. Adams, 1860a).
- 1981 *Odontostomia rissoides* sub-species *pupa* L.G. – Gougerot, p. 39, fig. 11 (*non* A. Adams, 1860a).

Material and dimensions – Height 1.6 mm, width 760 µm. **Sceaux-d’Anjou:** NHMW 2016/0103/2185 (1).

Discussion – This specimen is considered conspecific with *Odostomia pupa* Gougerot, 1969, described from the middle Miocene of the Loire Basin, France. It differs slightly from the holotype in having a deeper V-shaped suture and a weakly angular last whorl. The type B protoconch agrees with the figures given by Gougerot (1969, 1981). It was originally described as a variety of *O. rissoides* Hanley, 1844 (= *Brachystomia scalaris* Macgillivray, 1843). Unfortunately, the name is preoccupied by *Odostomia pupa* A. Adams, 1860, an extant species from

Japan. We propose the substitute name *Odostomia miopupa* nom. nov., which honours Gougerot’s concept for the trivial name. The extant European *O. scalaris* has a more strongly intorted protoconch and orthocone instead of prosocline growth lines, as seen in *O. miopupa*. In Assemblage I *O. miopupa* has so far only been found at Sceaux-d’Anjou.

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

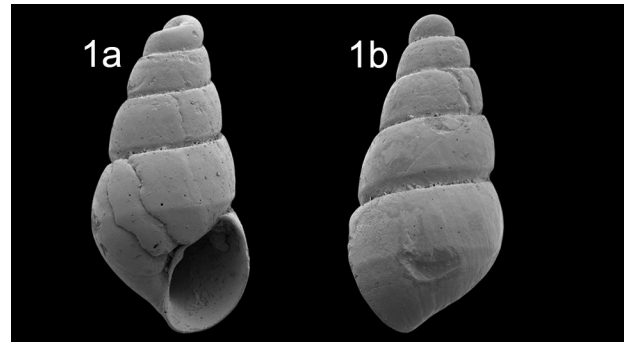


Plate 16. *Odostomia miopupa* nom. nov.; 1. NHMW 2016/0103/2185, height 1.6 mm, width 760 µm (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Odostomia robustissima* nov. sp.**

Plate 17, fig. 1

Type material – Holotype NHMW 2016/0103/1126, height 5.2 mm, width 2.0 mm.

Other material – Known only from holotype.

Etymology – Latin ‘robustus, -a’, reflecting very solid shell, using superlative. *Odostomia* gender feminine.

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

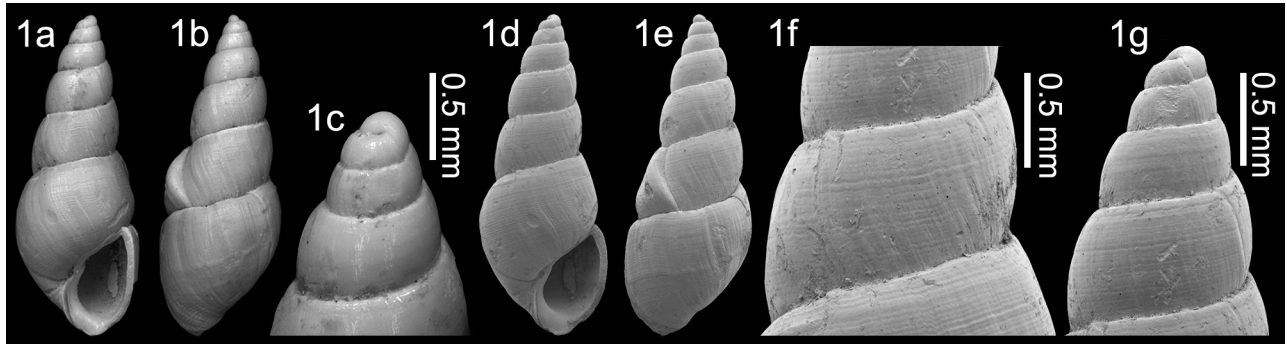


Plate 17. *Odostomia robustissima* nov. sp.; 1. **Holotype** NHMW 2016/0103/1126, height 5.2 mm, width 2.0 mm, 1c, g. detail of protoconch, 1f, detail of teleoconch sculpture (1d-g SEM images). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Odostomia* species of large size for genus, very robust, tall spired, relatively short last whorl, moderately weak columellar fold, fine spiral sculpture, strongly prosocline axial growth lines.

Description – Shell fusiform, tall spire, very solid. Protoconch type B. Teleoconch of six strongly convex whorls, separated by deeply impressed suture. Sculpture of very fine, weak spiral threads and strongly prosocline axial growth lines. Last whorl 54% total height, strongly convex, base not delimited, spiral sculpture slightly strengthened over base. Aperture small, ovate, 31% total height. Outer lip rounded, expanded, everted and spout-like abapically, columella short, broadly excavated with moderately well-developed fold placed adapically. Columellar callus strongly thickened and erect, bordering very narrow, small columellar chink. Parietal callus weak, forming narrow callus margin.

Discussion – *Odostomia robustissima* nov. sp. is an usually large, solid-shelled species. The holotype has a strong varix developed on the penultimate whorl above the aperture. We are unsure if this is a specific character or teratogenic following injury and repair.

The new species is very similar to the present-day European *O. striolata* Forbes & Hanley, 1850, from which it differs by its much taller and more slender outline, the more pointed apex, due to the elevated protoconch, lack of subsutural groove, and oblique suture.

Odostomia robustissima has so far only been found at St-Clément-de-la-Place .

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

Odostomia cf. *turonensis* Peyrot, 1938

Plate 18, figs 1-2

- cf. *1938 *Odontostomia turonensis* Peyrot, p. 54, pl. 2, fig. 44.
- cf. 1949a *Odostomia pallidaiformis* Sacco, 1892 – Glibert, p. 185, pl. 12, fig. 5 (*non* Sacco, 1892a).
- cf. 1981 *Odontostomia turonensis* Peyrot – Gougerot, p. 38, fig. 7.

Material and dimensions – Maximum height 2.5 mm, width 0.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2131 (1), NHMW 2016/0103/2264 (1).

Discussion – This species is characterised by its minute

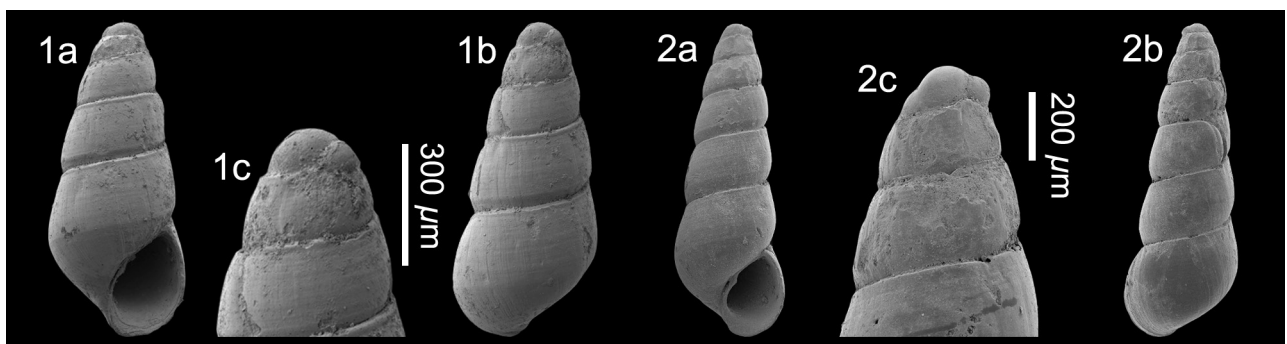


Plate 18. *Odostomia* cf. *turonensis* Peyrot, 1938; 1. NHMW 2016/0103/2131, height 1.8 mm, width 0.8 mm, 1c, detail of protoconch; 2. NHMW 2016/0103/2264, height 2.5 mm, width 0.9 mm, 2c, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

size, type A2 protoconch, three weakly convex teleoconch whorls forming a regularly conical spire separated by a deeply impressed V-shaped suture, and orthocone growth lines. The last two whorls are weakly angular at the periphery. The last whorl comprises 57% of the total height, the aperture is small, ovate, outer lip smooth within and the columellar fold is moderately developed. It is similar to *Odostomia turonensis* Peyrot, 1938 described from the Langhian middle Miocene of the Loire Basin in shell proportions (last whorl about half total height), having a type A2 protoconch, having a weakly angular last whorl, and lacking lirae within the outer lip. With some doubt, we follow Gougerot's (1981, p. 38) interpretation of the species, as Peyrot (1938) neither discussed nor figured the protoconch, and it is not illustrated on the MNHN Paris website. It differs from that species in having a deeper V-shaped suture and in having a weaker columellar fold. As discussed by Gougerot (1981, p.38) the specimen illustrated by Gilbert (1949a, pl. 12, fig. 5) as *Odostomia pallidaeformis* Sacco, 1892 is not that species (holotype figured in Ferrero Mortara *et al.*, 1984, pl. 10, fig. 7), which has strong lirae within the outer lip and therefore placed in the genus *Megastomia*.

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

Odostomia aff. *turrita* Hanley, 1844

Plate 19, fig. 1

- aff. *1844b *Odostomia turrita* Hanley, p. 18.
 aff. 2014 *Odostomia turrita* Hanley, 1844 – Giannuzzi-Savelli *et al.*, p. 48, fig. 80, appendix p.9, 57.

Material and dimensions – Maximum height 1.6 mm, width 730 μm . **Sceaux-d'Anjou**: NHMW 2016/0103/2178 (1).

Discussion – The specimen figured (Pl. 19, fig. 1) from Sceaux-d'Anjou is characterised by its minute size, spire whorls with slightly concave profile separated by a deep V-shaped suture, weakly angular base, prosocline growth lines, and medium-strength columellar fold. There is also a suggestion of spiral sculpture. In protoconch type and weak spiral sculpture it is similar to *O. turrita* Hanley, 1844, but in that species the whorls are convex and the suture is less impressed and not V-shaped. This small odostomiid is also similar to *Odostomia* cf. *turonensis* Peyrot, 1938 discussed above, but differs in whorl profile, protoconch shape, prosocline as opposed to orthocone growth lines, and in the suggestion of spiral sculpture absent in *Odostomia* cf. *turonensis*. Wienrich (2007, pl. 127, fig. 2) figured a very similar shell under the name *Odostomia* (*Megastomia*) cf. *pallidaeformis* from the middle Miocene of the North Sea Basin, Germany that might be conspecific. *Megastomia pallidaeformis* (Sacco, 1892) (holotype figured in Ferrero Mortara *et al.* 1984, pl. 10, fig. 7) differs in having a type B protoconch, and

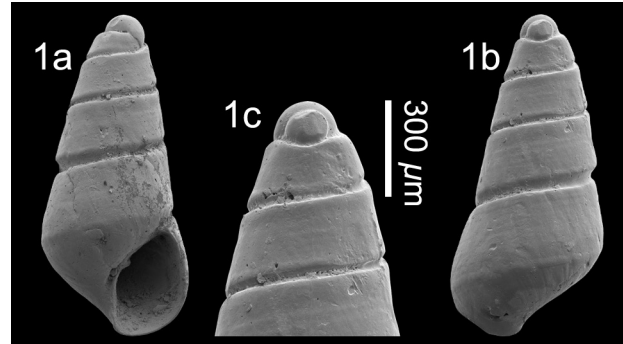


Plate 19. *Odostomia* aff. *turrita* Hanley, 1844; 1. NHMW 2016/0103/2178, height 1.6 mm, width 730 μm , 1c, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

in the generic character of lirae within the outer lip. It differs from the present day *Odostomia verhoeveni* Van Aartsen, Gittenberger & Goud, 1998, in having clearly prosocline, instead of “slightly opisthocline and sinuous” growthlines.

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

Odostomia unidentata (Montagu, 1803)

Plate 20, fig. 1

- *1803 *Turbo unidentatus* Montagu, p. 324.
 1846 *Turbonilla albella* Lovén, p. 19.
 1857 *Odostomia unidentata* Montague [sic] – Wood, p. 317, pl. 31, fig. 11.
 1892a *Odontostomia unidentata* (Mont.) – Sacco, p. 38.
 1892a *Odontostomia unidentata* var. *perpyramidata* Sacco, p. 38, pl. 1, fig. 82.
 1892a *Odontostomia unidentata* var. *savonensis* Sacco, p. 38, pl. 1, fig. 83.
 1892a *Odontostomia unidentata* var. *pseudoturrita* Sacco, p. 38, pl. 1, fig. 84.
 1892a *Odontostomia unidentata* var. *pseudopallida* Sacco, p. 39, pl. 1, fig. 85.
 1914 *Odontostomia unidentata* Mtg. – Cerulli-Irelli, p. 255, pl. 22, figs 38-39.
 1925 *Odostomia unidentata* (Montagu) – Harmer, p. 830, pl. 64, figs 6, 7.
 1933 *Odostomia litoris* Coen, p. 192.
 1964 *Odostomia* (*Odostomia*) *unidentata* (Montagu, 1803) – Van Regteren Altena *et al.*, p. 4, fig. 195.
 1969 *Odontostomia unidentata* (Montagu) – Fekih, p. 16, pl. 2, fig. 7.
 1985 *Odostomia unidentata* (Montagu, 1803) – Micali, p. 35, fig. 2.
 non 1987 *Odostomia unidentata* (Montagu, 1803) – Van Aartsen, p. 11, fig. 17 (*O. turgida* Sars, 1878).
 non 1988 *Brachystoma albella* (Lovén, 1846) – Graham, p. 588, figs 256, 253, 252.8 [*Brachystomia carrozzai* (Van Aartsen, 1987)].

- 1988 *Odostomia unidentata* (Montagu, 1803) – Graham, p. 604, fig. 263, 258, 252.7.
- ?1992 *Odostomia (Odostomia) unidentata* (Montagu, 1803) – Cavallo & Repetto, p. 158, fig. 445.
- 1993 *Odostomia (O.) unidentata* (Montagu, 1803) – Marquet, p. 94, pl. 4, figs 11, 12.
- non 1997 *Brachystoma albella* (Lovén, 1846) – Marquet, p. 107, pl. 9, fig. 11 [*Brachystomia carrozzai* (Van Aartsen, 1987)].
- 1996 *Odostomia unidentata* (Montagu, 1803) – Peñas *et al.*, p. 54, figs 114-115.
- 1998 *Odostomia (O.) unidentata* (Montagu, 1803) – Ferrero *et al.*, p. 49, 52, pl. 2, fig. 3.
- 1998 *Odostomia (O.) unidentata* (Montagu, 1803) – Marquet, p. 198, fig. 170.
- 1999b *Odostomia unidentata* (Montagu, 1803) – Peñas & Rolán, p. 63, figs 153-161.
- 2011 *Odostomia unidentata* (Montagu, 1803) – Chirli & Micali, p. 65, pl. 22, figs 4-11.
- 2011 *Odostomia unidentata* (Montagu, 1803) – Chirli & Linse, p. 203, pl. 78, fig. 3.
- 2013 *Odostomia unidentata* (Montagu, 1803) – Öztürk *et al.*, p. 150, fig. 21A-B.
- 2014 *Odostomia unidentata* (Montagu, 1803) – Giannuzzi-Savelli *et al.*, p. 48, figs 76, 77, appendix p. 9, 57.
- 2014 *Odostomia unidentata* (Montagu, 1803) – Høisæter, p. 38, figs 63-67.

Material and dimensions – Maximum height 3.2 mm, width 1.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1130 (1).

Discussion – *Odostomia unidentata* (Montagu, 1803) is characterised by its tall conical spire, type A2 helicoid protoconch, almost flat sided teleoconch whorls, the last whorl angular at the periphery, prosocline growth lines and well-developed columellar fold. Peñas & Rolán (1999b) noted the variability seen in this species in the extant faunas, and we note that the specimen illustrated here has a very tall conical spire and deep suture, similar to the specimen illustrated by those authors from Madeira

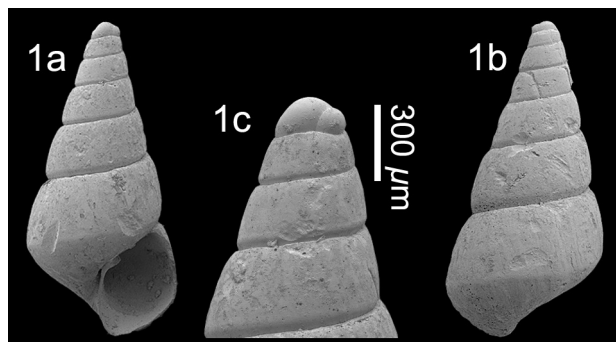


Plate 20. *Odostomia unidentata* (Montagu, 1803); 1. NHMW 2016/0103/1130, height 3.5 mm, width 1.7 mm, 1c, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(Peñas & Rolán, 1999b, fig. 158). Similar variability was reported by Chirli & Micali (2011) in the Italian Pliocene, and again our specimen is similar to one illustrated by those authors (2011, pl. 22, fig. 7).

In Assemblage I *Odostomia unidentata* has so far only been found at St-Clément-de-la-Place.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1925); western Mediterranean, Tunisia (Fekih, 1969); central Mediterranean, Italy (Sacco, 1892a; Guioli *et al.*, 2009; Chirli & Micali, 2011). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1853; Harmer, 1925), Kruisschans and Oorderen Sands, Belgium (Marquet, 1993, 1998); western Mediterranean, Estepona Basin (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a; ?Cavallo & Repetto, 1992; Ferrero *et al.*, 1998). Upper Pliocene-Pleistocene: North Sea Basin, Netherlands (Van Regteren Altena *et al.*, 1964). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1925); central Mediterranean, Italy (Cerulli-Irelli, 1914; Gianolli *et al.*, 2010; Brunetti, 2011); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: Ireland (Harmer, 1925). Present-day: Eastern Atlantic frontage from North Iceland, Norway to British Isles, south to Canaries, Cabo Verde to Angola (Peñas *et al.*, 2009), into Mediterranean (Graham, 1988; Peñas *et al.*, 1996; Giannuzzi-Savelli *et al.*, 2014; Høisæter, 2014), eastern Mediterranean (Öztürk *et al.*, 2013).

Odostomia sp.

Plate 21, figs 1-2

Material and dimensions – Maximum height 2.0 mm, width width 990 µm. **St-Clément-de-la-Place**: NHMW 2016/0103/2270-2271 (1), LC (X), FVD (X).

Description – Shell small, with regularly conical spire. Protoconch type B tending to C. Teleoconch of four whorls. Spire whorls almost straight sided, separated by

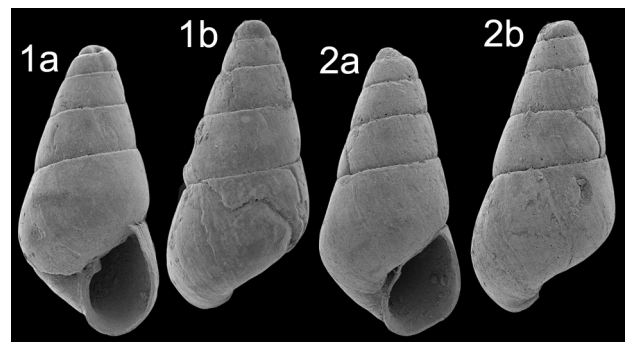


Plate 21. *Odostomia* sp.; 1. NHMW 2016/0103/2270, height 1.8 mm, width 880 µm; 2. NHMW 2016/0103/2271, height 2.0 mm, width width 990 µm (SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

weakly impressed, linear suture. Surface smooth, apart from strongly prosocline growth lines. Last whorl 63% total height, roundly angled at periphery, base convex, small umbilical chink. Aperture 35% of height, outer lip rounded, weakly flared abapically, smooth within. Columella concave, with strong fold developed at adapical end.

Discussion – In the extant European faunas *O. lukisii* Jeffreys, 1859 has a flatter C type protoconch and more convex whorls. *Odostomia striolata* Forbes & Hanley, 1850 also has a conical spire composed of almost flat-sided whorls, but differs in its type B protoconch, slightly more elevated than in the French species, and the teleoconch whorls are usually covered in spiral microsculpture. This species differs from the present-day *O. dijkhuizeni* Van Aartsen, Gittenberger & Goud, 1998 in having strongly prosocline growth lines, the more superficial suture and less angulated periphery.

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

Genus *Ondina* de Folin, 1870

Type species (by subsequent monotypy) – *Ondina semiornata* de Folin in de Folin & Périer, 1872 [= *Ondina warreni* (Thompson, 1845)], present-day, France (Atlantic).

- 1847b *Auriculina* Gray, p. 159. Type species (by original designation): *Odostomia obliqua* Alder, 1844, present-day, British Isles. Junior homonym of *Auriculina* Grateloup, 1838 [Ringiculidae].
- 1870 *Ondina* de Folin, p. 200.

Note – The relationship between the genera *Ondina* de Folin in de Folin & Périer, 1870 and *Odetta* de Folin in de Folin & Périer, 1870 were discussed by Van Aartsen (1984), and the European species were reviewed in a subsequent paper (Van Aartsen, 1987). More recent review of extant northern European species was given by (Høisæter, 2014).

Ondina species are relatively thin shelled, elongated and cyrtocoenoid in profile, with a broad type B or C protoconch, opisthocline growth lines, the sinus placed close to the adapical suture, they often bear spiral sculpture on the abapical part of the whorls, although some species are smooth, the aperture is pyriform, and the columellar fold is weakly developed. Based on molecular data, Schander *et al.* (2003, fig. 2) stated that *Ondina* appeared to be monophyletic.

***Ondina* cf. *micropeas* (Boettger, 1902)**

Plate 22, figs 1-3

- cf. *1902 *Odostomia (Ondina) micropeas* Boettger, p. 100.
cf. 1934 *Macrostomia micropeas* Boettger – Zilch, p. 237, pl. 11, fig. 12.

Material and dimensions – Maximum height 6.6 mm, width 2.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1133 (1), NHMW 2016/0103/1134 (1), NHMW 2016/0103/2233 (2), FVD (1). **Renauleau**: NHMW 2016/0103/1732 (9), LC (2).

Discussion – This relatively large *Ondina* species is characterised by its tall spire, large inflated last whorl, type B protoconch and fine irregular spiral microsculpture covering the entire surface. The peristome is continuous and there is just a suggestion of a columellar fold. It is closely similar to *Ondina micropeas* (Boettger, 1902) from the middle Miocene Paratethys of Romania, but differs in being higher spired. We have not seen that species, but the lectotype illustrated by Zilch (1934, pl. 11, fig. 12) does not show any spiral sculpture. However, the microsculpture is abraded in specimens that are not fresh (Pl. 22, fig. 3). Boettger clearly described the spiral microsculpture “...microscopice densissime spiraliter striati...” (1902, p. 100) in his species.

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

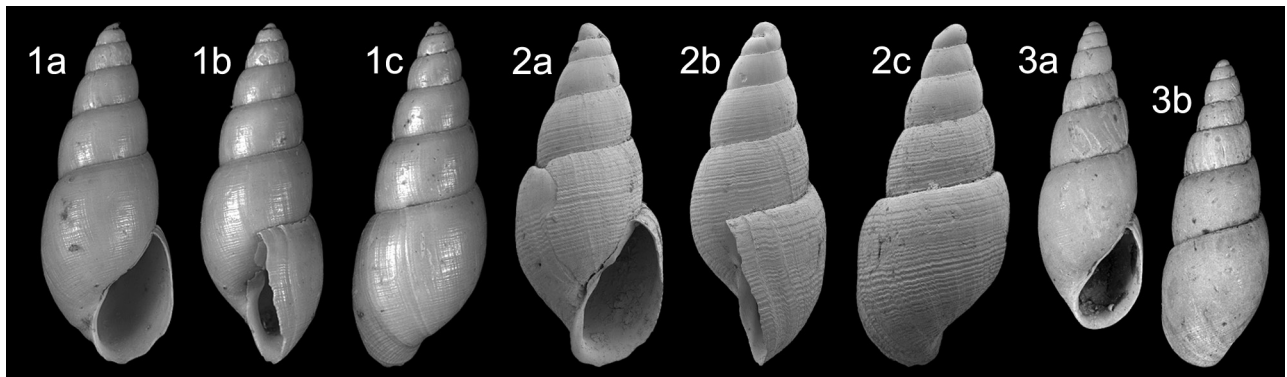


Plate 22. *Ondina* cf. *micropeas* (Boettger, 1902); 1. NHMW 2016/0103/1133, height 6.6 mm, width 2.5 mm (digital image); 2. NHMW 2016/0103/1134, height 6.4 mm, width 2.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place (SEM image). 3. NHMW 2016/0103/1732, height 6.5 mm, width 2.5 mm (digital image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Pseudoscilla* Boettger, 1902

Type species (by monotypy) – *Oscilla* (*Pseudoscilla*) *miocaenica* Boettger, 1902, Miocene, Romania.

1902 *Pseudoscilla* Boettger, p. 113.

1921 *Miraldiella* Cossmann, p. 263. *Type species* (by monotypy): *Parthenia exarata* Carpenter, 1857a, present-day, Pacific, Mexico.

***Pseudoscilla breitenbergeri* nov. sp.**

Plate 23, figs 1, 2

Type material – Holotype NHMW 2016/0103/2188, height 1.4 mm, width 700 μ m; paratype 1 NHMW 2016/0103/2189, height 1.3 mm, width 680 μ m; paratype 2 RGM.1352639, height 1.3 mm; paratype 3 RGM.1352640, height 1.3 mm.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2220 (1). **Sceaux-d'Anjou:** NHMW 2016/0103/2167 (2), RGM.718037 (40). **Renauleau:** LC (1).

Etymology – It gives me pleasure to name this species after Anton E. Breitenberger (Austria), passionate molluscan palaeontologist, good friend and travel companion of the first author (BL). *Pseudoscilla* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pseudoscilla* species of minute size, squat ovate shape, type C protoconch, low spire, strongly bicarinate, axial sculpture reduced to inconspicuous growth lines.

Description – Shell minute, ovate with short spire. Protoconch type C. Teleoconch of three strongly bicarinate whorls separated by impressed suture; carinae sharp and strongly elevated, adapical carina forming high-placed shoulder, delimiting narrow, slightly concave subsutural ramp; abapical carina placed mid-way between mid-whorl

and suture; whole profile between carinae concave. Axial sculpture reduced to inconspicuous, weak, slightly proscloine growth lines. Last whorl 64% total height, third carina develops at level of insertion of outer lip, delimits weakly convex base; narrow umbilical chink. Aperture 38% total height; outer lip angled at terminations of carinae, slightly flared abapically. Columella oblique, with low fold placed mid-aperture. Columellar callus thickened abapically, erect, forming medial border of columellar chink.

Discussion – The genus *Pseudoscilla* Boettger, 1902 includes highly characteristic shells with Type B tending to C or C protoconchs, strongly bicarinate teleoconch whorls, usually (but not always) with strongly developed axial growth lines, in some species elevated and lamelliform, and the aperture is angular at the terminations of the carinae. The genus is thermophilic, and today occurs on both sides of the tropical Atlantic and Pacific (Peñas & Rolán, 1999a).

The type species *Pseudoscilla miocaenica* Boettger, 1902 was described from the middle Miocene Paratethys of Kostej, Romania (Boettger, 1902, p. 113; illustrated in Zilch, 1934, pl. 11, fig. 6). Further specimens of *P. miocaenica* at hand from Lapugiu de Sus, Romania (NHMW coll.) show that the species attains a slightly greater maximum height, up to 3.0 mm, and fully adult shells have an extra whorl and are relatively slender. Peñas & Rolán (1999a, figs 1-2) figured a shell from the middle Miocene Atlantic Loire Basin of France, allegedly from the MNHN collection (Paris – no collection number given), as the holotype of *P. miocaenica*. This is clearly a *lapsus*. If the shell is from the Langhian of the Loire Basin, it is the only record of the species in those deposits. In any case, *P. miocaenica* differs from *Pseudoscilla breitenbergeri* nov. sp. in having a type B tending to C protoconch and a taller, conical spire with at least one extra teleoconch whorl. Its axial sculpture is relatively weak, but not as reduced as in the Assemblage I species.

Pseudoscilla bussanensis Sosso, Dell'Angelo & Bonfitto, 2009, described from the central Mediterranean lower Pliocene of Italy and also present in the western Mediterranean upper Pliocene Estepona Basin of Spain (Landau & Micali, in prep.) differs from *P. breitenbergeri* in also having a type B tending to C protoconch and a taller,

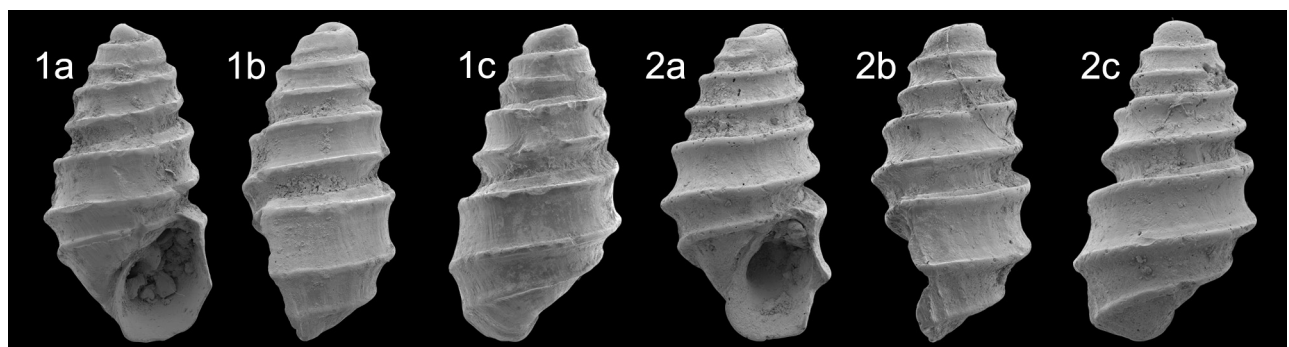


Plate 23. *Pseudoscilla breitenbergeri* nov. sp.; 1. **Holotype** NHMW 2016/0103/2188, height 1.4 mm, width 700 μ m; 2. **Paratype 1** NHMW 2016/0103/2189, height 1.3 mm, width 680 μ m (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

scalate spire with an extra teleoconch whorl.

The present-day West African species were reviewed by Peñas & Rolán (1999a). All the species discussed by those authors are taller spired. *Pseudoscilla bilirata* (de Folin, 1870) from Madeira and West Africa is again taller spired, and has lamellar axial growth lines. It is most similar in shape to *P. bussaensis* (for comparison see Sosso *et al.*, 2009, p. 108, tab. 1). *Pseudoscilla verdensis* Peñas & Rolán, 1999 from the Cape Verde Archipelago is distinguished by its spirally striate protoconch. *Pseudoscilla saotomensis* Peñas & Rolán, 1999 from São Tomé Island has a protoconch with a single apical cord and a micropustular surface. The teleoconch is tall and slender, like the other West African species discussed above. *Pseudoscilla pauciemersa* Peñas & Rolán, 1999 from Senegal, is the smallest of the West African species, similar in size to *P. breitenbergeri*, and like it has a teleoconch of only three whorls. However, it differs in being less squat, having a type B protoconch and stronger axial growth lines. In Assemblage I *Pseudoscilla breitenbergeri* has only been found at Sceaux-d'Anjou.

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

Genus *Pyramistomia* Cossmann, 1921

Type species (by original designation) – *Odostomia deubeli* Boettger, 1902, Miocene, Paratethys, Romania.

1921 *Pyramistomia* Cossmann, p. 211, 240.

Note – Landau *et al.* (2013, p. 311) considered *Pyramistomia* Cossmann, 1921 a separate genus from *Odostomia* Fleming, 1813, a position followed by Thivaïou *et al.* (2019). Other recent authors have used it at subgeneric status (*i.e.* Van Aartsen *et al.*, 1998), whilst others have synonymised it with *Odostomia* (*e.g.* Peñas & Rolán, 1999b). Pending a molecular phylogeny, we continue to use the genus *Pyramistomia* for strongly spirally sculptured *Odostomia*-like species, as this seems to be a strongly thermophilic group that extended up to north-

western France in the late Miocene, but disappeared from the European Atlantic frontage and Mediterranean already in the Pliocene. Today it occurs in West Africa south of the Azores (Van Aartsen *et al.*, 1998; Peñas & Rolán, 1999b).

Pyramistomia inaequilirata (Gougerot, 1969)

Plate 24, figs 1-3

*1969 *Cingulina* (*Oscilla*) *inaequilirata* Gougerot, p. 933, pl. 29, fig. 7.

Material and dimensions – Maximum height 2.9 mm, width 1.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0995 (23), FVD (6). **Sceaux-d'Anjou**: RGM.718036 (50+), RGM.1352710 (1). **Renauleau**: NHMW 2016/0103/2049-2050 (2), NHMW 2016/0103/0996 (50+), LC (11), FVD (7).

Discussion – *Pyramistomia inaequilirata* (Gougerot, 1969) was described from the middle Miocene of France. Most of the Assemblage I specimens are closely similar to the holotype from Paulmy, Indre-et-Loire, Loire Basin, in having a small evenly conical shell, the whorls sculptured by three spiral cords, the central cord weaker than the ad- and abapical cords. Some specimens from Assemblage I differ in being more slender for the same number of whorls and lacking the central cord, and are discussed below.

Pyramistomia aliakmoni Thivaïou, Harzhauser & Koskeridou, 2019 from the lower Miocene eastern Mediterranean of Greece and the type species *P. deubeli* (Boettger, 1902) from the middle Miocene Paratethys, which is also found in the eastern Mediterranean of Turkey (Landau *et al.*, 2013) both have more subdued sculpture composed of less elevated spiral bands than those seen in the two French Miocene species described herein. These two species are remarkably similar to each other and both have type B protoconchs, but *P. deubeli* has a subsutural spiral cord absent in *P. aliakmoni*. *Pyramistomia suprasulcata* (Peñas & Rolán, 1999) and *P. funiculustriata* (Peñas & Rolán, 1999) from present-day West Africa also have sculpture composed of broad, low rounded cords, but in those species the protoconch is of type A2, whereas in

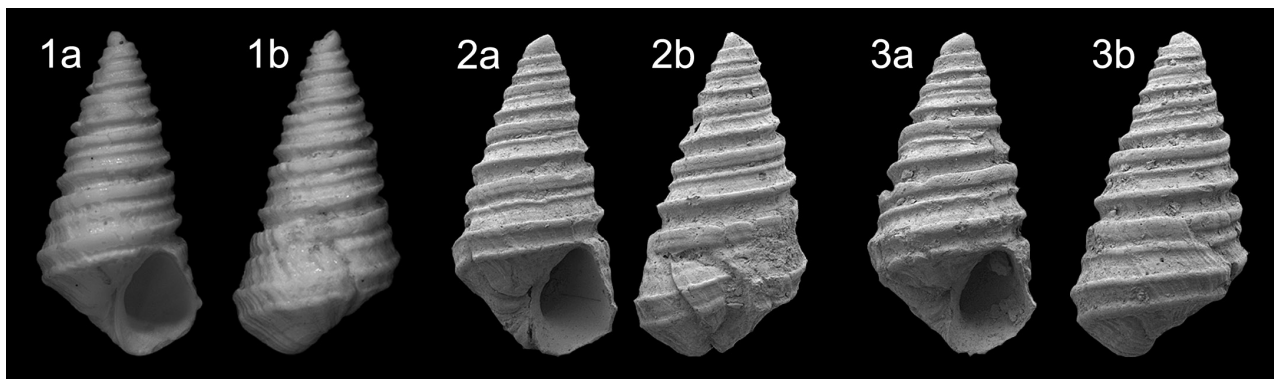


Plate 24. *Pyramistomia inaequilirata* (Gougerot, 1969); 1. NHMW 2016/0103/0996, height 2.9 mm, width 1.5 mm (digital image); 2. NHMW 2016/0103/2049, height 2.5 mm, width 1.2 mm; 3. NHMW 2016/0103/2050, height 2.2 mm, width 1.2 mm (SEM images). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

all the Miocene species and *P. fehrae* (Van Aartsen, Gittenberger & Goud, 1998) from the present-day Azores it is of type B.

This genus is also present in the Caribbean, where it is represented by *P. didyma* (Verrill & Bush, 1900), which is extremely similar to *P. aliakmoni*, but differs in being more slender conical and having a sharper abapical cord. The protoconch in the Caribbean shell is also of type B. *Pyramistomia inaequilirata* is widespread in Assemblage I, found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Middle Miocene: Loire Basin, France (Gougerot, 1969). Upper Miocene (Tortonian): NW France (Gougerot, 1969).

***Pyramistomia cf. inaequilirata* (Gougerot, 1969)**

Plate 25, figs 1, 2

Material and dimensions – Maximum height 4.0 mm, width 1.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0992-0993 (2), NHMW 2016/0103/0994 (7), FVD (1), LC (8). **Sceaux-d'Anjou:** NHMW 2016/0103/2066 (1), NHMW 2016/0103/2067 (1). **Renauleau:** NHMW 2016/0103/2108 (12), LC (3), FVD (2).

Description – Shell solid, slender conical. Protoconch planorbid, of type B. Teleoconch of five strongly bicarinate whorls, adapical carina just below suture, abapical carina stronger, placed about two-thirds whorl height; whorl profile between carinae and between abapical carina and suture slightly concave. Weak secondary spiral threads developed in some specimens. Suture linear, deeply impressed, narrowly canaliculate. Growthlines strongly prosocline. Last whorl strongly carinate, with third carina delimiting concave base. Outer lip produced at terminations of carinae. Umbilicus lacking. Columellar fold moderately developed.

Discussion – In each of the localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau a small number of specimens differ from typical *Pyramistomia inaequilirata* (Gougerot, 1969) in being more slender and lacking

the central spiral cord (Pl. 25, fig. 1), or almost so (Pl. 25, fig. 2). The rest of the shell characters are similar.

Pyramistomia cf. inaequilirata is extremely similar to *Pyramistomia fehrae* (Van Aartsen, Gittenberger, & Goud, 1998), an extant species from the Azores, but differs in being taller spired with an extra teleoconch whorl (5 vs 4 in *P. fehrae*), in having the shoulder carina more strongly developed and the abapical carina, placed just above the suture in *P. fehrae*, is situated higher, at about two-thirds whorl height. For further comparison see above. *Pyramistomia cf. inaequilirata* superficially resembles the shell illustrated as *Pseudoscilla miocaenica* (Boettger, 1902) from the middle Miocene of the Loire Basin of France illustrated by Sosso *et al.* (2009, figs 24I, J), but compared to specimens of that species from Lapugiu de Sus (Romania; NHMW coll.), *P. miocaenica* is taller, more slender, the carinate spiral cords are far more elevated, and the axial growth lines are more marked.

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

Tribe Chrysallidini Saurin, 1958

Tribe Chrysallidini Saurin, 1958

Genus *Ividella* Dall & Bartsch, 1909

Type species (by original designation) – *Odostomia (Ividia) navisa* Dall & Bartsch, 1904, present-day, Californian and Panamic Pacific.

- 1884 *Funicularia* Monterosato, p. 85. Type species (by subsequent designation, Dall & Bartsch, 1909, p. 172): *Rissoa excavata* Philippi, 1836, Recent, Mediterranean (*non* Forbes, 1845 [Cnidaria: Penatulidae]). Also unavailable due to being proposed conditionally *fide* Gofas pers. comm. 2012 [PIL]; Dall & Bartsch, 1909, p. 172, senior homonym '*Funicularia* Lamarck' is probably an error for *Furcularia* Lamarck, 1816 [Rotifera].
- 1907 *Ividia* spp. of Dall & Bartsch, p. 517 (based on a misinterpretation of the type species, *Parthenia armata* Carpenter, 1857).
- 1909 *Ividella* Dall & Bartsch, pp. 14, 172.

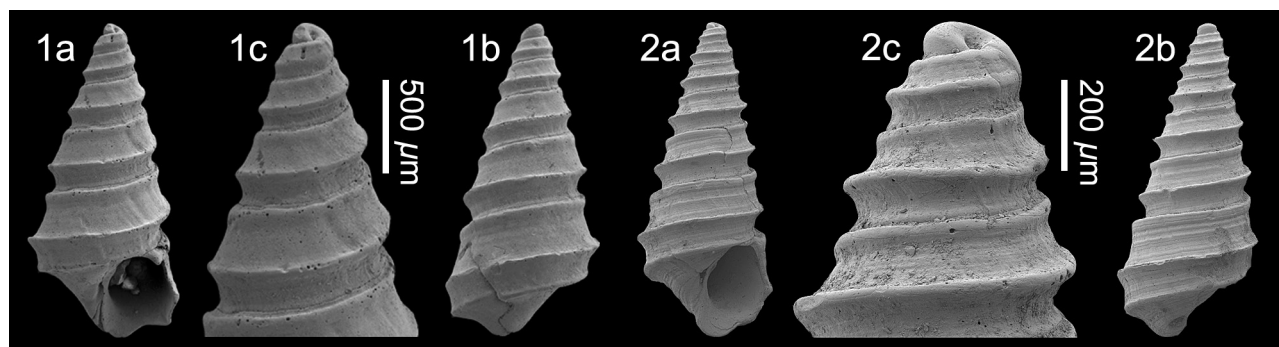


Plate 25. *Pyramistomia cf. inaequilirata* (Gougerot, 1969); 1. NHMW 2016/0103/0992, height 2.9 mm, width 1.4 mm, 1c, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/2066, height 4.0 mm, width 1.6 mm, 2c, detail of protoconch (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Note – Placement of the European species *Rissoa excavata* Philippi, 1836 remains controversial. Most authors have placed it in the genus *Folinella* Dall & Bartsch, 1904. However, Landau & LaFollette (2015, p. 24) argued for placement in the genus *Ividella* Dall & Bartsch, 1909, as done by some earlier European authors (Fretter *et al.*, 1986; Graham, 1988, p. 560). Peñas & Rolán (2017, p. 63) again highlighted the controversy and placed *Ividella* in synonymy with *Folinella* with a question mark. They argued for the use of *Folinella* “...the type species *Odosotomia (Ividia) navisa* Dall & Bartsch, 1904 superficially resembles *Folinella excavata* but also has a type B protoconch instead of type C, therefore its treatment as congeneric with the latter is no more convincing than for *F. anguliferens*.” (Peñas & Rolán, 2017, p. 63). Until molecular data are available to resolve this matter, we prefer to include these species in the genus *Ividella*.

Ividella Dall & Bartsch, 1909 species are characterised by having shells with elevated ribs, spiral sculpture formed by cords almost equal in strength to the ribs that overrun the ribs forming a strongly reticulated surface sculpture, and a base with some spiral cords, but no axials. The protoconch is of type B or C.

Ividella excavata (Philippi, 1836)

Plate 26, fig. 1

- *1836 *Rissoa excavata* Philippi, p. 154.
- 1892a *Pyrgulina (Miralda) excavata* var. *turritastensis* Sacco, p. 70, pl. 1, fig. 116.
- 1914 *Parthenina (Miralda) excavata* (Phil.) – Cerulli-Irelli, p. 439, pl. 55, figs 15-17.
- 1920 *Miralda excavata* (Philippi) – Harmer, p. 580, pl. 49, fig. 50.
- 1960 *Chrysallida (Ividella) excavata* (Philippi) – Pelosio, p. 147, pl. 2, fig. 1.
- 1970 *Chrysallida (Parthenina) excavata* (Philippi) – Greco, p. 288, pl. 4, figs 6, 7.
- 1984 *Miralda excavata* (Philippi) – Chirli, p. 25, fig. 3.
- 1986 *Ividella excavata* (Philippi, 1836) – Fretter *et al.*, p. 571, figs 388, 389.
- 1987 *Chrysallida (Parthenina) excavata* (Philippi 1836) – Cuerdo Barceló, 326, pl. 30, fig. 10.
- 1988 *Ividella excavata* (Philippi, 1836) – Graham, p. 560, fig. 241.
- 1992 *Chrysallida excavata* (Philippi, 1836) – Van der Linden & Eikenboom, p. 45, figs 58, 59.
- 1992 *Folinella excavata* (Philippi, 1836) – Cavallo & Repetto, p. 154, fig. 431.
- 1992 *Folinella excavata* (Philippi, 1836) – Crovato & Micali, p. 121.
- 1996 *Chrysallida excavata* (Philippi, 1836) – Peñas *et al.*, p. 18, figs 60-61.
- 2010 *Folinella excavata* (Philippi, 1836) – Sosso & Dell’Angelo, p. 52, 67, top row 2nd fig.
- 2011 *Chrysallida excavata* (Philippi, 1836) – Chirli & Micali, p. 24, pl. 8, figs 1-5 (*cum syn.*).
- 2011 *Chrysallida excavata* (Philippi, 1836) – Chirli & Linse, p. 194, pl. 72, fig. 3.

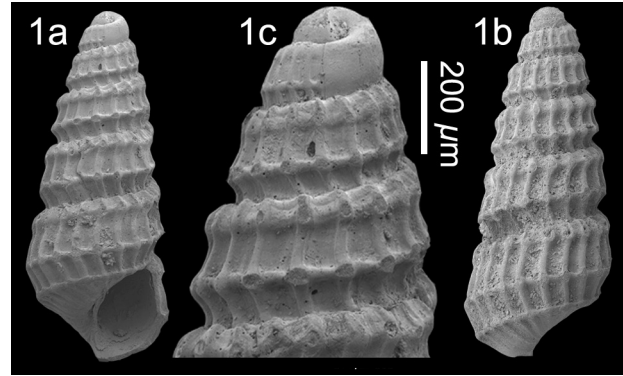


Plate 26 *Ividella excavata* (Philippi, 1836); 1. NHMW 2016/0103/2092, height 2.2 mm, width 800 μm , 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- 2011 *Chrysallida excavata* (Philippi, 1836) – Öztürk *et al.*, p. 60, figs 6A-D.
- 2014 *Folinella excavata* (Philippi, 1836) – Giannuzzi-Savelli *et al.*, p. 60, figs 136-137, appendix p. 16, 63.
- 2018 *Folinella excavata* (Philippi, 1836) – Brunetti & Cresti, p. 106, fig. 462.

Material and dimensions – Maximum height 2.0 mm, width 0.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2116 (1). **Sceaux-d’Anjou**: NHMW 2016/0103/2092 (1), NHMW 2016/0103/2105 (1).

Discussion – *Ividella excavata* (Philippi, 1836) is a distinctive species, with its strongly elevated axials and spirals forming coarse cancellate sculpture, with small, rounded tubercles developed at the intersections. There is a slight difference in the degree of intortion of the protoconch between the Assemblage I and extant specimens. The protoconch of present-day specimens is more depressed and was indicated as type B tending to C (Van der Linden & Eikenboom, 1992, p. 46) or type C (Giannuzzi-Savelli *et al.*, 2014, appendix p. 16, 63), while specimens from Assemblage I have a more elevated, type B tending to C, sharply delimited protoconch. *Ividella ghisottii* (Van Aartsen, 1984) from the present-day Mediterranean differs in having a squatter shell and three primary cords on the last whorl, the central cord somewhat weaker. This is the oldest stratigraphic record for *I. excavata* that we are aware of.

In Assemblage I this species has been found at St-Clément-de-la-Place and Sceaux-d’Anjou.

Distribution – Upper Miocene (Tortonian): NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli, 1984; Crovato & Micali, 1992; Guioli *et al.*, 2009; Chirli & Micali, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a; Greco, 1970; Cavallo & Repetto, 1992; Crovato & Micali, 1992; Ragaini & Bernieri, 2007; Sosso & Dell’Angelo, 2010;

Chirli & Micali, 2011; Brunetti & Cresti, 2018). Lower Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1914; Pelosio, 1960; Crovato & Micali, 1992); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: central Mediterranean, Italy (Crovato & Micali, 1992). Holocene: Atlantic, Northern Ireland (Harmer, 1920). Present-day: eastern Atlantic frontage from Scotland to Senegal, Mediterranean (Graham, 1988; Van der Linden & Eikenboom, 1992, Peñas *et al.*, 1996), eastern Mediterranean (Öztürk *et al.*, 2011).

***Ividella ligeriensis* nov. sp.**

Plate 27, figs 1, 2

Type material – Holotype NHMW 2016/0103/2241, height 2.0 mm, 760 μm ; paratype 1 NHMW 2016/0103/2242, height 2.2 mm, width 840 μm ; paratype 2 NHMW 2016/0103/2243, height 2.1 mm, width 810 μm ; paratype 3 NHMW 2016/0103/2244, height 2.0 mm, width 780 μm .

Other material – Known from type series only.

Etymology – Named after the Ligerian Gulf, in which this species lived. *Ividella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Ividella* species of small size, type C protoconch, up to 4.5 slightly coronate teleoconch whorls, strongly cancellate sculpture consisting of 20-22 ribs and two abapical cords on spire whorls, three on last whorl, small aperture, moderate strength columellar fold, small umbilical chink.

Description – Shell small, slender cylindrical spire, with blunt apex. Protoconch type C. Teleoconch of up to 4.5 whorls, convex, slightly angular at spirals, separated by impressed undulating suture. Sculpture of 20-22 narrow

rounded prosocline axial ribs on penultimate whorl, 24-26 on last whorl, overrun by two elevated narrow primary cords placed abapically on spire whorls, forming cancellate pattern, with axials slightly predominant with weak tubercles developed at intersections. Axials and spirals about one-quarter width of their interspaces. At adapical suture axials weakly elevated, giving whorl slightly coronate appearance. Last whorl 48% total height, with axials persisting over base, third primary cord developed at level of insertion outer lip delimiting base, small umbilical chink. Aperture small, 28% total height, ovate, outer lip slightly expanded abapically, columellar fold moderate strength.

Discussion – *Ividella ligeriensis* nov. sp. is separated from *I. excavata* (Philippi, 1836) by the absence of the adapical spiral cord seen in that species and having two abapical spirals on spire whorls as opposed to one in *I. excavata*, and three abapical spirals on the last whorl as opposed to two. *Ividella tuberculata* nov. sp. (see below) has a more scalate spire, more numerous spiral cords and much stronger tubercles developed at the sculptural intersections than in *I. ligeriensis*. The extant European *I. ghisottii* Van Aartsen, 1984 has two strong and a much weaker third central spiral cord. *Ividella holthuisi* (Van Aartsen, Gittenberger & Goud, 1998) from Mauritania also has three spiral cords on the spire whorls, but the shell is squatter than *I. ligeriensis*. *Ividella spinosula* (Micali, 1992) from the Pliocene of Italy also has a type C protoconch, but differs in having fewer axial ribs, and broader flattened cords, with small spines developed at the intersections instead of tubercles.

Ividella ligeriensis has so far only been found at St-Clément-de-la-Place.

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

***Ividella tuberculata* nov. sp.**

Plate 28, fig. 1

Type material – Holotype NHMW 2016/0103/1358, height 2.8 mm, width 1.0 mm; paratype 1 NHMW

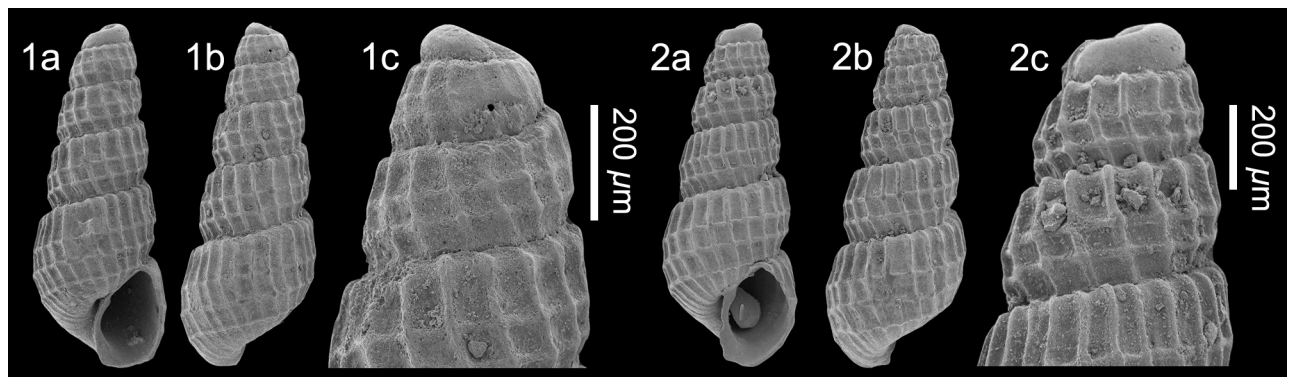


Plate 27. *Ividella ligeriensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/2241, height 2.0 mm, 760 μm , 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/2242, height 2.2 mm, width 840 μm , 2c, detail of protoconch (SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

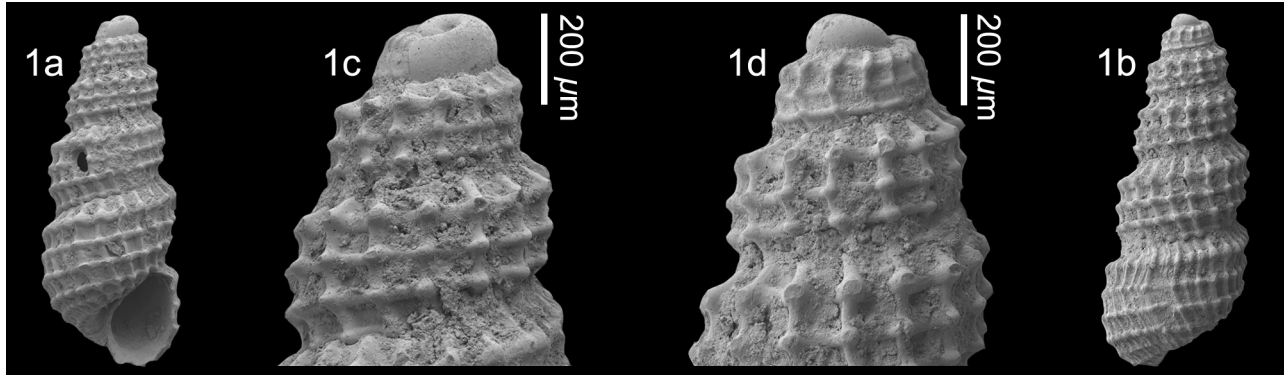


Plate 28. *Ividella tuberculata* nov. sp.; 1. **Holotype** NHMW 2016/0103/1358, height 2.8 mm, width 1.0 mm, 1c-d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

2016/0103/1454, height 2.4 mm, width 950 µm; paratype 2 NHMW 2016/0103/2051, height 2.3 mm, width 940 µm; paratype 3 NHMW 2016/0103/2052, height 2.4 mm, width 960 µm, **Renauleau**. Paratype 4 RGM.1352634, height 1.8 mm; paratype 5 RGM.1352635, height 2.0 mm, **Sceaux-d'Anjou**.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/2212 (1). **Sceaux-d'Anjou**: RGM.718021 (50+). **Renauleau**: NHMW 2016/0103/2053 (4), LC (1).

Etymology – Latin ‘*tuberculatus*, -a’, adjective meaning warty or tuberculate. *Ividella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Ividella* species of small size, type C protoconch, up to 4.75 scalate teleoconch whorls with well-developed subsutural ramp, strongly cancellate sculpture consisting of narrow ribs and three cords on spire whorls, small aperture, weak columellar fold, umbilicate.

Description – Shell small, slender cylindrical scalate spire, with blunt apex. Protoconch type C. Teleoconch of up to 4.75 whorls, with sharply delimited subsutural ramp, weakly convex below, separated by impressed undulating suture. Sculpture of 20–22 narrow rounded prosocline axial ribs on penultimate whorl, 25–30 on last whorl, overrun by three strongly elevated primary cords, fourth appearing at abapical suture on penultimate whorl, forming evenly cancellate pattern with spirals predominant with prominent tubercles developed at intersections. Axials and spirals about one-third width of their interspaces. Last whorl 49% total height, with sharply developed subsutural ramp, convex below, four primary cords above level of insertion outer lip, two further cords over base, prominent umbilical chink. Aperture small, 26% total height, ovate, outer lip slightly expanded abapically, columellar fold weak.

Discussion – With its strong sculpture and prominent tubercles developed at the intersections, *Ividella tuber-*

culata nov. sp. is impossible to confuse with any of its Assemblage I congeners. We have placed it in the genus *Ividella* Dall & Bartsch, 1909 on account of its sharp cancellate sculpture. The genus is represented in the European faunas by *I. excavata* (Philippi, 1836) having two strong spiral cords, and *I. ghisottii* (Van Aartsen, 1984) having two strong and a much weaker third central cord. *Ividella holthuisi* (Van Aartsen, Gittenberger & Goud, 1998) from Mauritania also has three spiral cords on the spire whorls, but the shell is squatter than *I. tuberculata*, composed of fewer whorls, and the sculpture is not as sharp. The most similar species in both shape and sculpture is *Ividella spinosula* (Micali, 1992) from the Pliocene of Italy, which also has a type C protoconch, but differs in having fewer axial ribs, and broader flattened cords, with small spines developed at the intersections instead of tubercles.

Ividella tuberculata is fairly widespread in Assemblage I, found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

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

Genus *Parthenina* Bucquoy, Dautzenberg & Dollfus, 1883

Type species (by original designation) – *Turbo interstinctus* J. Adams, 1797, present-day, British Isles.

- 1883 *Parthenina* Bucquoy, Dautzenberg & Dollfus, p. 158, 168.
- 1917 *Pyrguleta* Cossmann & Peyrot, p. 334. Type species (by original designation): *Pyrgulina degran-gei* Cossmann & Peyrot, 1917, Miocene, France.
- 1933 *Tiberiella* Coen, p. 164. Type species (by monotypy): *Tiberia pretiosa* Coen, 1933 (= *Turbo interstinctus* J. Adams, 1797), present-day, Mediterranean.
- 1958 *Prestoniella* Saurin, p. 64. Type species (by original designation): *Pyrgulina prestoni* Dautzenberg & H. Fischer, 1907, present-day, Vietnam.

1972b *Perparthenina* Nordsieck, p. 94. Type species (by original designation): *Chemnitzia terebellum* Philippi, 1844, present-day, Mediterranean.

Note – The genus *Parthenina* Bucquoy, Dautzenberg & Dollfus, 1883 includes species with conspicuous axial sculpture, spiral sculpture of strong basal cord plus one or more threads in the interspaces between the axials, not covering the entire whorl (Peñas & Rolán, 2017, p. 66). Based on molecular data, Schander *et al.* (2003, fig. 2) suggested that *Parthenina* appeared to be monophyletic.

***Parthenina brebioni* nov. sp.**

Plate 29, figs 1, 2

Type material – Holotype NHMW 2016/0103/2082, height 2.4 mm, width 1.1 mm; paratype 1 NHMW 2016/0103/2083, height 2.0 mm, width 0.8 mm, **Sceaux-d’Anjou**. Paratype 2 RGM.1352727, height 2.7 mm, **St-Clément-de-la-Place**.

Other material – **Renauleau**: NHMW 2016/0103/2129 (2).

Etymology – Named after Philippe Brébion of the Museum national d’Histoire naturelle, Paris, in recognition of his work on the French Redonian assemblages. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type C protoconch, 4.5 teleoconch whorls with 20-22 sinuous flattened ribs, 3-4 spiral cords placed abapically on spire whorls, last whorl five cords above insertion outer lip, 2-3 over base, well-developed columellar fold, small umbilical chink.

Description – Shell small, fusiform-conical, with blunt

apex. Protoconch type C. Teleoconch of 4.5 convex whorls. Suture linear, impressed, at 81° to main shell axis. Sculpture consists flexuous flattened ribs, 20-22 on penultimate whorl, about equal in width to their interspaces, crossed by three narrow spiral cords placed on abapical half of whorl on first two teleoconch whorls, fourth weaker cord appears above on penultimate whorl. Last whorl 58% total height, slightly inflated, evenly convex, with five spiral cords above level of insertion outer lip, 2-3 weaker cords over base, axials weaken over base, well-developed umbilical chink. Aperture ovate, 36% total height, outer lip flared abapically. Columella bearing stout fold at adapical end. Columellar callus somewhat thickened, erect, forming medial border of umbilical chink; parietal callus forming narrow callus margin.

Discussion – *Parthenina brebioni* nov. sp. is similar in shape, in having flexuous axial ribs and a well-developed umbilicus to *P. flexiornata* Gougerot, 1969 from the middle Miocene Loire Basin of France, but that species differs in only having two spiral cords placed abapically on the spire whorls. It is most similar to the Pliocene to present-day *P. juliae* (de Folin, 1872), which differs in having more regularly convex whorls, the ribs are more flexuous near the adapical suture, the spiral cords are weaker and occupy a more abapical portion of the spire and last whorl, and the columellar fold is weaker. In Assemblage I *Parthenina brebioni* has been found at St-Clément-de-la-Place, Sceaux-d’Anjou and Renauleau.

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

***Parthenina chauvereauensis* nov. sp.**

Plate 30, fig. 1

Type material – Holotype NHMW 2016/0103/2272, height 1.9 mm, width 855 µm.

Other material – Known from holotype only.

Etymology – Named after the type locality of Le Grand

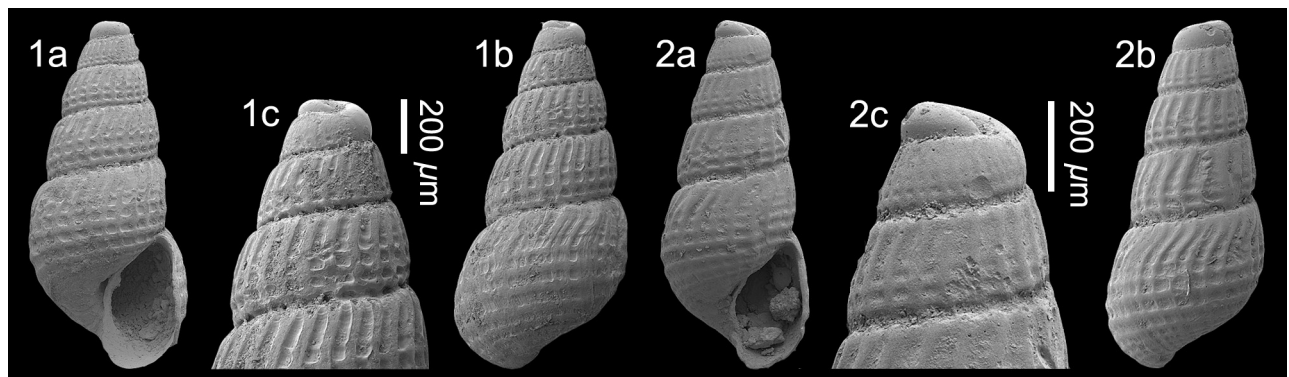


Plate 29. *Parthenina brebioni* nov. sp.; 1. **Holotype** NHMW 2016/0103/2082, height 2.5 mm, width 1.1 mm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/2083 height 2.0 mm, width 840 µm, 2c, detail of protoconch (SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

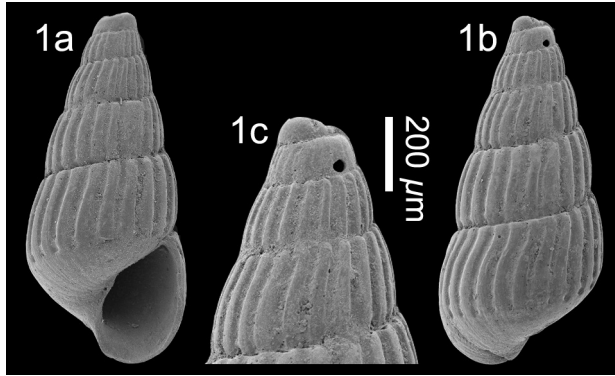


Plate 30. *Parthenina chauvereauiensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/2272, height 1.9 mm, width 855 µm, 1c, detail of protoconch (SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Chauvureau, St-Clément-de-la-Place. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type B tending to C protoconch, 4.5 teleoconch whorls with 20 broad flattened ribs, one subobsolete spiral just above suture, ribs stop abruptly at basal disc on last whorl, base imperforate, subobsolete columellar fold.

Description – Shell small, conical spire, with blunt apex. Protoconch type B tending to C. Teleoconch of 4.5 weakly convex whorls. Suture linear, impressed. Sculpture of broad flattened ribs, 20 on penultimate whorl, equal to slightly wider than their interspaces, crossed by one subobsolete spiral cord placed just above the suture. Last whorl 58% total height, convex, 24 slightly flexuous opisthocline flattened ribs ending abruptly at basal disc, crossed by one suboblete spiral cord placed just above disc; base convex, smooth, imperforate. Aperture ovate, 34% total height, outer lip slightly flared abapically. Columella bearing subobsolete fold at adapical end.

Discussion – *Parthenina chauvereauiensis* nov. sp. is characterised by having broad ribs, single spiral cord placed just above the suture that is subobsolete, and a smooth base. The most similar species is the present-day Mediterranean *Parthenina monterosati* (Clessin, 1900), that shows crowded ribs and only one spiral cord, but differs in having the two initial teleoconch whorls smooth. In Assemblage I *Parthenina chauvereauiensis* has so far only been found at St-Clément-de-la-Place.

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

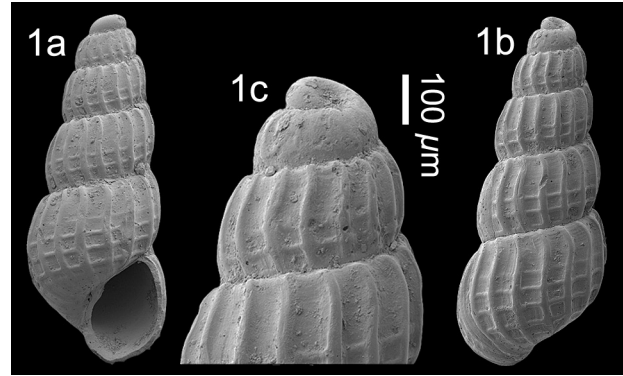


Plate 31. *Parthenina* cf. *clathrata* (Jeffreys, 1848); 1. NHMW 2016/0103/2080, height 2.1 mm, width 0.8 mm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Parthenina* cf. *clathrata* (Jeffreys, 1848)**

Plate 31, fig. 1

- cf. *1848 *Odostomia clathrata* Jeffreys, p. 345.
- cf. 1992 *Chrysallida clathrata* (Jeffreys, 1848) – Van der Linden & Eikenboom, p. 27, fig. 36.
- cf. 2011 *Chrysallida clathrata* (Jeffreys, 1848) – Chirli & Micali, p. 20, pl. 6, figs 1-5.
- cf. 2014 *Chrysallida clathrata* (Jeffreys, 1848) – Giannuzzi-Savelli *et al.*, p. 68, figs 188-190, appendix p. 22, 69.

Material and dimensions – Maximum height 2.1 mm, width 0.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2213 (8). **Sceaux-d'Anjou:** NHMW 2016/0103/2080 (1), RGM.1352730 (1), RGM.734942 (4).

Discussion – This species is extremely similar to the European Pliocene to present-day *P. clathrata* (Jeffreys, 1848) from which it differs in having fewer and narrower axial ribs and having a third cord on the penultimate whorl that is weaker than the other two.

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

***Parthenina clementiensis* nov. sp.**

Plate 32, figs 1-2

Type material – Holotype NHMW 2016/0103/2251, height 1.6 mm, width 405 µm; paratype 1 NHMW 2016/0103/2252, height 1.8 mm, width 620 µm.

Other material – Known from type series only.

Etymology – Named after the type locality of St-Clément-de-la-Place, Maine-et-Loire, North West France. *Parthenina* gender feminine.

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

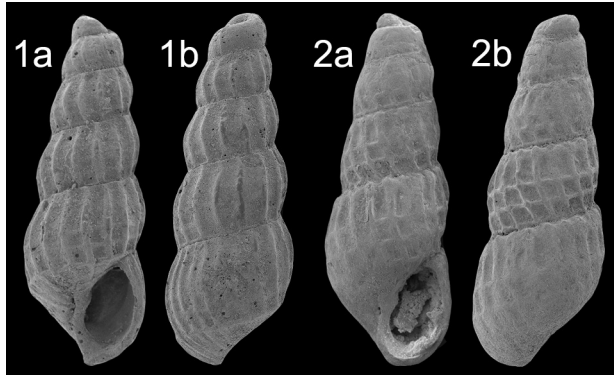


Plate 32. *Parthenina clementiensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/2251, height 1.6 mm, width 405 μm ; 2. **Paratype 1** NHMW 2016/0103/2252, height 1.8 mm, width 620 μm (SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type B tending to C protoconch, tall narrow spire, whorls broadly angled mid-height, suture strongly oblique, 14-15 narrow, widely spaced prosocline axial ribs crossed by two spiral cords on spire whorls, three on last whorl, mid-strength columellar fold.

Description – Shell small, slender, tall spire, with slightly angular whorls. Protoconch type B tending to C. Teleoconch of 4.5 convex whorls, widely angled just below mid-whorl marking periphery. Suture linear, impressed, strongly oblique. Sculpture consists of narrow, widely spaced, weakly prosocline axial ribs, 14-15 on penultimate whorl, separated by interspaces 2-3 times the width of ribs. Spire whorls with two spiral cord, slightly weaker than ribs, placed on lower third of whorl, upper delimits periphery, not swollen at intersections. Last whorl 52% total height, bearing three spiral cords, lower cord delimiting base, axial ribs extend over the base, base imperforate. Aperture ovate, 28% total height; outer lip rounded, hardly expanded abapically. Columella bearing mid-strength fold mid-aperture.

Discussion – In shell profile *Parthenina clementiensis* nov. sp. is reminiscent of the extant West African *P. josae* (van Aartsen, Gittenberger & Goud, 2000) from the Cape Verde Islands, but that species has one teleoconch whorl less, fewer, broader axial ribs and narrower spiral cords, placed in the abapical third of the whorl, that persist onto the base. *Parthenina mauritanica* (Peñas & Rolán, 1998), originally described from West Africa, but also occurring in the French Assemblage I deposits (see below), has similar sculpture, but is taller, less slender, with more convex whorls, the base bears a small umbilical chink and the columellar fold is weaker than in *Parthenina clementiensis*. *Parthenina sceauxensis* nov. sp. is less slender, composed

of more pagodiform whorls, with the periphery placed lower, the suture is less strongly oblique, the last whorl is more rounded, and the columellar fold is weaker. In Assemblage I *Parthenina clementiensis* has so far only been found at St-Clément-de-la-Place.

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

Parthenina emaciata (Brusina, 1866)

Plate 33, fig. 1

- 1865 *Turbonilla pygmaea* Brusina, p. 22 (*non* d'Orbigny, 1852).
- *1866 *Turbonilla emaciata* Brusina, p. 69 [*nom. nov. pro T. pygmaea* Brusina, 1865, *non Turbonilla pygmaea* (Grateloup, 1838), considered secondary homonym].
- 1868 *Turbonilla ambigua* Weinkauff, p. 216.
- 1972b *Chrysallida (Perparthenina) emaciata* form *minor* Nordsieck, p. 97.
- 1977 *Chrysallida emaciata* (Br.) – Van Aartsen, p. 56, fig. 17.
- 1992 *Chrysallida emaciata* (Brusina, 1866) – Van der Linden & Eikenboom, p. 13, fig. 21.
- 1996 *Chrysallida (Perparthenina) emaciata* (Brusina, 1866) – Van Aartsen & Menkhorst, p. 49, fig. 8.
- 1996 *Chrysallida emaciata* (Brusina, 1866) – Peñas *et al.*, p. 16, figs 36-37.
- 1998 *Chrysallida emaciata* (Brusina, 1866) – Peñas & Rolán, p. 44, figs 127-128.
- 1998 *Chrysallida emaciata* (Brusina, 1866) – Wilke & Van Aartsen, p. 9, pl. 1, fig. 1a-c.
- 2011 *Chrysallida emaciata* (Brusina, 1866) – Öztürk *et al.*, p. 58, fig 5A-C.
- 2013 *Chrysallida emaciata* (Brusina, 1866) – Landau *et al.*, p. 312, pl. 75, fig. 5.
- 2014 *Parthenina emaciata* (Brusina, 1866) – Giannuzzi-Savelli *et al.*, p. 64, fig. 154, appendix page 19, 66.

Material and dimensions – Maximum height 1.6 mm, width 0.6 mm. **Renauleau**: NHMW 2016/0103/1731 (1), NHMW 2016/0103/2124 (6).

Discussion – The specimens from Assemblage I are minute, slender cylindrical with a blunt apex, and type B tending to C protoconch. The teleoconch consists of 3-4 whorls separated by a broad V-shaped suture. Sculpture consists of narrow, prosocline, very slightly arched axial ribs, 17 on penultimate whorl, separated by interspaces about three times wider than the ribs. Spire whorls bear one spiral cord, equal in strength to the ribs, placed at one-quarter whorl height, with a second cord appearing at the abapical suture near the end of the penultimate whorl. The entire surface is covered in fine irregular spiral microsculpture. The last whorl has two spiral cords, the lower cord delimiting base, axial ribs are subobsolete over base, and a small umbilical chink is present. The

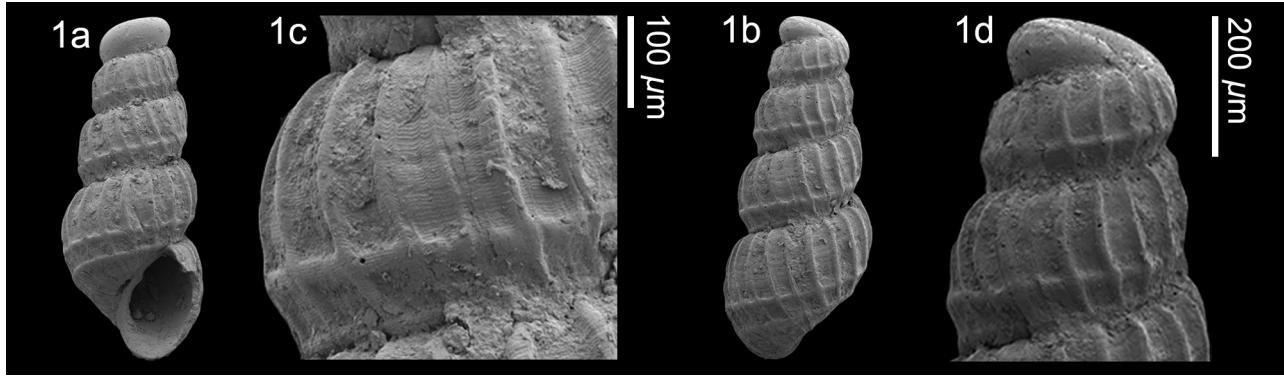


Plate 33. *Parthenina emaciata* (Brusina, 1866); 1. NHMW 2016/0103/1731, height 1.4 mm, width 0.6 mm, 1c, detail of teleoconch sculpture, 1d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

aperture is small, ovate, and the columella bears a small fold mid-height.

Parthenina emaciata (Brusina, 1866) is variable in shape. As this species may have up to six whorls, the specimens from Assemblage I are all immature and we have not found any fully grown specimen. The spiral microsculpture seen in the shell illustrated (Pl. 33, fig. 1c) is described by Van der Linden & Eikenboom (1992, p. 13), although the protoconch is at the limit between types B and C. Several extant European and West African Atlantic congeners, such as *P. interstincta* (J. Adams, 1797) and *P. pytelilla* (Schander, 1994), are sculptured by widely spaced axial ribs and one abapical spiral cord on the spire whorls, two on the last whorls, but neither of these species have such convex whorls nor any secondary spiral sculpture. *Parthenina monozona* (Brusina, 1869) [*Pyrgulina intermixta* Monterosato, 1884 is a synonym] from the Pliocene to present-day Mediterranean has similar sculpture, but the axials are broader and orthocline to weakly opisthocline, and the suture is deeper. In Assemblage I *P. emaciata* is most similar in sculpture to *P. lamellata* nov. sp., but differs in having a proportionately larger protoconch, the spire whorls are less scalate, but most importantly, *P. lamellata* lacks the distinct spiral teleoconch microsculpture seen in *P. emaciata*. This species is extremely uncommon, and so far found only at Renauleau.

Distribution – Middle Miocene: Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene (Tortonian): NW France (this paper). Present-day: Atlantic, south coast of Portugal (Van der Linden & Eikenboom, 1992), Canary Islands, Angola (Peñas & Rolán, 1998), Mediterranean (Peñas *et al.*, 1996; Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean (Öztürk *et al.*, 2011), Black Sea (Wilke & Van Aartsen, 1998).

***Parthenina indistincta* (Montagu, 1808)**

Plate 34, fig. 1

- *1808 *Turbo indistinctus* Montagu, p. 129.
- 1992 *Chrysallida indistincta* (Montagu, 1808) – Van der

- Linden & Eikenboom, p. 31, figs. 11, 12, 43-45.
- 2011 *Chrysallida indistincta* (Montagu, 1808) – Chirli & Micali, p. 33, pl. 10, figs 11-15 (*cum syn.*).
- 2011 *Chrysallida indistincta* (Montagu, 1808) – Öztürk *et al.*, p. 64, fig 10A-D.
- 2014 *Parthenina indistincta* (Montagu, 1808) – Giannuzzi-Savelli *et al.*, p. 70, figs 197, 198, appendix p. 22, 70.
- 2014 *Parthenina indistincta* (Montagu, 1808) – Høisæter, p. 15, fig. 5.
- 2018 *Parthenina indistincta* (Montagu, 1808) – Ceulemans *et al.*, p. 131, pl. 8, fig. 4 (*cum syn.*).

Material and dimensions – Maximum height 2.0 mm, width 0.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2214 (5). **Sceaux-d’Anjou:** NHMW 2016/0103/2102 (1).

Discussion – *Parthenina indistincta* (Montagu, 1808) is characterised by its slender cylindrical to slightly conical shell with a blunt apex, type C protoconch, teleoconch composed of 4-7 flat sided to slightly convex whorls that are slightly inflated below mid-whorl and taper inwards abapically to the oblique suture, and sculpture of orthocline ribs, straight on early whorls, sinuous on later

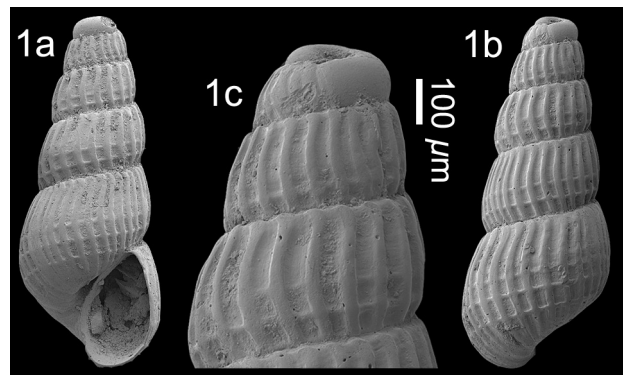


Plate 34. *Parthenina indistincta* (Montagu, 1808); 1. NHMW 2016/0103/2102, height 2.0 mm, width 0.8 mm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorls and narrow spirals; 2-3 on early whorls, 3-4 on penultimate, 4-7 on last whorl. The umbilicus is hardly developed and columellar fold absent. For comparison with related species we refer to Van der Linden & Eikenboom (1992, p. 33) although we note that *P. flexuosa* (Monterosato, 1874) and *P. palazzii* (Micali, 1984) are not synonyms as suggested by those authors (see Micali *et al.*, 1993; Lygre *et al.*, 2011).

In Assemblage I *Parthenina indistincta* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene (Tortonian): NW France (this paper). Lower Pliocene: Atlantic, northwestern France (Ceulemans *et al.*, 2018); western Mediterranean, Tunisia (Fekih, 1969); central Mediterranean, Italy (Forli *et al.*, 1999; Chirli & Micali, 2011). Upper Pliocene: North Sea Basin, Oorderen Sands, Belgium (Marquet, 1993, 1997, 1998); central Mediterranean, Italy (Cavallo & Repetto, 1992; Ferrero *et al.*, 1998). Pliocene (indeterminate): North Sea Basin, Netherlands (Van Regteren Altena *et al.*, 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914). Present-day: Eastern Atlantic frontage Norway (Høisæter, 2014), British Isles (Graham, 1988) to Mediterranean (Fretter *et al.*, 1986; Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean (Öztürk *et al.*, 2011).

***Parthenina indistincta* (J. Adams, 1797)**

Plate 35, figs 1, 2

- *1797 *Turbo interstinctus* J. Adams, p. 66, pl. 13, figs 23, 24.
- 1827 *Jasminia obtusa* Brown pl. 50, figs 27, 28.
- 1872 *Elodia hortensiae* de Nansouty in de Folin & Périer, p. 48, pl. 2, fig. 2.
- 1883 *Odostomia jeffreysi* var. *flexicostata* Bucquoy, Dautzenberg & Dollfus, p. 171, pl. 20, fig. 10.
- 1892a *Pyrgulina indistincta* var. *subappennina* Sacco, p. 66, pl. 1, fig. 108.
- 1914 *Parthenina indistincta* (Mtg. [sic]) – Cerulli-Irelli, p. 434, pl. 54, figs 61-66.
- 1914 *Parthenina indistincta* var. *bicinctulata* Brugn. – Cerulli-Irelli, p. 434, pl. 54, figs 67, 68.
- 1914 *Parthenina indistincta* var. *tristriata* Cerulli-Irelli, p. 434, pl. 54, fig. 69.
- 1914 *Parthenina indistincta* var. *quadristriata* Cerulli-Irelli, p. 434, pl. 54, fig. 70.
- non 1920 *Pyrgulina indistincta* (Montagu [sic]) – Harmer, p. 576, pl. 49, fig. 48.
- 1921 *Pyrgulina (Parthenina) indistincta* (Montagu [sic]) – Cossmann, p. 258, pl. 6, figs 28-31.
- 1923 *Pyrgulina indistincta* Mont. – Friedberg, p. 455, pl. 28, fig. 7.
- 1933 *Tiberia (Tiberiella) pretiosa* Coen, p. 51, 164, pl. 4, fig. 32.
- 1955 *Chrysallida indistincta* (Adams) – Moroni, p. 102, pl. 4, fig. 22.
- 1963 *Chrysallida (Pyrgulina) indistincta* (Adams) – Venzo & Pelosio, p. 76, pl. 4, figs 15-17.
- 1969 *Pyrgulina (Parthenina) indistincta* (Montagu.) –

- Fekih, p. 18, pl. 2, fig. 12.
- 1970 *Chrysallida (Parthenina) indistincta* (Montagu) – Greco, p. 288, pl. 4, figs 10-11.
- 1972b *Chrysallida (Parthenina) indistincta* (Montagu, 1803) – Nordsieck, p. 92, pl. PI, fig. 8.
- 1972b *Chrysallida farolita* Nordsieck, p. 96, PI, fig. 22.
- 1974 *Chrysallida (Parthenina) indistincta* (Montagu, 1803) – Malatesta, p. 442, pl. 32, fig. 14.
- 1984 *Pyrgulina indistincta* var. *subappennina* Sacco, 1892 – Ferrero Mortara *et al.*, p. 78, pl. 11, fig. 10.
- 1988 *Chrysallida obtusa* (Brown, 1827) – Graham, p. 546, fig. 234.
- 1992 *Chrysallida obtusa* (Brown, 1827) – Van der Linden & Eikenboom, p. 23, figs 8, 9, 30-32.
- 1996 *Chrysallida indistincta* (J. Adams, 1797) – Peñas *et al.*, p. 22, figs 43-47, 51.
- 1998 *Chrysallida obtusa* (T. Brown, 1827) – Wilke & Van Aartsen, p. 10, pl. 4, fig. 19a-c.
- 2000 *Chrysallida (Parthenina) obtusa* (Brown, 1827) – Van Aartsen *et al.*, p. 28, fig. 33.
- 2003 *Chrysallida (Parthenina) indistincta* (Adams) – İslamoğlu & Taner, p. 45, pl. 2, fig. 14.
- 2004 *Chrysallida indistincta* (J. Adams, 1797) – Solustri & Micali, p. 64, fig. 5a.
- 2011 *Chrysallida indistincta* (Adams, J., 1797) – Chirli & Micali, p. 35, pl. 11, figs 6-10 (*cum syn.*).
- 2011 *Chrysallida indistincta* (Adams, J., 1797) – Chirli & Linse, p. 196, pl. 74, fig. 1.
- 2013 *Chrysallida obtusa* (Brown, 1827) – Landau *et al.*, p. 314, pl. 75, fig. 10 (*cum syn.*).
- 2014 *Parthenina indistincta* (J. Adams, 1797) – Høisæter, p. 16, figs 6-11.
- 2014 *Parthenina indistincta* (J. Adams, 1797) – Giannuzzi-Savelli *et al.*, p. 64, figs 158-162, appendix p. 19, 67.
- 2018 *Parthenina indistincta* (Adams J., 1797) – Brunetti & Cresti, p. 106, fig. 453.

Material and dimensions – Maximum height 2.0 mm, width 0.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2246-2247 (2).

Discussion – *Parthenina indistincta* (J. Adams, 1797) is characterised by its turritiform profile, type B tending to C protoconch, almost straight-sided spire whorls separated by a V-shaped suture, axial sculpture of about 20 elevated orthocone robust ribs, roughly equal in width to their interspaces, that weaken over the base and on spire whorls one or two thin spiral cords placed on the abapical half of the whorl, 2-3 on the last whorl. The columella bears a well-developed fold and there is no umbilicus. We have excluded the record of Harmer (1920, p. 576, pl. 49, fig. 48) as he described “...rows of obscure spiral striae below the periphery...”, a character that does not fit this species.

Other European Mediterranean Pliocene to present-day turritiform species with almost flat-side spire whorls and similar spiral sculpture are: *P. suturalis* (Philippi, 1844) that differs in being taller, more slender, with more numerous orthocone ribs that are flattened and somewhat

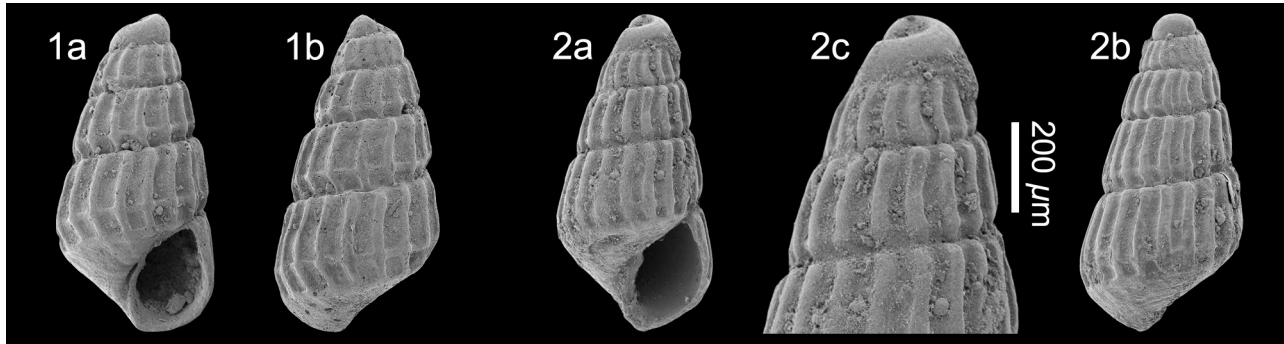


Plate 35. *Parthenina interstincta* (J. Adams, 1797); 1. NHMW 2019/0167/2246, height 1.3 mm, width 650 µm; 2. NHMW 2019/0167/2247, height 1.3 mm, width 645 µm (SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

flexuous, *P. terebellum* (Philippi, 1844) that is again taller, with the same number of ribs, but they are wider and flatter. *Parthenina tragulaeformis* (Fekih, 1969), from the Mediterranean Pliocene of Tunisia and Italy (Chirli & Micali, 2011), is even more slender and taller turri-form, with a deep, broad, V-shaped suture and 18–20 very broad, strongly prosocline flattened ribs. The specimens from Assemblage I are smaller than those from other fossil or present-day faunas, and until now found only at St-Clément-de-la-Place.

Distribution – Middle Miocene: Paratethys, Poland (Friedberg, 1923); Proto-Mediterranean (Serravallian): Antalya Basin, Turkey (İslamoğlu & Taner, 2003), Karaman Basin (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian), Proto-Mediterranean (Tortonian and Messinian), Italy (Moroni, 1955; Venzo & Pelosio, 1963). Lower Pliocene: central Mediterranean, Italy (Sacco, 1892a; Guioli *et al.*, 2009; Chirli & Micali, 2011; Brunetti & Cresti, 2018), Tunisia (Fekih, 1969). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a; Cossmann, 1921; Greco, 1970; Malatesta, 1974; Ferrero Mortara *et al.*, 1984); eastern Mediterranean, Rhodes (Chirli & Linse, 2011); central Mediterranean, Italy (Cerulli-Irelli, 1914; Gianolla *et al.*, 2010); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Present-day: Atlantic, Scandinavia, England (Nordsieck, 1972b; Graham, 1988; Høisæter, 2014), Madeira, south to Morocco, Canary Islands, Cape Verde Islands (Van Aartsen *et al.*, 2000;), into western Mediterranean (Peñas *et al.*, 1996), central Mediterranean (Nordsieck, 1972b; Giannuzzi-Savelli *et al.*, 2014), Black Sea (Wilke & Van Aartsen, 1998).

***Parthenina lamellata* nov. sp.**

Plate 36, fig. 1

Type material – Holotype NHMW 2016/0103/2093, height 1.7 mm, width 700 µm; paratype 1 RGM.1352632 (1), height 1.5 mm; paratype 2 RGM.1352633 (1), height 1.2 mm.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2224 (4). **Sceaux-d’Anjou:** RGM.1352740 (1 incomplete).

Etymology – Name describing the lamelliform axial ribs. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of minute size, type B protoconch, 3.5 teleoconch whorls with sinuous lamelliform ribs, 18 on penultimate whorl, crossed by one weakly developed abapical cord on spire whorls, two strong narrow cords on abapical portion of last whorl, third weaker cord placed mid-base.

Description – Shell minute, scalate spire. Protoconch type B. Junction with teleoconch sharply delimited. Teleoconch of 3.5 convex, scalate whorls, separated by deeply impressed suture. Sculpture of fine, elevated, orthocline sinuous lamelliform ribs, 18 on penultimate whorl, crossed by one weakly developed abapical cord on spire whorls. Last whorl 57% of total height, shoulder

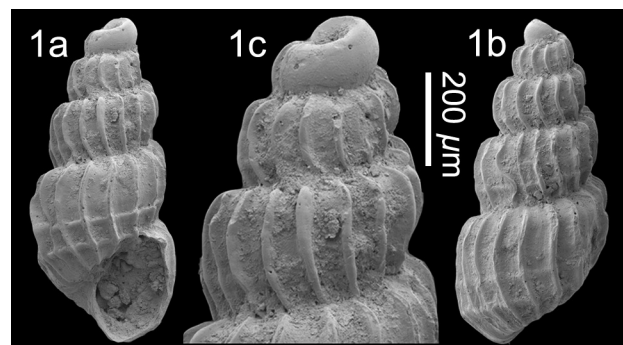


Plate 36. *Parthenina lamellata* nov. sp.; 1. **Holotype** NHMW 2016/0103/2093, height 1.7 mm, width 700 µm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

placed high, roundly angled at shoulder and base, with two fine cords that do not overrun ribs, lower cord placed at level of insertion of outer lip, upper placed mid-way between lower cord and shell periphery. Third weaker cord placed mid-base; umbilicus obscured by matrix. Aperture ovate, 30% of total height, apertural characters obscured by matrix.

Discussion – *Parthenina lamellata* nov. sp. is similar to some extreme forms of *P. flexuosa* (Monterosato, 1874) (see Giannuzzi-Savelli *et al.*, 2014, fig. 155), but differs in having a scalate spire, the suture is not V-shaped as in *P. flexuosa*, and the protoconch is of type B, as opposed to type C in *P. flexuosa*. Smaller specimens of the West African extant *P. connexa* (Dautzenberg, 1912) (see Peñas & Rolán, 1998, fig. 135) are also somewhat similar, but the spire is not scalate, the ribs broader, and the protoconch is of type C. It has been suggested to us that placement within the genus *Ividella* Dall & Bartsch, 1909 is also possible, but in members of that genus the axials and spirals are coarser and stronger, and placement in *Parthenina* is preferred herein.

This species has been found at St-Clément-de-la-Place and Sceaux-d’Anjou.

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

***Parthenina ligeriana* nov. sp.**

Plate 37, fig. 1

Type material – Holotype NHMW 2016/0103/2079, height 1.2 mm, width 600 μm .

Other material – Known only from type material.

Etymology – Named after the ‘Golfe Ligérien’, the name of the bay in which the species lived. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of minute size, type B protoconch, three convex teleoconch whorls, about 30 flexuous axial ribs, spiral sculpture of three primary cords on abapical half of whorls, fine spiral threads in interspaces between ribs on adapical half.

Description – Shell minute, fusiform, low spire. Protoconch type B. Teleoconch of three strongly convex whorls. Suture linear, impressed, at 78° to main shell axis. Sculpture of low curved ribs, 30 on penultimate whorl, flexuous ‘reverse-S shape’ just below suture, half to third width of their interspaces. Spiral sculpture of three primary cords placed on abapical half of spire whorls, slightly narrower than ribs, plus close-set spiral cordlets on adapical half of

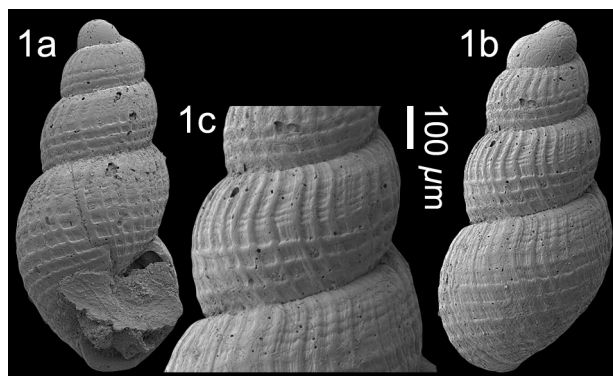


Plate 37. *Parthenina ligeriana* nov. sp.; 1. **Holotype** NHMW 2016/0103/2079, height 1.2 mm, width 600 μm , 1c, detail of teleoconch sculpture (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorl. Surface covered in prominent axial growth lines. Last whorl 61% total height, regularly convex, with axial and spiral sculpture persisting over base. Aperture ovate, 34% of height; apertural characters obscured by matrix.

Discussion – Despite being represented by a single specimen, this species is so distinctive that it warrants formal description. It is unusual for the genus in having fine spiral sculpture visible between the axial ribs on the adapical half of all teleoconch whorls. It is difficult to find similar species with which to compare; *Parthenina redoniana* nov. sp. sharing its minute size, squat profile and convex whorls, but, like most *Parthenina* species, lacks sculpture on the adapical half of the whorl. Gougerot (1978) described a minute species from the middle Miocene Loire Basin of France as *P. pseudodecussata*. The schematic drawings in that paper leave much to be desired, but, like *P. ligeriana*, it has rounded whorls (2 vs 3 in *P. ligeriana*) and similar sculpture of primary cords in strength and number, but no mention is made of any finer cords on the adapical half of the whorls in the detailed description given (Gougerot, 1978, p. 22). Therefore, we do not consider them to be conspecific.

Parthenina ligeriana as so far only been found at Sceaux-d’Anjou.

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

***Parthenina mauritanica* (Peñas & Rolán, 1998)**

Plate 38, figs 1, 2

*1998 *Chrysallida mauritanica* Peñas & Rolán, p. 50, figs 142-145.

Material and dimensions – Height 2.5 mm, width 950 μm . **St-Clément-de-la-Place:** NHMW 2016/0103/2262 (1), NHMW 2016/0103/2263 (1). **Sceaux-d’Anjou:** NHMW 2016/0103/2156 (1).

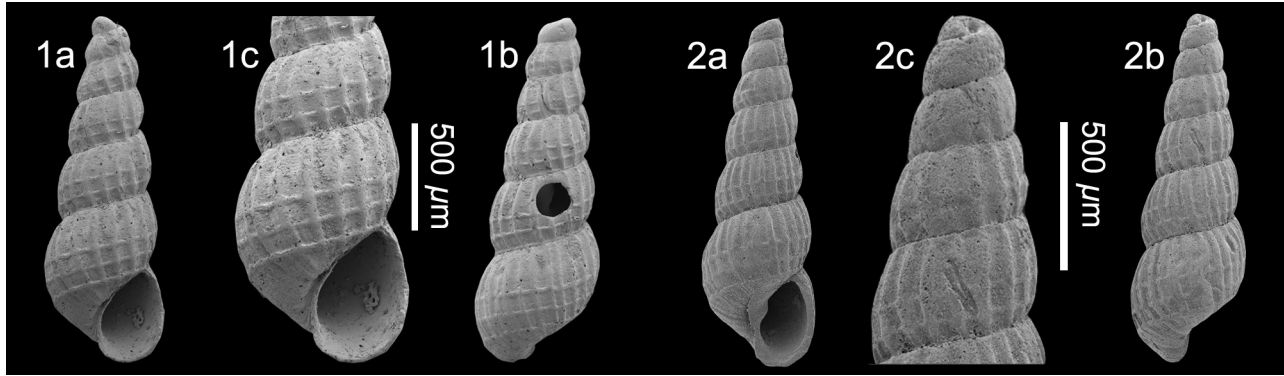


Plate 38. *Parthenina mauritanica* (Peñas & Rolán, 1998); 1. NHMW 2016/0103/2156, height 2.5 mm, width 950 µm, 1c, detail of teleoconch sculpture. La Presselière, Sceaux-d'Anjou, Maine-et-Loire. 2. NHMW 2016/0103/2262, height 2.4 mm, width 760 µm, 2c, detail of protoconch (SEM images). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – The single specimen from Sceaux-d'Anjou is almost identical to the holotype, except for having slightly thinner ribs. It is characterised by its type B protoconch (somewhat damaged in the fossil specimen), tall spire composed of strongly convex whorls, elevated weakly prosocline ribs, two spiral cords on spire whorls, three on last whorl and lack of columellar fold. Numerous European fossil and extant species are superficially similar; *P. monozona* (Brusina, 1869) and *P. interstincta* (J. Adams, 1797) both have fewer spirals and a well-developed columellar fold. *Parthenina clathrata* (Jeffreys, 1848) is similar in sculpture, number of axials and spirals, and has a weak columellar fold, but differs in whorl profile. In Assemblage I, *P. cf. clathrata* is less slender and has more spirals on the last whorl, *P. indistincta* (Montagu, 1808) again differs in whorl profile and has more numerous flexuous axials, *P. milleti* nov. sp. has the same number of spirals, but differs in shape and has more numerous axials, *P. sceauxensis* nov. sp. differs in whorl profile and has a weak columellar fold.

In Assemblage I *Parthenina mauritanica* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene (Tortonian): NW France (this paper). Present-day: Mauritania (Peñas & Rolán, 1998).

***Parthenina milleti* nov. sp.**

Plate 39, figs 1-3

Type material – Holotype NHMW 2016/0103/2069, height 2.5 mm, width 950 µm; Paratype 2 RGM.1352636, height 2.4 mm, width 900 µm, **Sceaux-d'Anjou**. Paratype 1 NHMW 2016/0103/1124, height 2.0 mm, width 800 µm; paratype 3 NHMW 2016/0103/1125, height 1.9 mm, width 820 µm, **St-Clément-de-la-Place**.

Other material – Maximum height 3.1 mm, width 1.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2245 (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. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of tall cylindrical shape, type B protoconch, 5.5 teleoconch whorls with 27-29 narrow orthocline axials and two spiral cords on spire whorls, three on last whorl, base covered in fine spiral threads, medium-strength columellar fold.

Description – Shell small, tall cylindrical, slightly scalate spire, with blunt apex. Protoconch type B. Teleoconch of 5.5 weakly convex whorls. Suture linear, impressed, at 80° to main shell axis. Sculpture consists of narrow, straight orthocline axial ribs, 27-29 on penultimate whorl, separated by interspaces about twice width of ribs. Spire whorls with two spiral cord, almost equal in strength to ribs, placed on lower third of whorl. Last whorl 48% total height, bearing three spiral cords, lower cord delimiting base, axial ribs persist over base, imperforate. Base bearing fine crowded threads. Aperture small ovate; outer lip not preserved. Columella bearing medium-strength fold at adapical end.

Discussion – *Parthenina milleti* nov. sp. is closely similar to *P. acuticostata* (Sorgenfrei, 1958) from the middle and upper Miocene North Sea Basin. The original figure may be misleading, as it is probably not a fully grown specimen at 1.7 mm in height. The specimens figured by Moths *et al.* (2010, pl. 23, fig. 13, pl. 46, fig. 2) attain 2.4 mm in height and have an extra teleoconch whorl. Although the original figure shows three spiral cords on the last whorl, the original description says 4-6 cords on last whorl (Sorgenfrei, 1958, p. 308). This agrees with

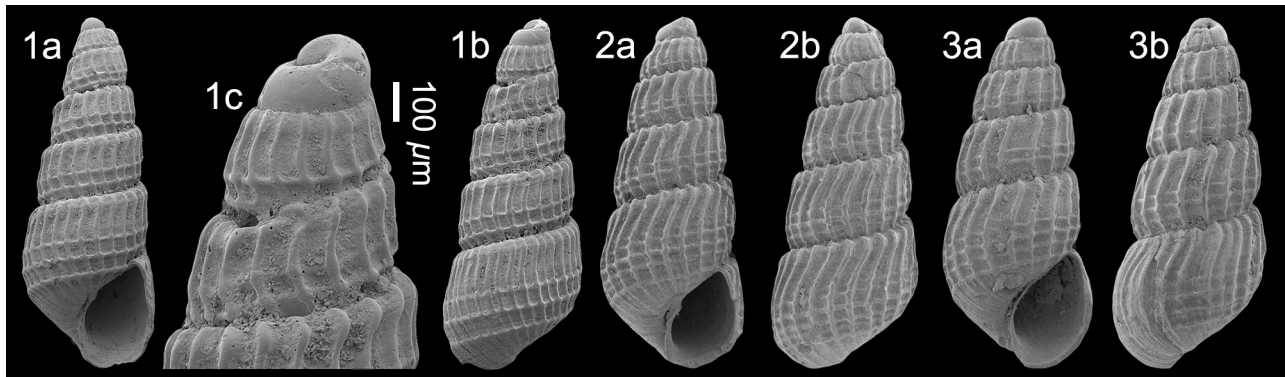


Plate 39. *Parthenina milleti* nov. sp.; 1. **Holotype** NHMW 2016/0103/2069, height 2.5 mm, width 950 μm , 1c, detail of protoconch. La Presselière, Sceaux-d'Anjou. 2. **Paratype 1** NHMW 2016/0103/1124, height 3.1 mm, width 1.2 mm; 3. **Paratype 2** NHMW 2016/0103/1124, height 1.9 mm, width 820 μm (all SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the figures given by Moths *et al.* (2010), which also show more cords on the spire whorls and the whorls tend to be more convex than in the French species. The specimen from the upper Pliocene of Italy figured as *P. cf. acuticostata* by Bongiardino & Micali (2018, fig. 1A) is so different from *P. milleti* that a comparison is not necessary.

In the recent faunas, *P. milleti* is similar to *P. dantarti* (Peñas & Rolán, in Peñas *et al.*, 2008) from Barcelona, northeastern Spain, but in that species the ribs are slightly fewer (about 24), broader, resulting in the axial sculpture being strongly predominant, whereas in *P. milleti* the ribs and cords are of equal strength. Furthermore, the ribs do not extend over the base, whereas they do in *P. milleti*. *Parthenina clathrata* (Philippi, 1848), widespread from the Mediterranean to the British Isles, is also similar, but in that species the axials are markedly prosocline, broader and flattened. *Parthenina indistincta* (Montagu, 1808), which shares a similar modern geographic range to the previous species, differs in having opisthocline axials that are again broader, slightly sinuous, and less numerous (28-30 on last whorl *vide* Fretter, 1988, p. 552 vs 36 in the French species).

In Assemblage I *Parthenina milleti* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

Parthenina monozona (Brusina, 1869)

Plate 40, fig. 1

- *1869 *Odostomia monozona* Brusina, p. 240.
- 1884 *Pyrgulina intermixta* Monterosato, p. 87.
- 1914 *Parthenina intermixta* Mtrs. – Cerulli-Irelli, p. 435, pl. 54, figs 7-9.
- 1969 *Pyrgulina (Parthenina) intermixta* Monterosato – Fekih, p. 19, pl. 3, fig. 3.
- 1992 *Chrysallida intermixta* (Monterosato, 1884) – Van der Linden & Eikenboom, p. 20, fig. 33.

- 1992 *Chrysallida rara* Gaglini, p. 149, fig. 130.
- 2011 *Chrysallida intermixta* (Monterosato, 1884) – Chirli & Micali, p. 34, pl. 11, figs 1-5.
- 2014 *Parthenina monozona* (Brusina, 1869) – Giannuzzi-Savelli *et al.*, p. 64, figs 163-168, appendix p. 19, 67.
- 2015 *Parthenina monozona* (Brusina, 1869) – Micali *et al.*, p. 521, figs 1-12 (*cum syn.*)

Material and dimensions – Maximum height 2.5 mm, width 0.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2225 (3). **Sceaux-d'Anjou:** NHMW 2016/0103/2073 (1), NHMW 2016/0103/2074 (2). **Renauleau:** NHMW 2016/0103/2111 (7).

Discussion – *Parthenina monozona* (Brusina, 1869) is characterised by its tall conical shell, type B protoconch, up to 6-7 weakly convex teleoconch whorls, sculpture of 18-22 strong, orthocline ribs slightly narrower than half the width of their intervals, crossed by a single abapical cord on spire whorls, two on the last whorl. The synonymy of *Pyrgulina intermixta* Monterosato, 1884 was discussed at length by Micali *et al.* (2015), and a detailed

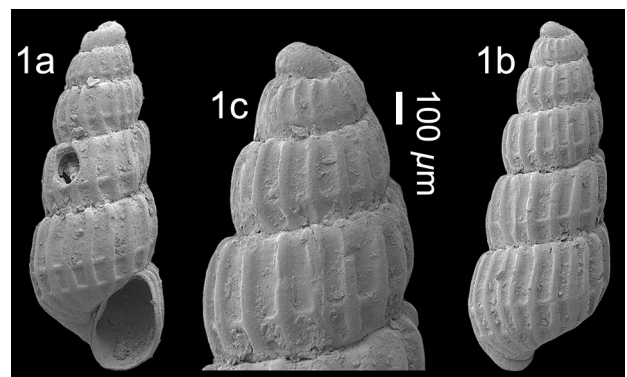


Plate 40. *Parthenina monozona* (Brusina, 1869); 1. NHMW 2016/0103/2073, height 2.5 mm, width 0.9 mm, 1c, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

chresonymy given. The specimens from Assemblage I fit within the relatively wide range of variability seen in this species, although the microscopic spiral threads described by Van der Linden & Eikenboom (1992, p. 27), Chirli & Micali (2011, p. 35) and Micali *et al.* (2015, p. 523) do not seem to be present. However, this micro-sculpture is only visible in very fresh specimens.

In Assemblage I *Parthenina monozona* has been found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene (Tortonian): NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli & Micali, 2014), Tunisia (Fekih, 1969). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914). Present-day: Atlantic from NW Spain southwards into whole Mediterranean (Van der Linden & Eikenboom, 1992; Micali *et al.*, 2015).

***Parthenina pouweri* nov. sp.**

Plate 41, fig. 1

Type material – Holotype NHMW 2016/0103/2152, height 1.3 mm, width 590 μm .

Other material – Known from holotype only.

Etymology – Named after Ronald Pouwer, collection manager Cainozoic Mollusca at the Naturalis Biodiversity Center in Leiden, in recognition of his hard work and enormous support in this project. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of minute size, type B protoconch, four scalate teleoconch whorls, strong prosocline ribs, 17 on penultimate whorl, no spiral sculpture, strong peribasal cord delimiting smooth concave base, small aperture, weak columellar fold.

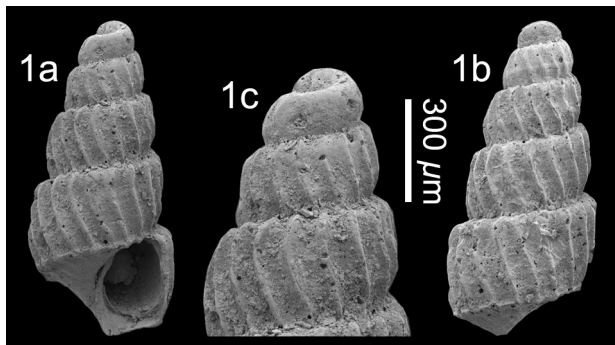


Plate 41. *Parthenina pouweri* nov. sp.; 1. **Holotype** NHMW 2016/0103/2152, height 1.3 mm, width 590 μm , 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell minute, scalate spire. Protoconch type B. Teleoconch of just under four weakly convex to straight-sided, scalate whorls, separated by deeply impressed suture. Sculpture of sharp, elevated, prosocline ribs, 17 on penultimate whorl, extending between sutures. No spiral sculpture. Last whorl 53% total height, shoulder placed at suture, almost straight sided below to strong, elevated, peribasal cord; ribs forming small tubercles where they abruptly end at peribasal cord. Base sharply delimited, angular at peribasal cord, smooth, small umbilical chink. Aperture small, ovate, 23% total height, outer lip angular at insertion peribasal cord, with small spout-like expansion abapically. Peristome continuous, columella weakly excavated, thickened and erect forming medial border of umbilical chink, with small fold placed just above mid-aperture.

Discussion – *Parthenina pouweri* nov. sp. is a most unusual species that differs from all its congeners in having sharp prosocline ribs that are not intersected by cords. The inclusion of this species in the genus *Parthenina* Bucquoy, Dautzenberg & Dollfus, 1883 stretches the genus concept that historically includes species that have spiral sculpture consisting of a strong basal cord plus one or more threads in the interspaces between the axials, not covering the entire whorl (Peñas & Rolán, 2017, p. 66), here a strong peribasal cord is present and no threads. In shape it is similar to two other Assemblage I species described herein; *P. lamellata* nov. sp. and *P. silvae* nov. sp., but both of those have cords on the abapical half of at least the last two whorls. We cannot find any further species with which to compare *P. pouweri*. This species has so far only been found at Sceaux-d'Anjou.

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

***Parthenina redoniana* nov. sp.**

Plate 42, figs 1, 2

Type material – Holotype NHMW 2016/0103/2165, height 1.0 mm, width 460 μm ; paratype 1 NHMW 2016/0103/2086, height 2.4 mm, width 600 μm ; paratype 2 RGM.1352738, height 2.3 mm; paratype 2 RGM.1352739, height 2.2 mm.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2215 (10). **Sceaux-d'Anjou:** NHMW 2016/0103/2087 (2), RGM.734943 (9).

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

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

Stratum typicum – Tortonian, upper Miocene.

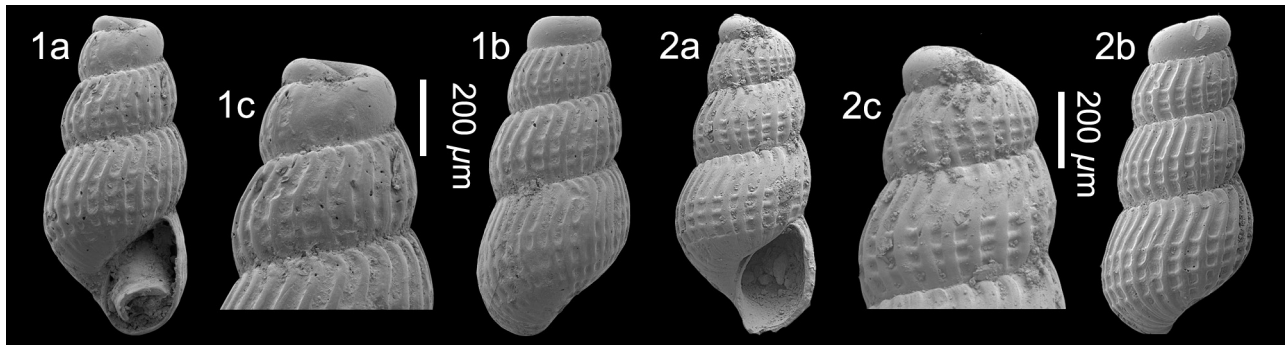


Plate 42. *Parthenina redoniana* nov. sp.; 1. **Holotype** NHMW 2016/0103/2165, height 1.0 mm, width 460 µm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/2086, height 2.4 mm, width 0.6 mm, 2c, detail of protoconch (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type C protoconch, low spire composed of three convex whorls, 22 flexuous axial ribs, three narrow cords on spire whorls, four on last whorl, subobsolete columellar fold.

Description – Shell small, squat cylindrical, short spire. Protoconch type C. Teleoconch of three convex whorls. Suture linear, impressed, at 81° to main shell axis. Sculpture of rounded ribs, 22 on penultimate whorl, strongly flexuous just below suture, slightly narrower than their interspaces, three narrow spiral cords placed on abapical half of spire whorls visible only in interspaces between ribs, with fourth appearing at lower suture on penultimate whorl. Last whorl 56% total height, bearing three or four cords, lower cord delimiting base, axial ribs extend over base, narrow umbilical chink. Aperture ovate, 33% of height; outer lip somewhat flared abapically. Columella fold weak, hardly developed.

Discussion – *Parthenina redoniana* nov. sp. is closely similar in shape, whorl profile and sculpture to the shell from the middle Miocene of Denmark illustrated by Sorgenfrei (1958, fig. 223) as *Chrysallida* cf. *cimbrica* (Kautsky, 1925), but differs in having an extra spiral cord. Both the original figure given by Kautsky (1925, pl. 6, figs 27, 28) and A.W. Janssen (1984, pl. 14, fig. 2) figure far taller shells for that species, and A.W. Janssen illustrated a shell with more numerous spiral cords, similar in number to that seen in the Assemblage I specimen. *Parthenina redoniana* also bears a close resemblance to *Chrysallida* (*Parthenina*) sp. from the North Sea Basin Miocene of the Netherlands and Germany illustrated by A.W. Janssen (1984, pl. 14, fig. 6) and Wienrich (2007, pl. 122, fig. 3) respectively, and might be conspecific, however we hesitate to make a formal conclusion based on line drawings.

Parthenina feldi (Van Aartsen, Gittenberger & Goud, 2000) from the present-day Cape Verde Islands is also similar in shape and sculpture, but that species is even squatter, with one teleoconch whorl less. *Parthenina juliae* (de Folin, 1872) is also similar in sculpture, but differs in being taller, composed of at least four whorls that are not as convex as in *P. redoniana*. In addition, the first teleoconch whorl has more numerous, closer spaced and

less flexuous axial ribs, and the spiral cords occupy a smaller portion of the whorls.

Parthenina redoniana has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Parthenina sceauxensis* nov. sp.**

Plate 43, fig. 1

Type material – Holotype NHMW 2016/0103/2077, height 1.5 mm, width 0.9 mm; paratype 1 NHMW 2016/0103/2078, height 1.1 mm, width 0.7 mm; paratype 2 RGM.1352637, height 2.3 mm; paratype 3 RGM.1352638, height 1.8 mm.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2216 (16), FVD (2). **Sceaux-d'Anjou:** RGM. 718025 (21).

Etymology – Named after the type locality of Sceaux-d'Anjou, Maine-et-Loire, NW France. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type B protoconch, slightly pagodiform profile, angled at one-third whorl height, 16 narrow, widely spaced and strongly prosocline axial ribs crossed by two spiral cords on spire whorls, three on last whorl, spiral grooves in axial interspaces in portion above spiral cords, weak columellar fold.

Description – Shell small, tall conical, angular whorls. Protoconch type B. Teleoconch of five whorls, with slightly pagodiform outline, widely angled at one-third whorl height marking periphery, convex below. Suture linear, deeply impressed, at 79° to main shell axis. Sculpture

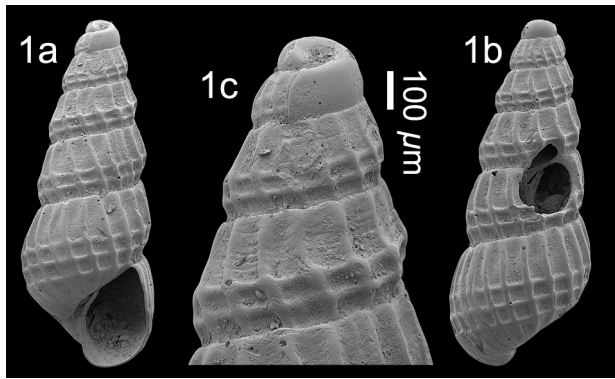


Plate 43. *Parthenina sceauxensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/2077, height 1.5 mm, width 0.9 mm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ture consists of narrow, widely spaced, strongly prosocline axial ribs, 16 on penultimate whorl, separated by interspaces 3-4 times the width of ribs. Spire whorls with two spiral cord, almost equal in strength to ribs, placed on lower third of whorl, upper delimits periphery, slightly swollen at intersections where they cross axial sculpture. Fine spiral grooves seen in interspaces between ribs on adapical portion above spiral cords. Last whorl 49% total height, bearing three spiral cords, lower cord delimiting base, axial ribs extend over the base, narrow umbilical chink. Aperture ovate, 29% total height; outer lip rounded, hardly expanded abapically. Columella bearing small fold at adapical end.

Discussion – With its angular whorls and widely spaced and strongly prosocline axials, *Parthenina sceauxensis* nov. sp. is a distinctive species. The spiral microsculpture is an important diagnostic character, but may be abraded in poorly preserved specimens. It is most similar to *Parthenina subalpina* (Sacco, 1892) (see Ferrero Mortara *et al.*, 1984, pl. 12, fig. 5) from the Pliocene of Italy, which also has a pagodiform profile and the same number of axial ribs and spiral cords, but in that species the ribs are opisthocline as opposed to prosocline in *P. sceauxensis*. Also somewhat similar is *P. fenestratoides* (Sacco, 1892) from the Italian Pliocene (holotype figured in Ferrero Mortara *et al.*, 1984, pl. 12, fig. 1) in whorl profile and in having two strong cords on the abaxial part of the spire whorls, but the Italian species differs in having more numerous axials that are slightly opisthocline and in having two cords also on the last whorl above the base, whereas *P. sceauxensis* has three. *Parthenina traguloides* (Gougerot, 1969) from the middle Miocene Loire Basin of France may be similar (the original photograph is very poor and seems to show an abraded shell; Gougerot, 1969, pl. 29, fig. 6), but according to the description, although the number of axial ribs is similar, they are orthocline and broader than in *P. sceauxensis*, and there is no mention of the spiral microsculpture in the detailed description.

Parthenina sceauxensis has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Parthenina tenuicostata* nov. sp.**

Plate 44, figs 1-3

*1978 *Chrysallida* (*Parthenina*) *delpretei* var. *tenuicostata* Gougerot, p. 20, fig. 12.

Type material – Holotype NHMW 2016/0103/2075, height 2.0 mm, width 800 µm, **Sceaux-d'Anjou**. Paratype 1 NHMW 2016/0103/2280, height 1.9 mm, width 910 µm; paratype 2 NHMW 2016/0103/2281, height 2.6 mm, width 1.0 mm, **St-Clément-de-la-Place**.

Other material – Maximum height 2.6 mm, width 1.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2218 (6), NHMW 2016/0103/2281 (1).

Etymology – Named honouring that given to this species by Gougerot (1978), which, being introduced after 1960 and infrasubspecific, is invalid. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of slender conical profile, type B tending to C protoconch, teleoconch of up to 5.5 convex whorls, sculpture of 20 flexuose ribs on penultimate whorl, crossed by one narrow spiral placed just above suture, two spirals on last whorl, columella with mid-strength fold.

Description – Shell small, slender-conical, with rounded apex. Protoconch type B, tending to C. Teleoconch of up to 5.5 convex whorls. Suture linear, impressed, at 79° to main shell axis. Sculpture of flattened ribs, 20 on penultimate whorl, opisthocline, strongly flexuose just below suture, slightly narrower than their interspaces, crossed by one narrow spiral cord placed just above suture. Last whorl 48% of total height, evenly convex, with two narrow spiral cords; abapical cord at level of insertion outer lip, sharply delimiting smooth convex base, adapical cord just above; small umbilical chink. Aperture ovate, small, 28% of total height, outer lip not flared abapically. Columella bearing mid-strength fold placed at adapical end. Columellar callus slightly thickened forming medial border of umbilical chink; parietal callus not developed.

Discussion – We interpret this as being conspecific with the taxon described by Gougerot (1978) as *Chrysallida* (*Parthenina*) *delpretei* var. *tenuicostata*. *Turbonilla delpretei* Sullioti, 1889 is now considered a junior synonym of *P. indistincta* (Montagu, 1808) (Micali *et al.*, 1993; Peñas & Rolán, 1998, p. 53). The French specimens differ from that species in having more flexuose ribs and a

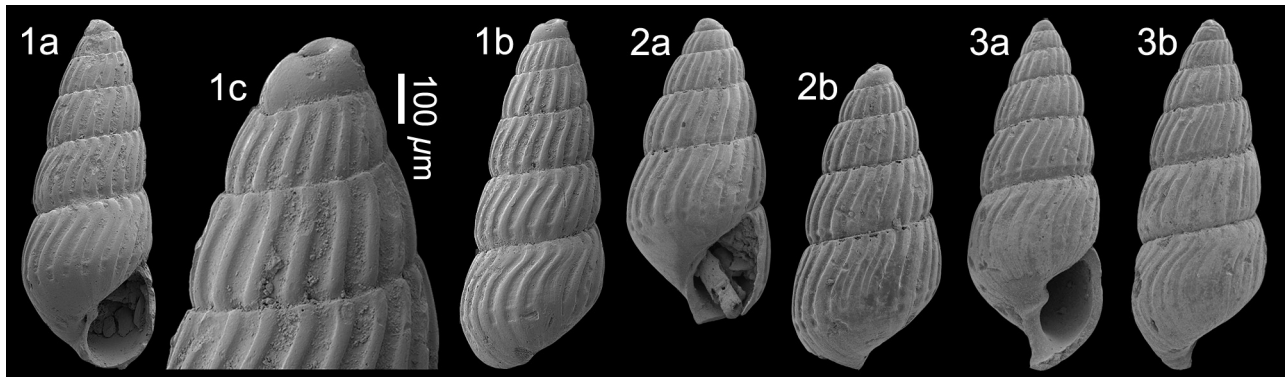


Plate 44. *Parthenina tenuicostata* nov. sp.; 1. **Holotype** NHMW 2016/0103/2075, height 2.0 mm, width 800 µm, 1c, detail of protoconch. La Presselière, Sceaux-d'Anjou. 2. **Paratype 1** NHMW 2016/0103/2280, height 1.9 mm, width 910 µm; 3. **Paratype 2** NHMW 2016/0103/2281, height 2.6 mm, width 1.0 mm (SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

stronger columellar fold, which is absent, or almost so in *P. indistincta*.

The name was erected by Gougerot (1978) as a variety. According to ICZN (1999) Art. 15.2, a new name published after 1960 expressly as the name of a “variety” is deemed to be infrasubspecific and as such is not regulated by the Code (Art.1.1.1), and is excluded from its provisions (Art. 1.3.4 et 45.6.3). Herein we make Gougerot’s name available, as it is not preoccupied, but authorship passes to the authors of this paper.

Parthenina tenuicostata nov. sp. and *P. brebioni* nov. sp. are the two Assemblage I species with flexuous axial ribs, but are easily separated by the greater number of spirals in *P. brebioni*. It is also similar to *P. flexiornata* Gougerot, 1969 from the middle Miocene Loire Basin of France, but that species differs in having two spiral cords placed abapically on the spire whorls that are almost as wide as the axials, and not thin as in *P. tenuicostata*. Moreover the base in *P. flexiornata* bears weaker cords, whereas it is smooth in the Assemblage I species.

Parthenina tenuicostata is also similar in axial sculpture to *P. curvicostata* (Wood, 1848) from the lower Pliocene Coralline Crag of England. We have not seen specimens or figures subsequent to the original description, and it is not figured or discussed by Harmer’s (1914-1924) subsequent revision of the Crag mollusca of England. *Parthenina curvicostata*, or one referred with some doubt to that species, has also been recorded from the Italian Pliocene (Seguenza, 1880; Pavia, 1976; Chirli & Micali, 2008, 2014). Although the character of the reverse S-shaped, strongly flexuous axial ribs is similar in both species, there are fewer ribs in the French species (22 vs about 30 on the last whorl, *vide* Chirli & Micali, 2008, p. 40; 2011, p. 22) and there is extremely fine spiral sculpture along the entire height of the whorl, whereas in *P. tenuicostata* there is only one cord placed a short distance above the suture at the periphery on the spire whorls. Another species to be compared is *P. cimbrica* (Kautsky, 1925) from the Miocene North Sea Basin of Germany and Denmark that also has strongly sinuous axial ribs, however, that species differs in having a shell with fewer whorls (3.5-4

maximum) and the apex is relatively broader and flatter. It also has two or more spiral cords on the abapical half of the spire whorls (see Sorgenfrei, 1958, pl. 66, fig. 223; A.W. Janssen, 1984, pl. 14, fig. 3; Moreno *et al.*, 2003, figs 62-66; Moths *et al.*, 2010, pl. 24, figs 1-2, pl. 46, fig. 3).

In Assemblage I *Parthenina tenuicostata* has been found at St-Clément-de-la-Place and Sceaux-d’Anjou.

Distribution – Middle Miocene: Loire Basin, France (Gougerot, 1978). Upper Miocene (Tortonian): NW France (this paper).

Parthenina cf. *terebellum* (Philippi, 1844)

Plate 45, fig. 1

- cf. *1844 *Rissoa terebellum* Philippi, p. 138, pl. 24, fig. 12.
- cf. 1992 *Chrysallida terebellum* (Philippi, 1844) – Van der Linden & Eikenboom, p. 15, figs 8, 9, 23, 24.
- cf. 2011 *Chrysallida terebellum* (Philippi, 1844) – Chirli & Micali, p. 45, pl. 15, figs 1-5.
- cf. 2014 *Chrysallida terebellum* (Philippi, 1844) – Giannuzzi-Savelli *et al.*, p. 66, figs 179-181, appendix p. 21, 68.

Material and dimensions – Maximum height 1.9 mm, width 0.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2228 (8), FVD (1). **Sceaux-d’Anjou:** NHMW 2016/0103/2084 (1), NHMW 2016/0103/2085 (2). **Renauleau:** NHMW 2016/0103/2130 (4), LC (2).

Discussion – *Parthenina terebellum* (Philippi, 1844) is characterised by its high turritiform shell. The protoconch is of type B (Van der Linden & Eikenboom, 1992, p. 15; Giannuzzi-Savelli *et al.*, 2014, p. 68). The teleoconch consists of 4-5 almost flat-sided to convex whorls, about 20 straight, occasionally broad, flexuous, opisthocline axial ribs that do not extend over the base and one abapical cord on spire whorls, two on the last whorl. *Parthenina terebellum* is today a very variable species. The specimen figured (Pl. 45, fig. 1) has the same shell profile and sculp-

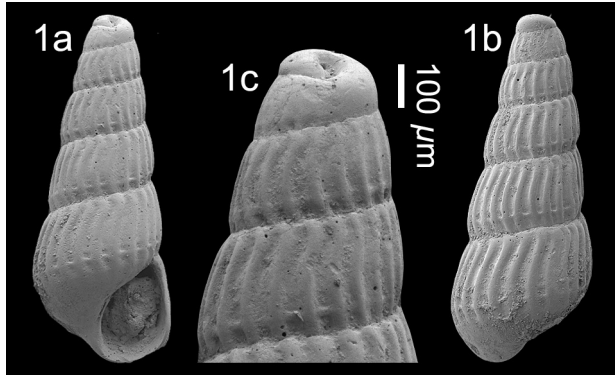


Plate 45. *Parthenina* cf. *terebellum* (Philippi, 1844); 1. NHMW 2016/0103/2084, height 1.9 mm, width 0.7 mm, 1c, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ture, but differs in having a type C protoconch, although there are signs of breakage and repair, which might have distorted the protoconch. *Parthenina terebellum* is similar to the Pliocene to present-day European Atlantic and Mediterranean *P. interstincta* (J. Adams, 1797), from which may be separated by the tall spire, more conical outline, and more pointed protoconch.

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

***Parthenina wesselinghi* nov. sp.**

Plate 46, figs 1, 2

Type material – Holotype NHMW 2016/0103/2088, height 1.9 mm, width 0.7 mm; paratype 1 NHMW 2016/0103/2089, height 1.1 mm, width 950 µm.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2261 (2).

Etymology – We dedicate this species to Frank Wesselingh, senior researcher at the Naturalis Biodiversity

Center in Leiden in recognition of his strong and unwaivering support during the production of this series. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of minute size, type B protoconch, tall spired, five weakly convex whorls with 20 curved orthocone axial ribs, two spiral cord on first two whorls, four on third and penultimate whorls, weak columellar fold.

Description – Shell minute, tall cylindrical, slightly scalate spire, with blunt apex. Protoconch type B. Teleoconch of five weakly convex whorls. Suture linear, impressed, oblique, at 73° to main shell axis. Sculpture consists of narrow, curved orthocone axial ribs, 20 on penultimate whorl, separated by interspaces about twice width of ribs. Two spiral cord on first two whorls, four on third and penultimate whorls, placed on lower half of whorl, that do not overrun and slightly narrower than ribs. Last whorl 50% of total height, regularly convex, bearing four strong spirals and a weaker fifth above level of insertion of outer lip, plus one weaker cords just below, ribs weaken over base, small umbilical chink. Aperture ovate, 28% of total height. Outer lip evenly rounded, not expanded abapically. Columella bearing very weak fold at abapical end.

Discussion – This species is extremely similar to the West African species *Parthenina willeminae* (Van Aartsen, Gittenberger & Goud, 2000), but differs in having less convex whorls and narrower ribs. The cords are also narrower and there is one extra cord than in the holotype of *P. willeminae*. Moreover, the last whorl comprises 60% of the total height vs 50% in *P. wesselinghi* nov. sp. *Parthenina decussata* (Montagu, 1803), which was been likened to *P. willeminae* by Van Aartsen *et al.* (2000), is quite different, with far more rounded whorls and the last whorl comprises about 70-75% of the total height. *Parthenina cylindrata* (Cerulli-Irelli, 1914) from the

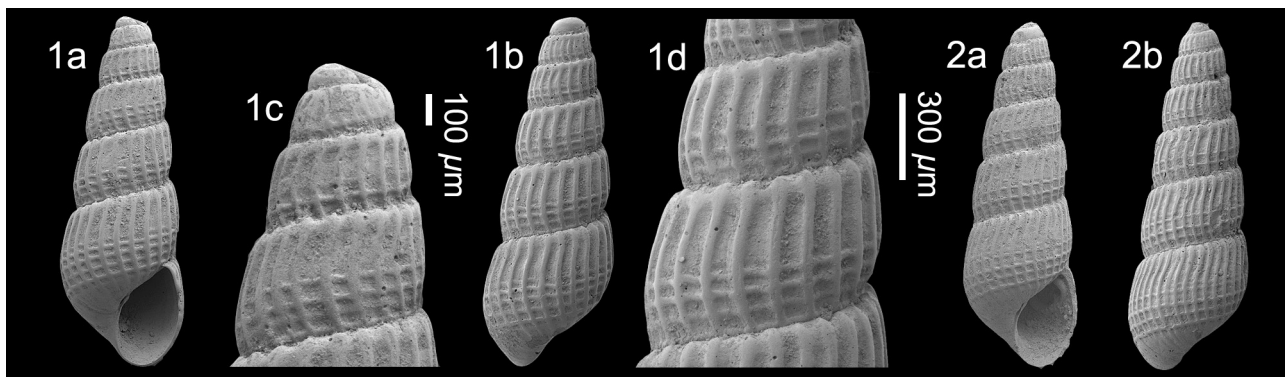


Plate 46. *Parthenina wesselinghi* nov. sp.; 1. **Holotype** NHMW 2016/0103/2088, height 1.9 mm, width 0.7 mm, 1c, detail of protoconch, 1d, detail of teleoconch sculpture; 2. **Paratype 1** NHMW 2016/0103/2089, height 1.1 mm, width 950 µm (all SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Pliocene and lower Pleistocene Mediterranean of Italy has similar sculpture, but is more slender, taller spired, with strongly convex whorls.

Parthenina degrangei (Cossmann & Peyrot, 1917) from the Atlantic lower Miocene of the Aquitaine Basin, France has similar shell profile and type B protoconch, but fewer, more flexuous ribs and fewer cords.

Parthenina wesselinghi has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Parthenina* sp.**

Plate 47, figs 1, 2

Material and dimensions – Maximum height 2.3 mm, width 900 μm . **St-Clément-de-la-Place**: 2016/0103/2238-2239 (2), NHMW 2016/0103/2240 (13).

Description – Shell medium size for genus, with regularly conical spire. Protoconch type C. Teleoconch of up to 4.5 almost straight-sided whorls, separated by impressed suture. Sculpture of low, poorly delimited, orthocline ribs, slightly narrower than their interspaces. Even weaker spiral cords present just above suture on penultimate whorls and periphery of last whorl. Last whorl 52% total height, weakly convex, roundly angled at periphery, base poorly delimited by weak cord, base smooth, small umbilical chink. Aperture about 31% total height, outer lip rounded, weakly flared abapically. Columella narrow, bearing weak fold mid-aperture.

Discussion – *Parthenina* sp. is atypical for the genus in having extremely weak sculpture. The axials are low and poorly defined and the spirals on the abapical half of the whorl so typical of the genus are hardly developed. The type series figured here illustrate the species variability; the sculpture relatively well developed in the holotype (Pl. 47, fig. 1) and almost completely absent in the paratype (Pl. 47, fig. 2). Intermediates exist amongst the unnumbered specimens from St-Clément-de-la-Place, but none

have stronger sculpture than the holotype. We hesitate to formally describe this species as subobsolete sculpture is also seen in populations of species such as *P. interstincta* (J. Adams, 1797), which occurs in Assemblage I and *P. monerosatii* (Clessin, 1900), especially those from brackish environments (PM, personal observation). We therefore leave it in open nomenclature.

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

Genus *Pyrgulina* A. Adams, 1863

Type species (by subsequent designation, P. Fischer, 1885, p. 788) – *Pyrgulina decussata* A. Adams, 1863 (as *O. decussata* “Montagu,” a *lapsus* corrected per ICZN (1999) Art 67.7), present-day, Shandong Prov., China.

1863 *Pyrgulina* A. Adams, p. 1, 4.

1910 *Eupyrulina* Melvill, p. 198. Type species (by subsequent designation, Schander *et al.*, 1999, p. 149): *Pyrgulina dautzenbergi* Melvill, 1910, present-day, India.

1956 *Contraxiala* Laseron, p. 421. Type species (by original designation): *Contraxiala obliqua* Laseron, 1956, present-day, Queensland, Australia.

Note – We follow Peñas & Rolán (2017, p. 131) in including in this genus species with conspicuous axial sculpture and spiral sculpture which occupies the entire height of the whorls, including the base. The spiral sculpture may be formed by grooves, threads or cordlets, and may be present only in the rib interspaces or override them.

***Pyrgulina cancellatissima* nov. sp.**

Plate 48, figs 1-3

Type material – Holotype NHMW 2016/0103/1121, height 2.6 mm, width 1.1 mm; paratype 1 NHMW 2016/0103/1122, height 2.3 mm, width 0.9 mm, paratype 4 RGM.1352731, height 2.6 mm, **St-Clément-de-la-**

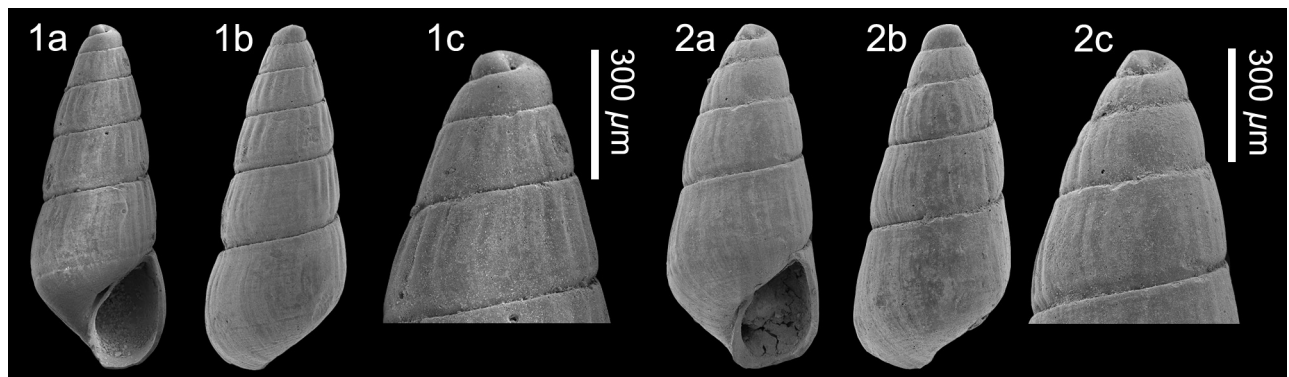


Plate 47. *Parthenina* sp.; 1. NHMW 2016/0103/2238, height 2.3 mm, width 900 μm , 1c, detail of protoconch; 2. NHMW 2016/0103/2239, height 1.8 mm, width 810 μm , 2c, detail of protoconch (all SEM images). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Place. Paratype 2 NHMW 2016/0103/2094 (1), height 2.2 mm, width 0.8 mm; paratype 3 RGM.1352725, height 2.1 mm, **Sceaux-d'Anjou.**

Other material – Maximum height 2.6 mm, width 1.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1121-1122 (2), NHMW 2016/0103/1123 (11), RGM.1352732 (7), RGM.1352735 (50+), FVD (2). **Sceaux-d'Anjou:** NHMW 2016/0103/2094 (1), RGM.718024 (50+). **Renauleau:** NHMW 2016/0103/1352 (4).

Etymology – Latin ‘*cancellatus*, -a, -um’, adjective, meaning reticulated or having a lattice/grid pattern, superlative used to reflect dense character of sculpture. *Parthenina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parthenina* species of small size, type B tending to C protoconch, four teleoconch whorls with finely cancellate sculpture, axials slightly predominant, pitted interspaces, weak columellar fold.

Description – Shell small, ovate-fusiform. Protoconch type B tending to C. Teleoconch of four convex whorls. Suture linear, impressed, at 77-75° to main shell axis. Sculpture finely cancellate with pitted interspaces, consists of orthocone arched axial ribs, 33-35 on penultimate whorl, interspaces roughly equal in width to ribs and slightly narrower spiral cords, 10-12 on last whorl. Last whorl 59-60% of total height; base not delimited, imperforate to very narrow umbilical chink. Aperture pyriform; outer lip weakly rounded, somewhat expanded abapically. Columella bearing weak single fold at adapical end.

Discussion – *Pyrgulina cancellatissima* nov. sp. is characterised by its dense cancellate sculpture, in which the axials are only slightly dominant, reducing the interspaces to small pits. It is most similar to several recently de-

scribed Italian Pliocene species such as *P. enricoi* (Chirli & Micali, 2011) that also has dense cancellate sculpture, but differs in having a more pupoid shell shape, channelled suture, fewer stronger spiral cords (7-8 vs 10-12), and the axials are more strongly predominant. *Parthenina variornata* (Sacco, 1892) from the upper Pliocene of Italy is also similar with dense cancellate sculpture. The original description indicates 5-6 spiral cords, although there seem to be more in the holotype figured by Ferrero Mortara *et al.* (1984, pl. 10, fig. 6). Either way, it differs from *P. cancellatissima* in having the axial sculpture more strongly predominant, whereas in the French species the axials and spirals are almost of equal strength. We have not seen any further specimens of *P. variornata*, although the specimen illustrated as *Chrysallida* sp. 1 by Cavallo & Repetto (1992, fig. 428) might represent that species.

Other similar species are *P. feldi* Van Aartsen, Gittenberger & Goud, 2000 from Cape Verde Islands, which has an even more involute protoconch (type C), has fewer teleoconch whorls and fewer, more sinuous axial ribs and only four spirals. The Mediterranean *P. juliae* (de Folin, 1872) and *P. palazzii* (Micali, 1984), both have fewer and more sinuous ribs and fewer cords. *Parthenina leptoclathrata* Gougerot, 1978 described from the middle Miocene Loire Basin of France is also closely similar. Unfortunately, the hand drawn sketches used in this publication to illustrate the species are not ideal, but the description given is detailed. That species reaches only half the height of *P. cancellatissima* (1.0-1.2 mm vs 2.2-2.5 mm), has fewer teleoconch whorls (maximum three whorls; 17 specimens; Gougerot, 1978, p. 23), has fewer axial ribs (approx. 25 on last whorl vs approx. 35), and some of the spiral cords are wider and equal in strength to the ribs, whereas in *P. cancellatissima* the cords are subequal, and always narrower than the ribs. Lastly, the columellar fold in *P. leptoclathrata* is more strongly developed than in the Assemblage I species. Indeed, *P. cancellatissima* has the densest cancellate sculpture we have seen in the genus. It bears a remarkable resemblance to group of finely sculptured extant South Pacific species including *Pyrgulina epitoniformis* Peñas & Rolán, 2017, *P. grovesi* Peñas & Rolán, 2017, and *P. textilisculpta* Peñas

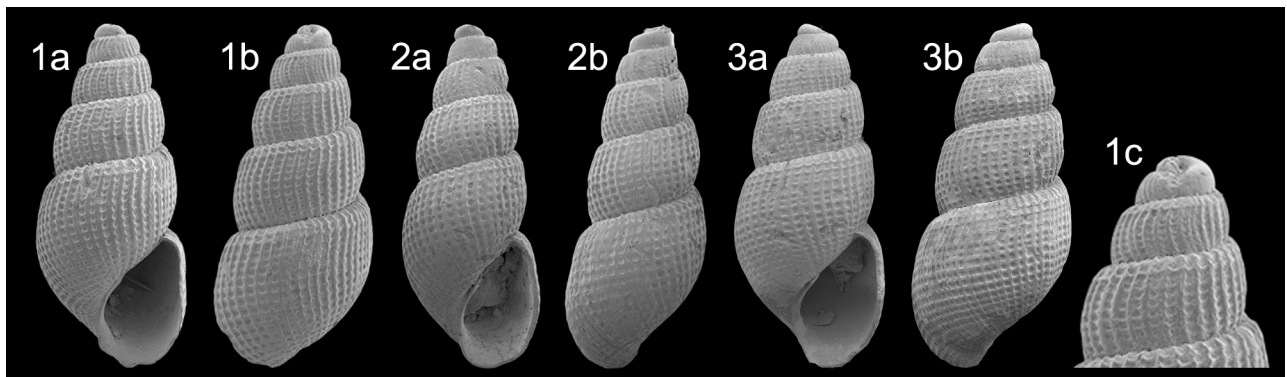


Plate 48. *Pyrgulina cancellatissima* nov. sp.; 1. **Holotype** NHMW 2016/0103/1121, height 2.6 mm, width 1.1 mm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1122, height 2.3 mm, width 0.9 mm. Le Grand Chauvèreau, St-Clément-de-la-Place. 3. **Paratype 2** NHMW 2016/0103/2094, height 2.2 mm, width 0.8 mm (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

& Rolán, 2017. *Pyrgulina cancellatissima* is found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, and is the most abundant *Pyrgulina/Parthenina* species.

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

***Pyrgulina parvula* (Nyst, 1845)**

Plate 49, fig. 1

- 1838 *Acteon pygmaea* Grateloup, p. 282, pl. 6, figs 77-78 (*non* Lea, 1833).
 *1845 *Tornatella parvula* Nyst, p. 429 (*nom. nov. pro Acteon pygmaea* Grateloup, 1838, *non* Lea, 1833).
 1847 *Acteon pygmaea* Grat. – Grateloup, pl. 11, figs 77-78.
 1902 *Parthenia (Pyrgisculus) scalaris* Phil. – Boettger, p. 106 [*non Turbonilla scalaris* Philippi, 1836)].
 1907 *Parthenia (Pyrgisculus) longula* Boettger, p. 122, no. 427.
 1917 *Chrysallida pygmaea* (Grat.) – Cossmann & Peyrot, p. 338, no. 198, pl. 9, figs 61-63.
 1921 *Actaeopyramis (Chrysallida) pygmaea* (Grat.) – Cossmann, p. 266, pl. 6, figs 13-16.
 1992 *Chrysallida interita* Van der Linden & Eikenboom, p. 41, fig. 53 (*nom. nov. pro Acteon pygmaea* Grateloup, 1838, *non* Lea, 1833).
 1934 *Chrysallida (Parthenia) longula* (Boettger) – Zilch, p. 234, pl. 11, fig. 96.
 2001 *Chrysallida interita* van der Linden & Eikenboom, 1992 – Lozouet *et al.*, p. 75.
 2013 *Chrysallida longula* (Boettger, 1907) – Landau *et al.*, p. 313, pl. 52, fig. 9, pl. 75, fig. 7.

Material and dimensions – Maximum height 3.0 mm, width 2.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1002 (1), NHMW 2016/0103/1003 (50+), RGM.1352736 (2), FVD (3). **Sceaux-d'Anjou:** RGM.718023 (27). **Renauleau:** NHMW 2016/0103/2205 (2).

Discussion – *Acteon pygmaea* Grateloup, 1838 from the lower Miocene Atlantic Aquitaine Basin is a junior hom-

onym of *Acteon pygmaeus* Lea, 1833, and was renamed *Chrysallida interita* Van der Linden & Eikenboom, 1992. These authors separated the Miocene populations from the closely similar Pliocene-Recent species *Pyrgulina stefanisi* (Jeffreys, 1869) on the basis of shell morphometrics. The Assemblage I specimens fall within the range of *P. interita* for measurements taken by Van der Linden & Eikenboom (1992, fig. 1) (LW = 53-58%, L/B = 2.4-2.5, B/b 1.7-1.8), but are even more slender. Apart from these morphometrics, the Assemblage I specimen clearly exhibits the flatter whorls, more scalate spire and more elevated ribs typical of the Miocene species. Landau *et al.* (2013, p. 313) considered the French Miocene species conspecific with *Pyrgulina (Pyrgisculus) longula* Boettger, 1907 from the middle Miocene Paratethys of Romania, and consider the older name to take priority. Both Linden & Eikenboom (1992) and Landau *et al.* (2013) missed the earlier replacement name *Tornatella parvula* Nyst, 1845, introduced for *Acteon pygmaea* Grateloup, 1838, *non* Lea, 1833, which has priority.

In Assemblage I *Pyrgulina parvula* is found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Lower Miocene: Atlantic (Aquitainian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1917; Lozouet *et al.*, 2001; Van der Linden & Eikenboom, 1992). Middle Miocene: Atlantic, Azores (Ferreira, 1955); Paratethys (Langhian-Serravallian), Romania (Boettger, 1902, 1907; Zilch, 1934); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene (Tortonian): NW France (this paper).

***Pyrgulina cf. peraffinis* Boettger, 1902**

Plate 49, fig. 2

- cf. *1902 *Pyrgulina peraffinis* Boettger, p. 105, no. 334.
 cf. 1934 *Chrysallida (Pyrgulina) peraffinis* (Boettger) – Zilch, p. 234, pl. 11, fig. 97.

Material and dimensions – Maximum height 3.7 mm, width 2.6 mm. **St-Clément-de-la-Place:** NHMW

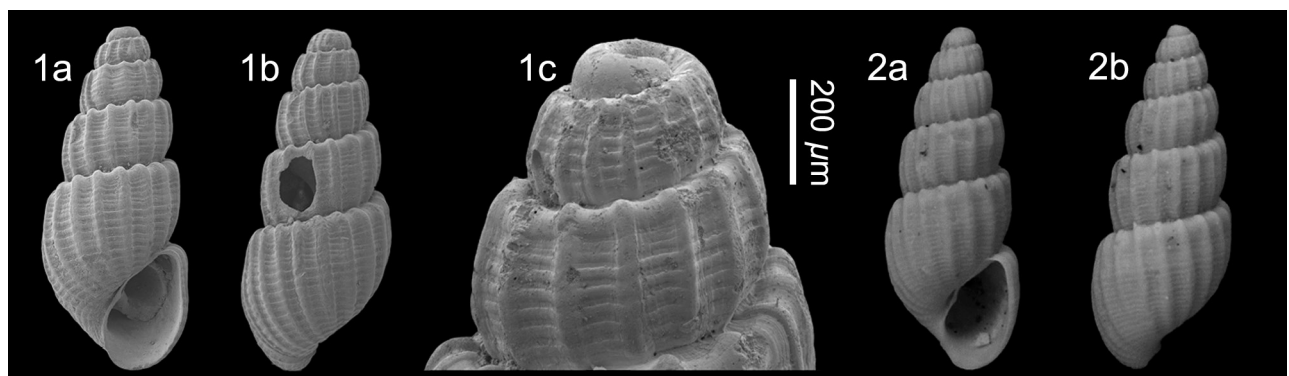


Plate 49. 1. *Pyrgulina parvula* (Nyst, 1845); NHMW 2016/0103/1002, height 3.0 mm, width 2.5 mm, 1c, detail of protoconch (SEM image). 2. *Pyrgulina cf. peraffinis* Boettger, 1902; NHMW 2016/0103/1004, height 3.1 mm, width 2.5 mm (digital image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

2016/0103/1004 (1), NHMW 2016/0103/2160 (1). **Sceaux-d'Anjou**: NHMW 2016/0103/2107 (1).

Discussion – The specimen figured (Pl. 49, fig. 2) is similar to *Pyrgulina parvula* (Nyst, 1845) (= *P. longula* Boettger, 1907; see above), but differs in having a more pointed apex, a more slender outline with narrower and proportionally higher aperture, finer spiral sculpture and a narrower subsutural shelf. We provisionally identify it as *Pyrgulina* cf. *peraffinis* Boettger, 1902, figured by Zilch (1934, pl. 11, fig. 97). *Pyrgulina sacyi* Cossmann & Peyrot, 1919 from the Atlantic lower Miocene Aquitanian of L'éognan, France (MNHN.F.J05608; https://science.mnhn.fr/institution/mnhn/collection/f/item/j05608?lang=en_US) has a less scalate profile and broader axial ribs.

Distribution – Middle Miocene: Paratethys, Romania (Boettger, 1902; Zilch, 1934). Upper Miocene: Atlantic (Tortonian): NW France (this paper).

***Pyrgulina presselierensis* nov. sp.**

Plate 50, fig. 1

Type material – Holotype NHMW 2016/0103/2199, 1.5 mm, width 550 μ m.

Other material – Known from holotype only.

Etymology – Named after the type locality of La Presselière, Sceaux-d'Anjou. *Pyrgulina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pyrgulina* species of minute size, type A2 protoconch, four teleoconch whorls, narrowly canalliculate suture, very weak sculpture, axials predominant, 27 low broad ribs, spirals irregular, subobsolete, last whorl evenly convex, base not delimited, weak columellar fold.

Description – Shell minute, ovate-fusiform. Protoconch type A2 helicoid. Teleoconch of just over four convex whorls, with periphery below mid-whorl. Suture linear, very narrowly canalliculate, deeply impressed, oblique, at 72° to main shell axis. Sculpture of very weak, low, broad, slightly prosocline axial ribs, 27 on penultimate whorl, separated by narrow interspaces. Spiral sculpture even weaker, subobsolete, composed of indistinct irregular cords separated by shallow grooves. Last whorl 53% total height, regularly convex, base not delimited, small umbilical chink. Aperture ovate, 30% total height. Outer lip evenly rounded, weakly expanded abapically. Peristome continuous, columella bearing very weak fold mid-aperture.

Discussion – Although represented by a single speci-

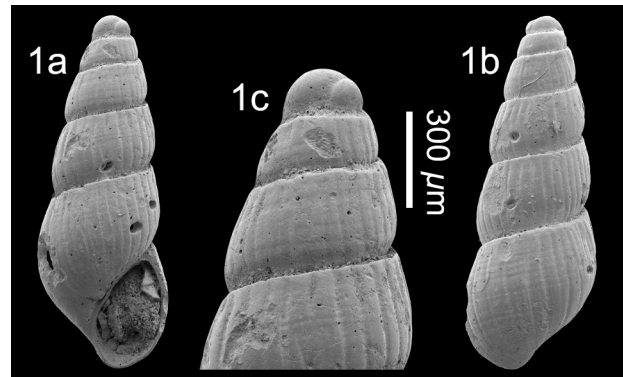


Plate 50. *Pyrgulina presselierensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/2199, height 1.5 mm, width 550 μ m, 1c, detail of teleoconch sculpture (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

men, this species is unusual and warrants description. We have placed it in the genus *Pyrgulina* A. Adams, 1863, as the shell characters match most closely those of the genus given by Peñas & Rolán (2017, p. 131), although the axial sculpture is much weaker than usual for the genus. It is difficult to find any species to compare this new taxon with, as all the European *Pyrgulina* species, i.e. *P. stefanisi* (Jeffreys, 1869) species group [see above under *P. longula* (Boettger, 1907)] have stronger sculpture.

Pyrgulina presselierensis has so far only been found at Sceaux-d'Anjou.

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

Genus *Spiralinella* Chaster, 1898

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

1840 *Spiralina* Hartmann, supposed senior homonym of *Spiralina* Chaster, 1898, but actually a *nomen nudum*, not made available until Martens, 1899. The name *Spiralina* appears only in the foldout table “*Systematische Übersicht der Europäischen Gattungen*”; bound between p. 227 and pl. 1 in SIL/BHL copy <https://www.biodiversitylibrary.org/page/32077880>, and “e-rara.ch” (Swiss electronic library) <http://dx.doi.org/10.3931/e-rara-9759>.

1869 *Partulida* Schaufuss, p. 6. Type species (by subsequent designation, Iredale, 1917): *Turbo spiralis* Montagu, 1803, present-day, British Isles. Unavailable, substitute name for “*Parthenia* Adams” [= misapplication, by H. & A. Adams, 1853 [The genera of Recent Mollusca, 1, p. 233] of *Parthenia* Lowe, 1841, non *Parthenia* Robineau-Desvoidy, 1830] (Corgan, 1973).

1898 *Spiralina* Chaster, p. 20.

- 1901 *Spiralinella* Chaster, p. 8. Unnecessary replacement name.
 1917 *Partidula* Iredale, p. 395. Name made available.

Note - *Spiralinella* Chaster, 1901 species are characterised by species with prominent ribs sharply interrupted at the periphery by strong spiral cords that continue over the base (Giannuzzi-Savelli *et al.*, 2014; p. 71; under *Partidula*, which is unavailable; see above). Based on molecular data, Schander *et al.* (2003, fig. 2) suggested that *Spiralinella* appeared to be monophyletic.

Spiralinella incerta (Milaschewitch, 1916)

Plate 51, fig. 1

- 1869 *Odostomia turbonilloides* Brusina, p. 240 (*non* Deshayes, 1861).
 1892a *Pyrgulina turbonilloides* var. *alpinoligustica* Sacco, p. 67, pl. 1, fig. 110.
 *1916 *Parthenina incerta* Milaschewitsch, 1916, p. 98.
 1921 *Pyrgulina Brusinai* Cossmann, p. 258. *Nom. nov. pro Odostomia turbonilloides* Brusina, 1869 *non* Deshayes, 1861.
 1933 *Pyrgulina coëni* Monterosato ms Coen, p. 52, 164, pl. 4, fig. 37.
 1933 *Pyrgulina brevicula* var. *rejecta* Coen, p. 54, 165, pl. 4, fig. 39.
 1984 *Pyrgulina turbonilloides* var. *alpinoligustica* Sacco, 1892 – Ferrero Mortara *et al.*, p. 79, pl. 10, fig. 8.
 1992 *Chrysallida brusinai* (Cossmann, 1921) – Van der Linden & Eikenboom, p. 11, fig. 20.
 1998 *Chrysallida brusinai* (Cossmann, 1921) – Peñas & Rolán, p. 36, figs 102-103.
 2004 *Chrysallida incerta* (Milaschewitsch, 1916) – Bogi & Chirli, p. 91, fig. 1o.
 2011 *Chrysallida incerta* (Milaschewitsch, 1916) – Chirli & Micali, p. 32, pl. 10, figs 6-10.
 2011 *Chrysallida incerta* (Milaschewitsch, 1916) – Öztürk *et al.*, p. 62, fig 9A-C.
 2014 *Partidula incerta* (Milaschewitsch, 1916) – Giannuzzi-Savelli *et al.*, p. 72, figs 203-211, appendix p. 23, 71.

- non* 2018 *Chrysallida incerta* (Milaschewitsch, 1916) – Brunetti & Cresti, p. 104, fig. 447.

Material and dimensions – Maximum height 2.7 mm, width 1.2 mm. **Sceaux-d’Anjou**: NHMW 2016/0103/2071 (1), NHMW 2016/0103/2072 (3), RGM.718020 (7), RGM.719003 (29), RGM.737054 (50+). **Renauleau**: NHMW 2016/0103/2112 (4).

Discussion – *Spiralinella incerta* (Milaschewitsch, 1916) is characterised by its conical shell with blunt apex, type C protoconch, up to five almost straight sided teleoconch whorls separated by a canalculated suture, with 20-25 orthocone to slightly prosocline strong rounded ribs ending abruptly at a robust cord placed just above the suture. On the last whorl a further robust cords develops at the level of the insertion of the outer lip, separated from the adapically placed robust cord by a deep narrow interspace, and two further cords weakening over the base.

The species from the upper Pliocene of Italy illustrated by Brunetti & Cresti (2018, fig. 447) as *Chrysallida incerta* has spiral sculpture above the strong abapical cord and probably does not represent this species.

The species illustrated by Gougerot (1978, fig. 5) as *Parthenina peyroti* variété *pseudoturbonilloides* (spelling in plate caption *pseudoturbonilloides*; 1978, p. 20) from the middle Miocene Loire Basin of France differs in not having cords on the base. We note that the varietal names of *Parthenina peyroti* Gougerot, 1978 introduced by that author in the same paper are not valid, as ICZN (1999) Art. 15.2 states: “A new name published after 1960 expressly as the name of a “variety” is deemed to be *infrasubspecific* and as such is not regulated by the Code (Art.1.1.1) and is excluded from its provisions (Art. 1.3.4 et 45.6.3)”.

In Assemblage I this species has been found at Sceaux-d’Anjou and Renauleau.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Sacco, 1892a; Ferrero Mortara *et al.*, 1984; Crovato & Micali, 1993; Bogi & Chirli, 2004; Chirli & Micali, 2011). Upper Pliocene: central Mediterranean, Italy (Crovato & Micali, 1993; Ragaini & Bernieri, 2007).

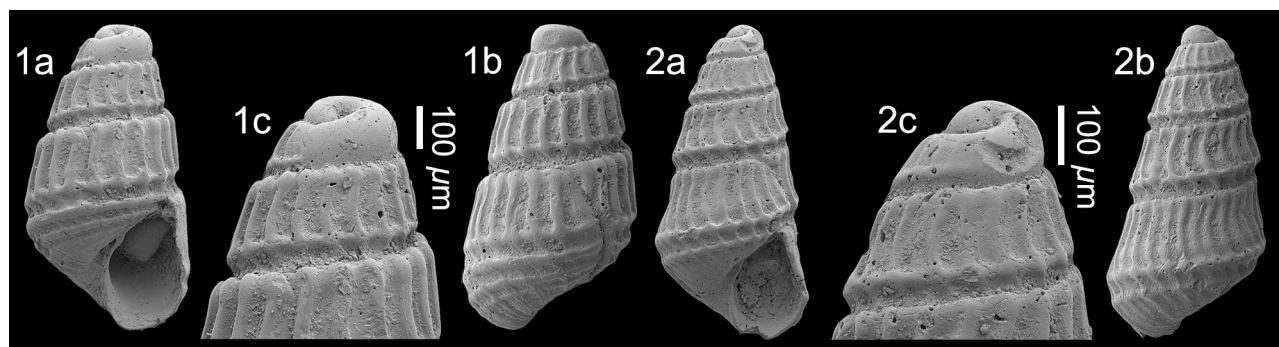


Plate 51. *Spiralinella* species: 1. *Spiralinella incerta* (Milaschewitsch, 1916); NHMW 2016/0103/2071, height 1.2 mm, width 615 µm, 1c, detail of protoconch; 2. *Spiralinella pagoda* nov. sp.: **holotype** NHMW 2016/0103/2070, height 1.5 mm, width 670 µm, 2c, detail of protoconch (SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Lower Pleistocene: central Mediterranean, Italy (Crovato & Micali, 1993). Upper Pleistocene: central Mediterranean, Italy (Crovato & Micali, 1993). Present-day: Atlantic, south Portugal to Angola (Peñas & Rolán, 1998), Mediterranean (Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean (Öztürk *et al.*, 2011).

***Spiralinella pagoda* nov. sp.**

Plate 51, fig. 2

Type material – Holotype NHMW 2016/0103/2070, height 1.5 mm, width 670 µm.

Other material – Known only from holotype.

Etymology – Name reflecting the ‘pagodiform’ shape of the spire whorls. *Spiralinella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Spiralinella* species of small size, protoconch type B tending to C, teleoconch with 3.75 concave whorls, curved axial ribs, 20 on penultimate, 25 on last whorl, one strong cord just above suture on spire whorls, second weaker cord at level of insertion outer lip on last whorl, no cords on base.

Description – Shell small, conical. Protoconch type B tending to C. Teleoconch of 3.75 weakly concave whorls separated by a canaliculated suture, at 80° to main shell axis. Sculpture of orthocone to slightly prosocline curved rounded ribs, extending between sutures and one robust spiral cord placed just above suture. Small rounded tubercles placed on cord at intersection with ribs. Last whorl 58% of total height, concave in profile, with 25 axial ribs, one further slightly weaker cord develops at level of insertion of outer lip, ribs weaken over base, small umbilical chink. Aperture pyriform, 32% of total height. Outer lip straight adapically, rounded abapically, not greatly expanded. Columella bearing weak fold at adapical end.

Discussion – *Spiralinella pagoda* nov. sp. is closely similar to *S. andersoni* (Spaink, 1968) from the North Sea Basin of the Netherlands and Germany, but that species differs in having a deep suture that is not as canaliculated as in *S. pagoda* and in having a single cord delimiting the base, whereas the French species has two. It is also similar to *Spiralinella incerta* (Milaschewitch, 1916), with which it co-occurs in Assemblage I (see above), but differs in having concave instead of straight sided whorls, in having narrower ribs and lacking further cords over the base. The protoconch in *S. incerta* is of type C, whereas that of *S. pagoda* is type B tending to C.

Spiralinella pagoda has so far only been found at Sceaux-d’Anjou.

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

Genus *Tragula* Monterosato, 1884

Type species (by original designation) – *Odostomia fenestrata* Jeffreys, 1848, present-day, British Isles.

1884 *Tragula* Monterosato, p. 86.

For generic synonymy see Ceulemans *et al.* (2018, p. 129).

***Tragula fenestrata* (Jeffreys, 1848)**

Plate 52, fig. 1

*1848 *Odostomia fenestrata* Jeffreys, p. 345.

1972b *Turbonilla (Tragula) fenestrata* (Forbes, 1848) – Nordsieck, p. 132, pl. PVI, fig. 17.

1998 *Chrysallida fenestrata* (Jeffreys, 1848) – Wilke & Van Aartsen, p. 9, pl. 2, fig. 17a, b.

2011 *Chrysallida fenestrata* (Jeffreys, 1848) – Chirli & Linse, p. 195, pl. 73, fig. 1.

2011 *Chrysallida fenestrata* (Jeffreys, 1848) – Öztürk *et al.*, p. 60, fig 7A-E.

2018 *Tragula fenestrata* (Jeffreys, 1848) – Ceulemans *et al.*, p. 133, pl. 8, fig 7 (*cum syn.*).

Material and dimensions – Height 1.9 mm, width 0.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2115 (1). **Sceaux-d’Anjou:** NHMW 2016/0103/1698 (1), NHMW 2016/0103/2091 (1), RGM.718028 (5).

Discussion – *Tragula fenestrata* (Jeffreys, 1848) is characterised by its very elongate slender shell, its intorted protoconch of type A1 tending to B. The shell has 5-7 teleoconch whorls, in which the upper two-thirds of the whorl are straight-sided and the lower third is convex, the lower part bearing two spiral cords on spire whorls

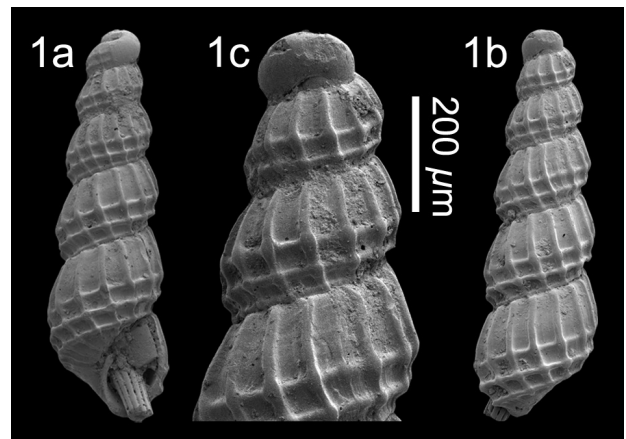


Plate 52. *Tragula fenestrata* (Jeffreys, 1848); 1. NHMW 2016/0103/1698, height 1.9 mm, width 0.5 mm (SEM image). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

and three on the last whorl. Peñas & Rolán (1998, p. 15) reported some variability; the West African shells having a larger protoconch, a more cylindrical teleoconch composed of more convex whorls, a less angular base and weak spiral sculpture on the adapical part of the whorls. The specimen from Assemblage III has slightly more convex whorls and finer axial ribs than usual for the species, but even within the Mediterranean there is some variability in these characters. The specimen figured here (Pl. 52, fig. 1) is similar in shape and sculpture to that illustrated by Giannuzzi-Savelli *et al.* (2014, fig. 229) from Turkey.

Italian Pliocene specimens illustrated by Chirli & Micali (2011, pl. 8, figs 11-15) are very tall and slender with a strongly oblique suture and more angular whorls than the Assemblage I specimen illustrated above, and similar to the extant Mediterranean specimen illustrated by Giannuzzi-Savelli *et al.* (2014, fig. 228). Therefore, some variability was also present in the Pliocene Mediterranean.

A further species occurs in the Italian Pliocene; *T. interstinctoides* Sacco, 1892 (holotype figured by Ferrero Mortara *et al.*, 1984, pl. 12, fig. 2). The holotype is not well preserved, but differs from *T. fenestrata* in being more slender, the outline of the early teleococonch whorls is more cylindrical, whorl profile less convex. In any case, the two species are very similar and *T. interstinctoides* could be a Pliocene offshoot. Anyway considering that the French specimens differ from *T. fenestrata*, as well as *T. interstinctoides*, and variability in *T. fenestrata s.l.* is quite large, we prefer to use the former name.

In Assemblage I *Tragula fenestrata* has been found at St-Clément-e-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (this paper). Lower Pliocene: Atlantic, NW France (Ceulemans *et al.*, 2018); central Mediterranean, Italy (Chirli & Micali, 2011); western Mediterranean, Tunisia (Fekih, 1969). Upper Pliocene: central Mediterranean, Italy (Sacco, 1896; Cavallo & Repetto, 1992; Sosso & Dell'Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914; Brunetti, 2011); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Present-day: Atlantic southwest of England and western Ireland (Nordsieck, 1972b; Graham, 1988), southwards to Angola (Peñas & Rolán, 1998), western Mediterranean (Peñas *et al.*, 1996), central Mediterranean (Nordsieck, 1972b; Giannuzzi-Savelli *et al.*, 2014; Peñas & Rolán, 1998), eastern Mediterranean (Öztürk *et al.*, 2011), Black Sea (Nordsieck, 1972b; Wilke & Van Aartsen, 1998).

Subfamily Turbonillinae Bronn, 1849

Tribe Syrnolini Saurin, 1958

Genus *Nisosyrnola* Landau, Harzhauser, İslamoğlu & Silva, C.M., 2013

Type species (by original designation) – *Niso concava*

Boettger, 1907, middle Miocene, Paratethys.

2013 *Nisosyrnola* Landau, Harzhauser, İslamoğlu & Silva, C.M., p. 307.

Nisosyrnola concava (Boettger, 1907)

Plate 53, fig. 1

*1907 *Niso concava* Boettger, p. 107, no. 377.

1934 *Niso concava* Boettger – Zilch, p. 233, pl. 11, fig. 94.

2003 *Eulimella* sp. 1 – Moreno *et al.*, p. 154, fig. 74.

2013 *Nisosyrnola concava* (Boettger, 1907) – Landau *et al.*, p. 307, text-fig. 28, pl. 52, figs 7, 8, pl. 74, fig. 11.

Material and dimensions – Height 3.0 mm, width 1.4 mm. **Sceaux-d'Anjou**: RGM.734950 (1).

Discussion – Although missing its protoconch, the shell from Assemblage I is closely similar to the holotype of *Nisosyrnola concava* (Boettger, 1907) figured by Landau *et al.* (2013, text-fig. 28). The base is possibly slightly flatter, but this is probably within the intraspecific variability. The *Niso*-like umbilicus that characterises the genus is clearly visible in the French specimen illustrated. The specimen illustrated by Moreno *et al.* (2003, fig. 74) as *Eulimella* sp. 1 from the middle Miocene of Barcelona, Spain also represents this species. These geographically scattered records suggest that it was probably widespread in the European Miocene, although rarely reported. For further discussion see Landau *et al.* (2013, p. 307).

In Assemblage I *Nisosyrnola concava* is extremely uncommon and has only been found at Sceaux-d'Anjou.

Distribution – Middle Miocene: Paratethys (Langhian-Serravallian): Romania (Boettger, 1907; Zilch, 1934); Proto-Mediterranean Sea (Serravallian): Barcelona, Spain (Moreno *et al.*, 2003), Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (this paper).

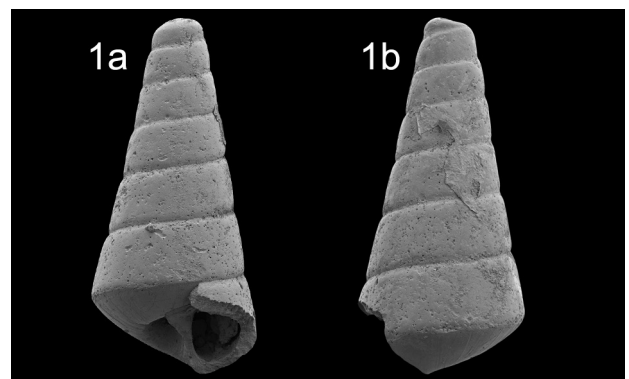


Plate 53. *Nisosyrnola concava* (Boettger, 1907); 1. RGM.734950, height 3.0 mm, width 1.4 mm (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Syrnola* A. Adams, 1860

Type species (by monotypy) – *Syrnola gracillima* A. Adams, 1860, present-day, Korea Strait.

- 1860b *Syrnola* A. Adams, p. 405.
- 1903 *Heida* Dall, p. 1600. Type species (by subsequent designation, Dall & Bartsch, 1904, p. 13) *Odontostomia (Syrnola) caloosaensis* Dall, 1892, Pliocene, North Carolina, USA.
- 1907 *Pachysyrnola* Cossmann, p. 213. Type species (by original designation): *Syrnola houdasi* Cossmann, 1907, Eocene, France.

Note – Species included in this genus have tall, slender shells, smooth, except for microscopic growth lines and an aperture with a conspicuous columellar fold (Peñas & Rolán, 2016, p. 218).

***Syrnola turoiensis* (Glibert, 1949)**

Plate 54, figs 1, 2

- *1949a *Odostomia (Syrnola) subumbilicata turoiensis* Glibert, p. 186, pl. 12, fig. 9.

Material and dimensions – Maximum height 11.0 mm, width 2.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1293-1294 (2), NHMW 2016/0103/2200 (10), FVD (4).

Discussion – Cossmann & Peyrot (1917) discussed *Syrnola subumbilicata* (Grateloup, 1838), from the lower Miocene Aquitanian and Burdigalian of the Aquitaine Basin, and noted differences in the French Atlantic middle Miocene populations. The middle Miocene Aquitanian form they named mut. *bearnensis* and subsequently Glibert (1949a) named the Loire Basin form as subspecies *turoiensis*. We prefer to give these forms full species

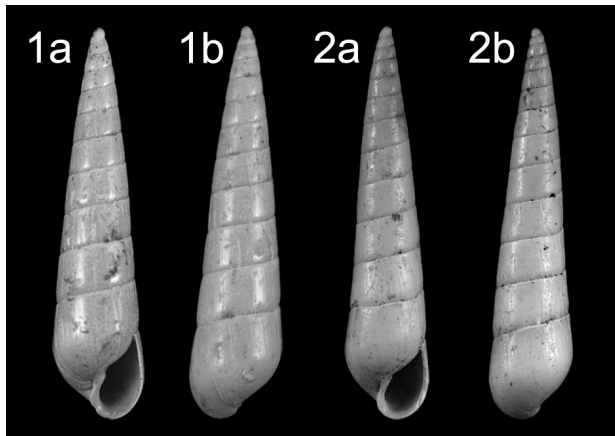


Plate 54. *Syrnola turoiensis* (Glibert, 1949); 1. NHMW 2016/0103/1293, height 9.4 mm, width 2.2 mm; 2. NHMW 2016/0103/1294, height 11.0 mm, width 2.3 mm (digital images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

rank. *Syrnola turoiensis* (Glibert, 1949) differs from *S. subumbilicata* in being less slender, in having lower spire whorls, a more angulated base, and in having a weaker columellar fold. *Syrnola bearnensis* (Cossmann & Peyrot, 1917) differs in having a wider apical angle, a weakly angular base and again a stronger columellar fold. In Assemblage I *Syrnola turoiensis* has only been found at St-Clément-de-la-Place.

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

Tribe Turbonillini Bronn, 1849
Genus *Careliopsis* Mörch, 1875

Type species (by monotypy) – *Monoptygma styliformis* Mörch, 1875, present-day, Caribbean.

- 1875 *Careliopsis* Mörch, p. 169.

***Careliopsis gallica* nov. sp.**

Plate 55, figs 1, 2

Type material – Holotype NHMW 2016/0103/2257, height 1.5 mm, width 550 µm; paratype 1 NHMW 2016/0103/2258, height 1.5 mm, width 580 µm.

Other material – Maximum height 1.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2258 (5).

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

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

Stratum typicum – Tortonian, upper Miocene.

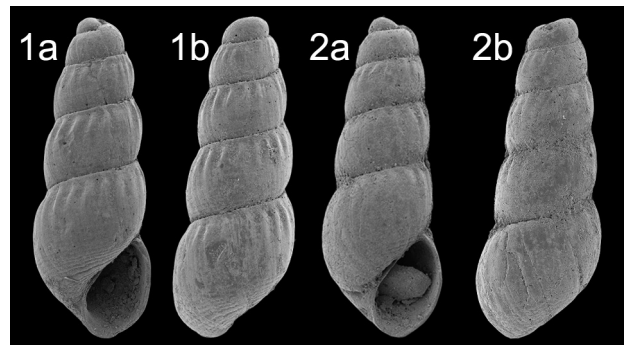


Plate 55. *Careliopsis gallica* nov. sp.; 1. **Holotype** NHMW 2016/0103/2257, height 1.5 mm, width 550 µm; 2. **Paratype 1** NHMW 2016/0103/2258, height 1.5 mm, width 580 µm (SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Careliopsis* species of small size, type B tending to C protoconch, four convex teleoconch whorls bearing low poorly delimited ribs on adapical half, fine weak spiral cords most clearly developed over base, small columellar chink, no columellar fold.

Description – Shell, small, pupoid. Protoconch type B tending to C. Teleoconch of four regularly convex whorls, separated by impressed linear suture. Sculpture of poorly delimited opisthocline axial ribs present on adapical half of whorls; ribs develop just below suture, weakening rapidly, obsolete by mid-whorl. Faint spiral sculpture most clearly developed over base. Last whorl 53% total height, evenly convex, base not delimited, very narrow umbilical chink. Aperture small, 30% total height, outer lip rounded, weakly flared abapically. Columella narrow, without fold.

Discussion – *Careliopsis gallica* nov. sp. is an unusual species that is most like *C. utdigitulus* Peñas & Rolán, 2017 from the Marquesas Archipelago in teleoconch sculpture, but that species has a type A protoconch. The extant Mediterranean *C. modesta* (de Folin, 1870) has less inflated whorls, stronger spiral sculpture that covers the entire whorl surface, weaker and narrower axial ribs, and differs in having a type A1 tending to B protoconch. The Caribbean type species *C. styliformis* (Mörch, 1875) is taller-shelled with stronger spiral cords separated by punctate interspaces, and again has an A1 tending to B protoconch. *Careliopsis gallica* has so far only been found at St-Clément-de-la-Place.

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

Genus *Chemnitzia* d’Orbigny, 1840

Type species (type species by monotypy) – *Melania campanellae* Philippi, 1836, present-day, Mediterranean.

1840 *Chemnitzia* d’Orbigny, p. 77.

Note – Species in this group are characterised by hav-

ing prominent axial ribs, which fuse or terminate at the suture, deeply-sunken interspaces starting at the adapical suture and terminating at or just above the abapical suture, no spiral sculpture beyond microscopic spiral striations, a smooth base and a straight columella (Dall & Bartsch, 1909; Landau & LaFollette, 2015). WoRMS does not accept this position, and synonymises *Chemnitzia* d’Orbigny, 1840 with *Turbonilla* Risso, 1826 (MolluscaBase, 2020). Based on molecular data, the results given by Schander *et al.* (2003, fig. 2) suggested that *Turbonilla lactea* (Linnaeus, 1758) and *T. subulina* Monterosato, 1889 were monophyletic. Both of these species would be included in *Chemnitzia*, as understood herein. Therefore, it is likely that *Chemnitzia* represents a true monophyletic group.

***Chemnitzia costellata* (Grateloup, 1828)**

Plate 56, fig. 1

- *1828 *Auricula costellata* Grateloup, p. 107.
- 1838 *Auricula costellata* Grat. – Grateloup, pl. 6, figs 69-70.
- 1847 *Auricula costellata* Grat.– Grateloup, pl. 11, figs 69-70.
- non 1856 *Turbonilla costellata* Grat. – Hörnes, p. 498, pl. 43, fig. 27 [= *Chemnitzia pseudocostellata* (Sacco, 1892)]
- 1917 *Turbonilla costellata* (Grateloup) – Cossmann & Peyrot (*partim*), p. 349, pl. 9, figs 79-81 (*non* 68-70).

Material and dimensions – Height 5.6 mm, width 1.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2253 (1).

Discussion – *Chemnitzia costellata* (Grateloup, 1828) is a poorly known species. The specimen illustrated on the MNHN (Paris) website (MNHN-F-J05646), also illustrated by Cossmann & Peyrot (1917, pl. 9, figs 79-81), from Moulin de Lagus, Aquitaine Basin, France compares well with the specimen illustrated here from Assemblage I. It has 16 robust opisthocline ribs on the penultimate whorl (15-18 *vide* Cossmann & Peyrot, 1917, p. 349), the interspaces equal or slightly narrower than

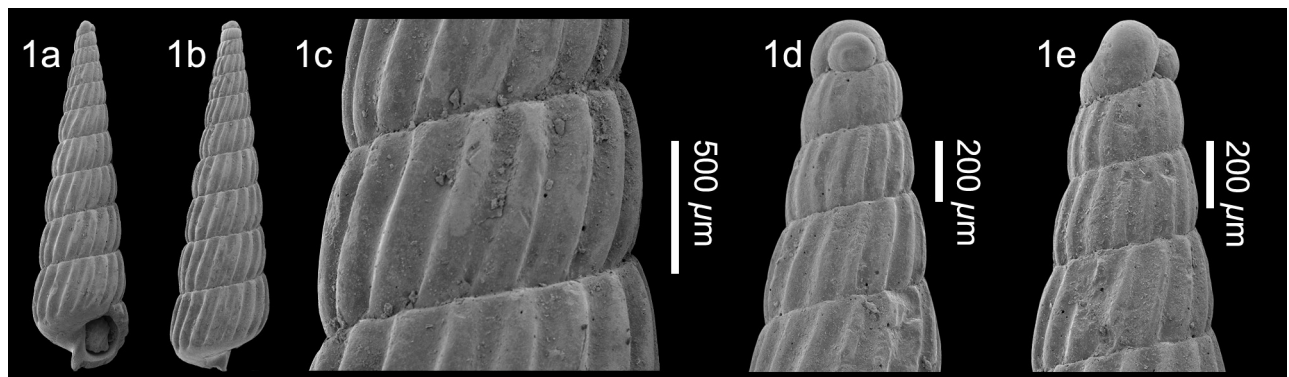


Plate 56. *Chemnitzia costellata* (Grateloup, 1828); 1. NHMW 2016/0103/2253, height 5.6 mm, width 1.6 mm, 1c, detail of teleoconch sculpture penultimate whorl, 1d-e, detail of protoconch (SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the ribs, and the ribs stop abruptly at the basal disc. The only appreciable difference is the apical angle in the Assemblage I specimen seems slightly wider than that illustrated on the MNHN website. The protoconch in the specimen illustrated (Pl. 56, figs 1d-e) is of type A2 with 2.25 whorls exposed. Unfortunately, the protoconch of the early Miocene specimens is not known.

In Assemblage I *Chemnitzia costellata* has only been found at St-Clément-de-la-Place.

Distribution – Lower Miocene: Atlantic (Burdigalian), France (Cossmann & Peyrot, 1917). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

Chemnitzia lactea (Linnaeus, 1758)

Plate 57, fig. 1

- *1758 *Turbo lacteus* Linnaeus, p. 765.
- 2011 *Turbonilla lactea* (Linné, 1758) – Chirli & Micali, p. 84, pl. 30, figs 7-18 (*cum syn.*).
- 2011 *Turbonilla lactea* (Linné, 1758) – Chirli & Linse, p. 207, pl. 82, fig. 1.
- 2013 *Turbonilla lactea* (Linnaeus, 1758) – Öztürk & Bitlis Bakir, p. 431, fig. 18.
- 2018 *Chemnitzia lactea* (Linnaeus, 1758) – Ceulemans *et al.*, p. 134, pl. 8, figs 9-11 (*cum syn.*).

Material and dimensions – Maximum height 6.0 mm, width 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1107-1108 (2), RGM.1347964 (1), RGM.1348340 (1 + 2 fragments), RGM.1352706 (10 fragments), RGM.1352708 (3 fragments). **Sceaux-d'Anjou:** RGM.1348608 (1 fragment), RGM.1352716 (1), RGM.718048 (15). **Renauleau:** LC (5).

Discussion – *Chemnitzia lactea* (Linnaeus, 1758) is characterised by its tall, slender shell, opisthocline axial ribs, equal in width to broader than their interspaces, not extending onto the base on the last whorl but ending abruptly at the base, absence of umbilicus or columellar fold, and by its type B protoconch. Peñas & Rolán (1997, p. 25) noted that the protoconch size differed amongst extant populations. The specimens from Assemblage I are very small, and the protoconch is not well preserved, but we consider them to represent this species. Other Miocene records for this species need to be confirmed.

In Assemblage I *Chemnitzia lactea* has been found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene: NW France (this paper). Lower Pliocene: Atlantic, northwestern France (Brébion, 1964; Ceulemans *et al.*, 2018), Guadalquivir Basin, Spain (Ruiz Muñoz *et al.*, 1997; Landau *et al.*, 2011); western Mediterranean, Tunisia (Fekih, 1969); central Mediterranean, Italy (Sacco, 1892a; Guioli *et al.*, 2009; Chirli & Micali, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (this paper); central Mediterranean, Italy (Sacco, 1892a; Greco, 1970; Malatesta, 1974; Cavallo & Repetto, 1992). Upper Pliocene-

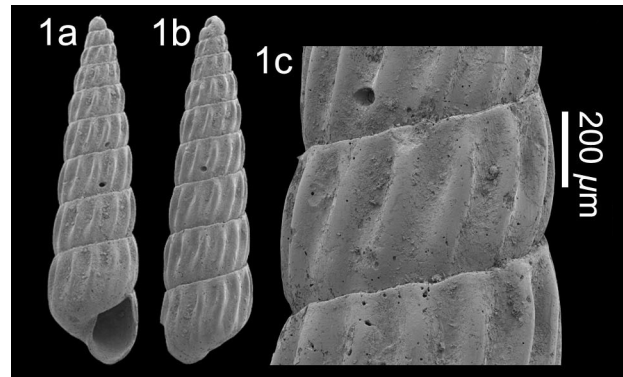


Plate 57. *Chemnitzia lactea* (Linnaeus, 1758); 1. NHMW 2016/0103/1107, height 3.4 mm, width 940µm, 1c, detail of teleoconch sculpture penultimate whorl (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Pleistocene: Atlantic, NW France (Brébion, 1964). Lower Pleistocene: Atlantic, St. Erth, England (Harmer, 1920); central Mediterranean, Italy (Cerulli-Irelli, 1914; Brunetti, 2011); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: English Channel, England (Harmer, 1920). Present-day: Eastern Atlantic frontage from North Norway to British Isles, North Sea (Raven, 2020), into Mediterranean (Graham, 1988), eastern Mediterranean (Öztürk & Bitlis Bakir, 2013), Canaries, Cabo Verde and São Tomé (Rolán, 2005; Peñas *et al.*, 2009).

Chemnitzia miogallica nov. sp.

Plate 58, figs 1, 2

Type material – Holotype NHMW 2016/0103/1112, height 6.0 mm, width 1.2 mm; paratype 1 NHMW 2016/0103/1113, height 5.1 mm, width 1.1 mm; paratype 2 NHMW 2016/0103/1109, height 6.0 mm, width 1.2 mm; paratype 3 NHMW 2016/0103/1110, height 5.0 mm, width 1.0 mm.

Other material – Maximum height 6.0 mm, width 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1441 (23), FVD (11). **Renauleau:** NHMW 2016/0103/2207 (4).

Etymology – Compound name; named after the Roman province of Gaul, Latin: ‘*Gallia*’, a region of Western Europe encompassing present-day France, and the prefix reflecting the Miocene epoch in which it lived. *Chemnitzia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Chemnitzia* species of small size, very slender, type A2 strongly protruding helicoid protoconch,

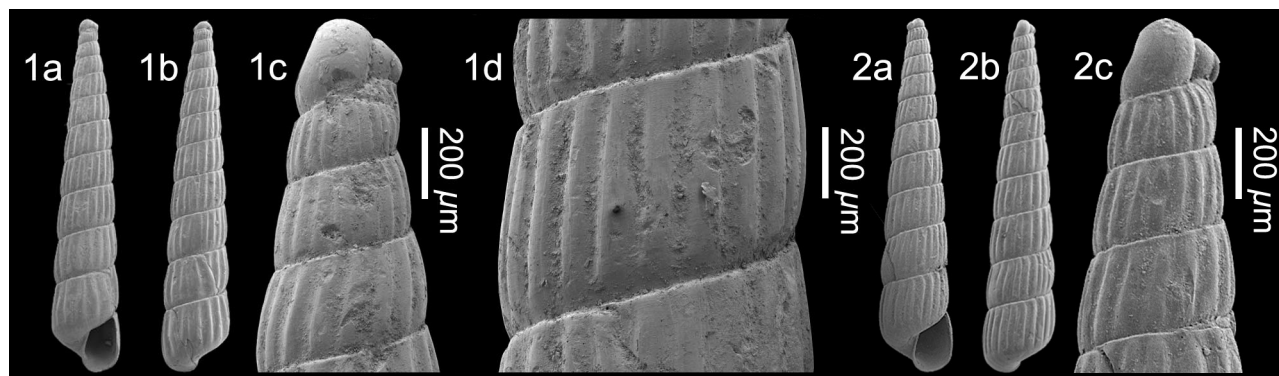


Plate 58. *Chemnitzia miogallica* nov. sp.; 1. **Holotype** NHMW 2016/0103/1112, height 6.0 mm, width 1.2 mm, 1c, detail of protoconch, 1d, detail of teleoconch sculpture penultimate whorl; 2. **Paratype 1** NHMW 2016/0103/1113, height 5.1 mm, width 1.1 mm, 2c, detail of protoconch (SEM images). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ten teleoconch whorls bearing 16-20 low rounded ribs that end relatively abruptly at periphery last whorl, basal disc not sharply developed, no umbilicus or columellar fold.

Description – Shell small for genus, tall, very slender. Protoconch strongly protruding helicoid type A2. Teleoconch of up to ten weakly convex whorls, slightly swollen just above suture, separated by moderately deeply impressed, oblique linear suture. Sculpture of 16-20 low, rounded, orthocone to weakly opisthocline ribs that extend between sutures, equal in width to their interspaces. Last whorl 28% of totally height, acutely rounded at periphery, ribs end relatively abruptly at base, basal disc not strongly developed; base depressed, imperforate. Aperture subquadrate, columella straight, leaning abaxially, no columellar fold.

Discussion – *Chemnitzia miogallica* nov. sp. differs in being the most slender *Chemnitzia* species, and in having all the teleoconch characters typical for the genus poorly developed: *i.e.* weak suture, low ribs, poorly delimited basal disc. *Chemnitzia lactea* (Linnaeus, 1758) differs in having a more strongly intorted protoconch (compare Pl. 58, fig 1c, 2c vs Chirli & Micali, 2011, pl. 30 figs 10, 16), in having the whorls separated by a deeper suture, in having the ribs much stronger, more elevated, more markedly opisthocline, and in having the basal disc more sharply delimited. *Chemnitzia plioperstricta* (Chirli & Micali, 2011) has much stronger ribs separated by deep interspaces, a deeper suture and an A2 protoconch with a much larger nucleus. *Chemnitzia hamata* (Nordsieck, 1972) differs in having stronger ribs, a deeper suture, a rounded base and the protoconch has one whorls less (Peñas *et al.*, 1996, figs. 189-192).

Chemnitzia miogallica has been found at St-Clément-de-la-Place and Renauleau.

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

Chemnitzia cf. pseudoterebralis (Sacco, 1892)

Plate 59, fig. 1

cf.*1892a *Turbonilla (Pyrgolampros) pseudoterebralis* Sacco, p. 88, pl. 2, fig. 94.

cf. 1984 *Turbonilla (Pyrgolampros) pseudoterebralis* Sacco, 1892 – Ferrero Mortara *et al.*, p. 83, pl. 13, fig. 4.

cf. 1998 *Turbonilla pseudoterebralis* Sacco, 1892 – Bogi & Cauli, p. 131, fig. 11.

cf. 2011 *Turbonilla pseudoterebralis* Sacco, 1892 – Chirli & Micali, p. 95, pl. 34, figs 13-18.

Material and dimensions – Height 6.0 mm, width 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0997 (1).

Discussion – This specimen is very similar to that identified as *Turbonilla (Pyrgolampros) pseudoterebralis* Sacco, 1892 by Chirli & Micali (2011, pl. 34, figs 13-18) from the lower Pliocene of Tuscany, differing for the opisthocline instead of orthocone ribs. The protoconch is the same, type A1 tending to A2. The specimen figured

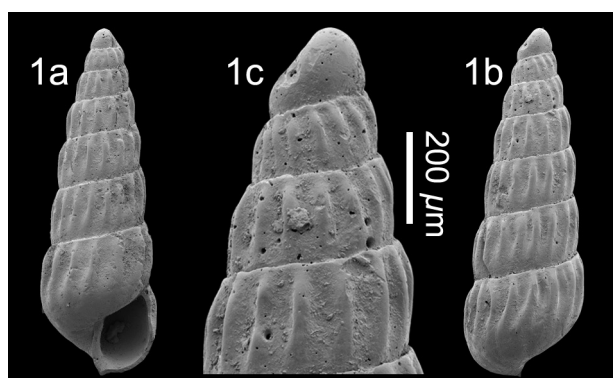


Plate 59. *Chemnitzia cf. pseudoterebralis* (Sacco, 1892); 1. NHMW 2016/0103/0997, height 6.0 mm, width 1.2 mm, 1c, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

by Glibert (1952b, pl. 4, fig. 15) from the upper Miocene North Sea Basin of Belgium clearly differs from our specimen in having stronger axial ribs that are orthocone, the shell profile is conical and the protoconch, based on the illustration, seems to be type A2. We believe that Glibert's figured shell is not conspecific with *Chemnitzia pseudoterebralis* described from the upper Miocene of Sant'Agata, Italy (syntype figured by Ferrero Mortara *et al.*, 1984, pl. 13, fig. 4), which has a narrower apical angle, straighter and slightly broader ribs that continue between sutures. Protoconch morphology was not described by Sacco, and is missing in the figured syntype.

The specimen figured by Sorgenfrei (1958, pl. 72, fig. 245) as *Turbonilla pseudoterebralis* is subadult, but differs from Glibert's specimen and the French specimen in having a slightly less tilted protoconch and the first two teleoconch whorls are devoid of axial sculpture. *Turbonilla (Pyrgolampros) pseudoterebralis* in Wienrich (2007, pl. 167, fig. 1 only) from the North Sea Basin lower-middle Miocene of Germany seems conspecific with Glibert's interpretation of the species. None of these three records correspond to *Turbonilla (Pyrgolampros) pseudoterebralis* Sacco, 1892 from Italy.

This species differs from *Chemnitzia lactea* (Linnaeus, 1758) in being more cylindrical, in having fewer whorls, narrower and more numerous ribs, the whorls slightly constricted mid-whorl, and a narrow subsutural ramp that produce a characteristic whorl profile.

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

***Chemnitzia robusticostata* nov. sp.**

Plate 60, fig. 1

Type material – Holotype NHMW 2016/0103/2276, height 5.4 mm, width 1.5 mm; paratype 1 NHMW 2016/0103/2277, height 5.8 mm, width 1.6 mm; paratype 2 NHMW 2016/0103/2278, height 4.8 mm, width 1.4 mm.

Other material – Maximum height 5.8 mm, width 1.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2279 (2).

Etymology – Compound name; Latin 'robustus, -a', adjective, meaning hard or solid, and 'costatus, -a, -um', adjective, meaning ribbed, reflecting the very prominent solid ribs seen in this species. *Chemnitzia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Chemnitzia* species of small size, very slender, type A2 tending to B, strongly protruding helicoid protoconch, ten teleoconch whorls bearing 16-20 low rounded ribs that end relatively abruptly at periphery last whorl, basal disc not sharply developed, no umbilicus or columellar fold.

Description – Shell small for genus, tall, slender, slightly scalate spire. Protoconch strongly protruding helicoid type A2 tending to B. Teleoconch of up to nine whorls, initially convex, later whorls almost straight sided, separated by deeply impressed, strongly undulating suture. Sculpture of 14-15 robust, elevated rounded, opisthocline ribs that extend between sutures, slightly coronate at adapical suture, equal in width to slightly narrower than their interspaces. Last whorl 33% of totally height, weakly angled at base, ribs end abruptly at strongly developed basal disc; base depressed, imperforate. Aperture subquadrate, columella straight, no columellar fold.

Discussion – *Chemnitzia robusticostata* nov. sp. is characterised by its strong opisthocline axial ribs that extend slightly above the suture, giving the whorls a slightly coronate appearance. In Assemblage I it is most similar to *Chemnitzia costellata* (Grateloup, 1828) (see above), but that species differs in having more convex whorls and although it also has strong axial sculpture, the ribs are not as elevated nor as strongly delimited as in *C. robusticostata*. Numerous European Neogene to present-day congeners have similar characters and need to be compared. *Chemnitzia acutissima* (Monterosato, 1884) from Pliocene to the present-day Mediterranean also has strong ribs that

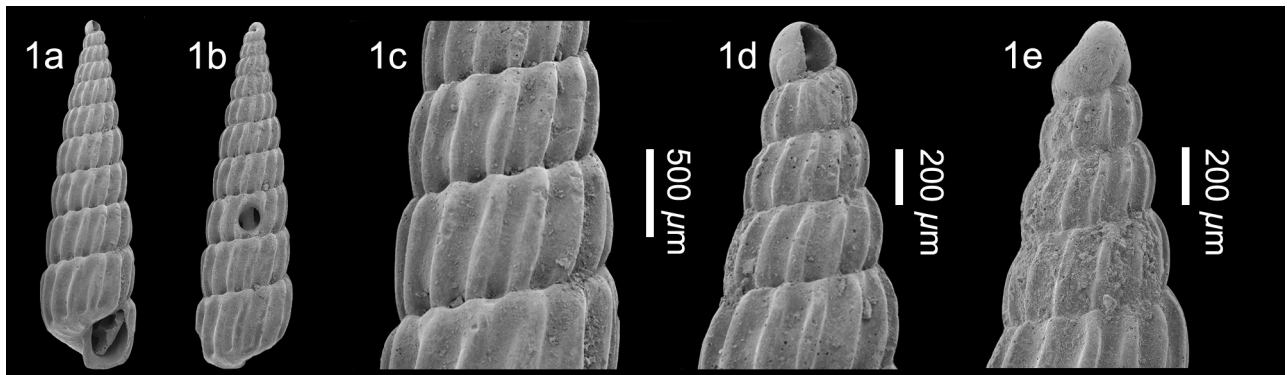


Plate 60. *Chemnitzia robusticostata* nov. sp.; 1. **Holotype** NHMW 2016/0103/2276, height 5.4 mm, width 1.5 mm, 1c, detail of teleoconch sculpture penultimate whorl, 1d-e, detail of protoconch (SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

coarsely crenulate the suture, but differs in having a clearly A2 protoconch, more numerous axial ribs (18-20; *vide* Chirli & Micali, 2011, p. 71), the spire is less scalate, and the basal disc is weaker. *Chemnitzia beidaensis* (Peñas & Rolán, 2000) originally described from present-day West Africa, but also recorded in the Pliocene of the central Mediterranean (Chirli & Micali, 2011), is similar in having a well-developed basal disc, but has weaker, more numerous axial ribs. *Chemnitzia intuspersulcata* (Sacco, 1892) from the Pliocene of the Mediterranean also has strong ribs and basal disc, but has a relatively broad, regularly conical profile, the whorls separated by a shallower suture, and the ribs are more numerous (18-20; *vide* Chirli & Micali, 2011, p. 82), and do not crenulate the suture. The widespread *C. lactea* (Linnaeus, 1758) (see above for distribution) does not have a scalate spire and has far more numerous ribs (20-25; *vide* Chirli & Micali, 2011, p. 86) that do not crenulate the suture. *Chemnitzia pliomagna* (Sacco, 1892) from the Pliocene Mediterranean has a similar number of ribs and a strong basal disc, but differs in having a conical spire, not scalate, the suture is very superficial for the genus, and the ribs are slightly flexuous. *Chemnitzia robusticostata* has so far only been found at St-Clément-de-la-Place.

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

Genus *Mormula* A. Adams, 1863

Type species (by subsequent designation, Verrill & Bush, 1900, p. 530) – *Mormula rissoina* A. Adams, 1863 [*Mormula philippiana* (Dunker, 1860)], present-day, Japan.

1863 *Mormula* A. Adams, p. 1, 2.

Note – The genus *Mormula* A. Adams, 1863 includes species with a rather solid shell, axial ribs and deeply incised spiral grooves, and irregular broad varices on the later teleoconch whorls. Dall & Bartsch (1909) included lirations of the outer lip in their characterisation of the

subgenus *Mormula* A. Adams, 1863. However, Higo *et al.* (2001, p. 135) published a figure of the type of *Mormula rissoina* [*Mormula philippiana* (Dunker, 1860)], which shows a thickened lip without obvious lirations within, and a small apparently intorted protoconch. Adams' (1863) descriptions of *Mormula* and *M. rissoina* do not mention lirations. The presence of lirations or nodes within the outer lip of turbonillids is an inconsistent character (Landau & LaFollette, 2015, p. 28). We separate this genus from *Pyrgostylus* Monterosato, 1884, in which the axial ribs stop abruptly at a well-developed basal disc and the base bears only spiral sculpture.

Mormula catherinae (Glibert, 1949)

Plate 61, figs 1-3

*1949a *Turbonilla (Mormula) catherinae* Glibert, p. 194, pl. 12, fig. 10.

1964 *Turbonilla (Mormula) catherinae* Glibert, 1949 – Brébion, p. 299, pl. 7, fig. 19.

2018 *Mormula* cf. *catherinae* (Glibert, 1949) – Bongiardino & Micali, p. 105, fig. 11.

Material and dimensions – Maximum height 11.3 mm, width 2.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1076-1077 (2), NHMW 2016/0103/1078 (24), RGM.1348052 (1), RGM.1348336 (2 + 5 fragments), RGM.1348842 (1), RGM.1352701 (6), FVD (8), LC (12). **Sceaux-d'Anjou:** NHMW 2016/0103/1079 (17), NHMW 2016/0103/2181 (1), RGM.1348062 (6), RGM.1348583 (1), RGM.1348926 (1 + 2 fragments), RGM.1352712 (1), RGM.718047 (50+), FVD (3). **Renauleau:** NHMW 2016/0103/1359 (1), LC (2). **Beugnon:** RGM.1352286 (1), RGM.1352683 (3 fragments).

Discussion – *Mormula catherinae* (Glibert, 1949) is immediately distinguished from all other turbonillids in Assemblage I by its relatively large size and very solid shell. The protoconch is of type A1. The axial ribs are low, about 19-20 on the last whorl, separated by intervals narrower than the ribs cut by close-set regular spiral grooves. On

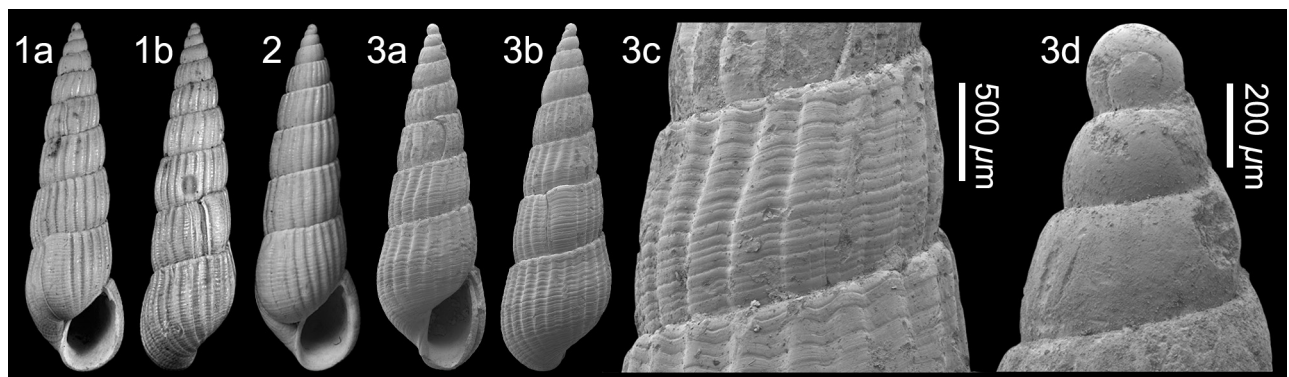


Plate 61. *Mormula catherinae* (Glibert, 1949); 1. NHMW 2016/0103/1076, height 10.2 mm, width 2.8 mm; 2. NHMW 2016/0103/1077, height 9.6 mm, width 2.8 mm. Le Grand Chauvèreau, St-Clément-de-la-Place. 3. NHMW 2016/0103/2181, height 9.4 mm, width 2.7 mm, 3c, detail of teleoconch sculpture penultimate whorl, 3d, detail of protoconch (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the last whorl the ribs weaken rapidly over the base, but not abruptly as in the genus *Chemnitzia* d'Orbigny, 1840. There are no internal labial denticles (see generic note above). The columella is short and straight and no fold is developed. The columellar and parietal calluses are continuous, forming a narrow callus rim. Bongiardino & Micali (2018, fig. 11) illustrated an incomplete shell from the upper Pliocene of Italy and assigned it to this species with some doubt due to the great geographic and stratigraphic gap between the Atlantic and Mediterranean specimens. However, this record of *M. catherinae* from the Atlantic upper Miocene of France and well preserved specimens occur in the upper Pliocene western Mediterranean of the Estepona Basin, Spain (Landau & Micali, in prep.), partially close the stratigraphic gap and increase the geographic distribution of the species.

Brébion (1964, p. 300) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Renauleau and St-Michel, to which we add St-Clément-de-la-Place and Beugnon.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949a). Upper Miocene: Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Bongiardino & Micali, 2018).

Genus *Pyrgisculus* Monterosato, 1884

Type species (by monotypy) – *Melania scalaris* Philippi, 1836, present-day, Mediterranean.

1884 *Pyrgisculus* Monterosato, p. 88.

Note – Species in this group are characterised by having a scalate spire composed of strongly convex whorls, usually shouldered, the shoulder placed high, just below the suture, with strong lamellose axial ribs and fine spiral cords in the interspaces, subquadrate aperture, and lack of columellar fold (Monterosato, 1884, p. 88). Thiele (1929, p. 237) synonymised *Pyrgisculus* Monterosato,

1884 with *Dunkeria* Carpenter, 1857 (type species by subsequent designation, Bucquoy *et al.*, 1898, *Chemnitzia paucilirata* Carpenter, 1857, present-day, Pacific Mexico). Until molecular phylogeny proves the monophylogeny of European genus *Pyrgisculus* with eastern Pacific *Dunkeria*, we prefer to consider them separate.

***Pyrgisculus jeffreysii* (Jeffreys, 1848)**

Plate 62, fig. 1

- 1836 *Melania scalaris* Philippi, p. 157 (*non* Spix, 1827, in Wagner, *nec* Sowerby, 1829).
- *1848 *Odostomia scalaris* var. *Jeffreysii* Jeffreys, p. 346.
- 1884 *Pyrgisculus scalaris* – Monterosato, p. 82.
- 1892a *Pyrgulina* (*Pyrgisculus*) *scalaris* (Phil.) – Sacco, p. 71.
- 1892a *Pyrgulina* (*Pyrgisculus*) *scalaris* var. *basidepressa* Sacco, p. 71, pl. 1, fig. 117.
- 1892a *Pyrgulina* (*Pyrgisculus*) *scalaris* var. *pliopercossata* Sacco, p. 71, pl. 1, fig. 118.
- 1892a *Pyrgulina* (*Pyrgisculus*) *scalaris* var. *subfasciolata* Sacco, p. 71, pl. 1, fig. 119.
- 1914 *Turbonilla* (*Pyrgisculus*) *scalaris* Phil. – Cerulli-Irelli, p. 450, pl. 55, figs 64-67.
- 1920 *Pyrgulina scalaris* (Philippi) – Harmer, p. 577, pl. 49, fig. 43.
- 1988 *Turbonilla jeffreysi* [*sic*] Forbes & Hanley, 1850 [*sic*] – Graham, p. 632, fig. 275.
- 1992 *Turbonilla jeffreysii* (Jeffreys, 1848) – Cavallo & Repetto, p. 162, fig. 460.
- 1994 *Turbonilla scalaris* (Ph.) – Tabanelli & Segurini, p. 13, pl. 2, fig. 12.
- 1996 *Turbonilla jeffreysii* (Jeffreys, 1848) – Peñas *et al.*, p. 64, fig. 154.
- 1997 *Turbonilla jeffreysii* (Jeffreys, 1848) – Peñas & Rolán, p. 53, figs 131-132.
- 2011 *Turbonilla jeffreysi* [*sic*] (Jeffreys, 1848) – Chirli & Micali, p. 82, pl. 30, figs 1-6 (*cum syn.*).
- 2011 *Turbonilla jeffreysi* [*sic*] (Jeffreys, 1848) – Chirli & Linse, p. 207, pl. 81, fig. 3.
- 2013 *Turbonilla jeffreysii* (Jeffreys, 1848) – Öztürk & Bitlis Bakir, p. 430, fig 17A-C.

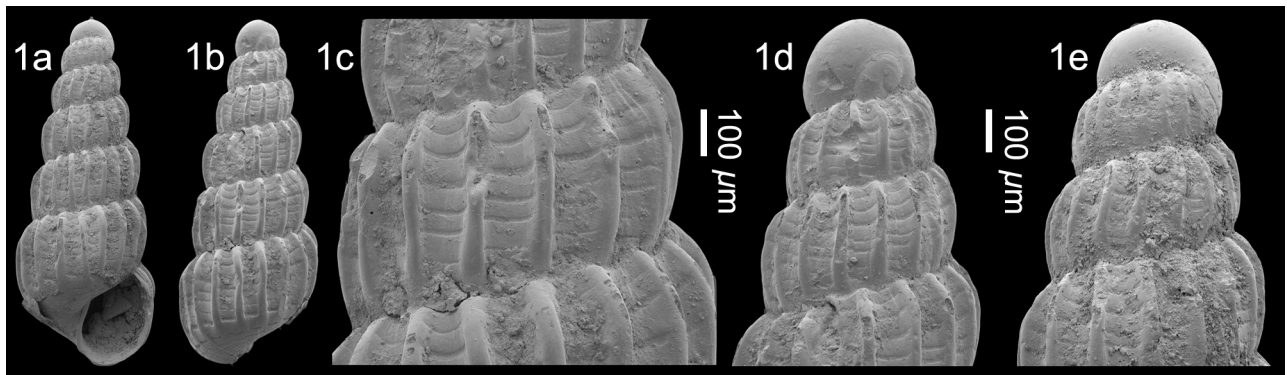


Plate 62. *Pyrgisculus jeffreysii* (Jeffreys, 1848); 1. NHMW 2016/0103/2101, height 2.5 mm, width 1.0 mm, 1c, detail or teleoconch sculpture penultimate whorl, 1d-e detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- 2014 *Pyrgiscus jeffreysii* (Forbes & Hanley, 1850-1851) – Høisæter, p. 67, figs 6-11.
 2014 *Dunkeria jeffreysii* (Forbes & Hanley, 1850) – Giannuzzi-Savelli *et al.*, p. 84, fig. 273, appendix p. 32, 80.

Material and dimensions – Height 2.5 mm, width 1.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/2231 (24), FVD (2). **Sceaux-d'Anjou:** NHMW 2016/0103/2101 (1), NHMW 2016/0103/2102 (2).

Discussion – *Pyrgisculus jeffreysii* (Jeffreys, 1848) is characterised by its turritiform, scalate profile, type A1 protoconch, teleoconch of 6-7 shouldered whorls, separated by a deep undulating suture. Sculpture consists of 16-18 raised, sharp, narrow orthocone ribs separated by broad interspaces and 8-10 spirals cords visible only in the interspaces. The cords are highly irregular in width and disposition, separated by narrow-relatively wide spiral grooves. The aperture is small, ovate, with a straight columella bearing the suggestion of a weak fold adapically.

As commented by Høisæter (2014, p. 68), the history of the name is complex. It has often been attributed to Forbes & Hanley (1850, p. 251), although the name was introduced earlier by Jeffreys (1848, p. 346). There are no further congeners in the European Neogene to extant faunas.

In Assemblage I *Pyrgisculus jeffreysii* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli & Micali, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a; Cavallo & Repetto, 1992; Tabanelli & Segurini, 1994). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: English Channel, England (Harmer, 1920). Present-day: Atlantic southern British Isles (Graham, 1988) to Canary Islands and Angola (Peñas & Rolán, 1997), into Mediterranean (Peñas *et al.*, 1996), eastern Mediterranean (Öztürk & Bitlis Bakir, 2013), more northern Atlantic records need to be verified (Høisæter, 2014).

Genus *Pyrgiscus* Philippi, 1841

Type species (by subsequent designation Dall & Bartsch in Arnold, 1903, p. 274) – *Melania rufa* Philippi, 1836, present-day, Mediterranean.

- 1841 *Pyrgiscus* Philippi, p. 50.
 1841 *Ortostelis* Aradas & Maggiore, p. 27. Type species (by subsequent designation, Dall & Bartsch, 1909, p. 74): *Melania rufa* Philippi, 1836, present-day, Mediterranean. Junior objective synonym of *Pyrgiscus* Philippi, 1841. Simultaneously published,

Pyrgiscus given precedence by First Reviser's choice by Dall & Bartsch (1907, p. 504).

- 1884 *Pyrgostelis* Monterosato, p. 89. Type species (by subsequent designation, Crosse, 1885, p. 141): *Melania rufa* Philippi, 1836, present-day, Mediterranean. Junior objective synonym of *Pyrgiscus* Philippi, 1841 and *Ortostelis* Aradas & Maggiore, 1841.

Note – Species in this group are characterised by having shells with sculpture composed of axial ribs and strongly incised spiral grooves. These species do not have varices or internal liration on the outer lip (Dall & Bartsch, 1909). Based on molecular data, Schander *et al.* (2003, fig. 2) suggested that *Pyrgiscus* appeared to be monophyletic.

Pyrgiscus rufus (Philippi, 1836)

Plate 63, figs 1, 2

- *1836 *Melania rufa* Philippi, p. 156, pl. 9, fig. 7.
 2011 *Turbonilla rufa* (Philippi, 1836) – Chirli & Micali, p. 98, pl. 35, figs 13-18, pl. 36, 1-18 (*cum syn.*).
 2011 *Turbonilla rufa* (Philippi, 1836) – Chirli & Linse, p. 208, pl. 82, fig. 3.
 2013 *Turbonilla rufa* (Philippi, 1836) – Öztürk & Bitlis Bakir, p. 432, fig 24A-D.
 2018 *Pyrgiscus rufus* (Philippi, 1836) – Ceulemans *et al.*, p. 136, pl. 8, figs 12-14 (*cum syn.*).
 2018 *Pyrgiscus rufus* (Philippi, 1836) – Brunetti & Cresti, p. 114, fig. 504.

Material and dimensions – Maximum height 6.1 mm, width 1.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1105 (1), NHMW 2016/0103/1106 (44), RGM.1348341 (2), RGM.1352704 (10), FVD (6), LC (1). **Sceaux-d'Anjou:** NHMW 2016/0103/2139 (1), RGM.718052 (50+). **Renauleau:** LC (1).

Discussion – Two similar species occur in the European extant fauna; *Pyrgiscus rufus* (Philippi, 1836) and *P. crenatus* (Brown, 1827), which have sometimes been synonymised (e.g. Van Aartsen, 1981, p. 75). Peñas & Rolán (2011, p. 396) argued for the separation of the two taxa: *P. rufus* with a smaller protoconch (255- 260 µm) and a narrow shell, and *P. crenatus* with a larger protoconch (300-310 µm) and a broader shell. *Pyrgiscus crenatus* has a distribution that extends further north, up to British Islands. However, those authors caution that they do not exclude the possibility that *P. rufus* and *P. crenatus* could be morphotypes of a single species. Peñas & Rolán (1997) describe various species similar to *P. rufus* extant along the West African coast, such as *P. rafaëli* (Peñas & Rolán, 1997).

The protoconch of the specimen illustrated (diameter 340 µm; Pl. 63, fig. 1c) is even larger than the range given for *P. crenatus*, as well as for *P. rafaëli*. As discussed by Ceulemans *et al.* (2018, p. 137), it is possible that such a distinction did not exist in the Miocene and Pliocene, as many of the Italian Pliocene shells illustrated by Chirli

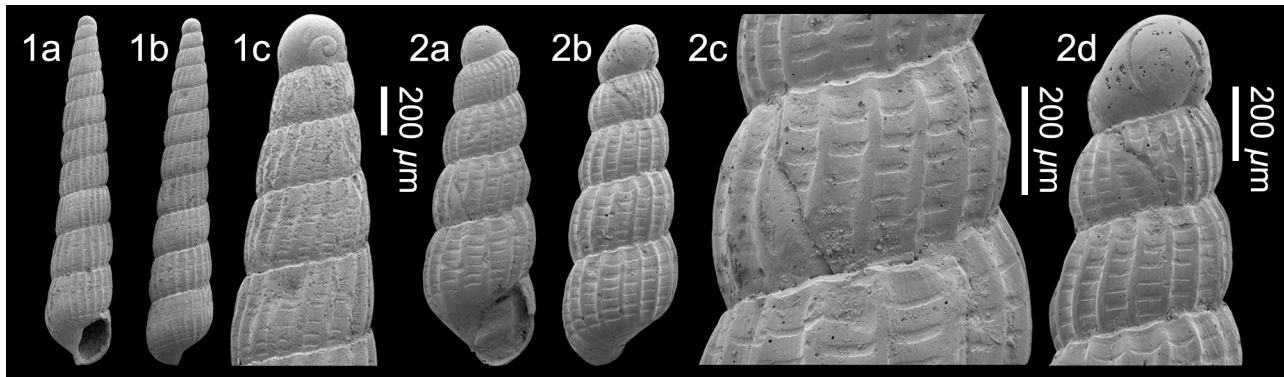


Plate 63. *Pyrgiscus rufus* (Philippi, 1836); 1. NHMW 2016/0103/1105, height 6.1 mm, width 1.2 mm, 1c, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place. 2. NHMW 2016/0103/2139, height 2.3 mm, width 740 µm, 2c, detail of teleoconch sculpture penultimate whorl, 2d, detail of protoconch (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

& Micali (2011) are quite broad (2011, pl. 35, fig. 13, pl. 36, fig. 15) and the shells illustrated here from the upper Miocene Atlantic of NW France are of the narrow *rufus* form rather than the *crenatus* form, as would be expected in the Atlantic. *Pyrgiscus rafaëli* described from Ghana is the most similar to fossil French specimens in outline and spiral sculpture.

Indeed, the variability seen in the late Miocene and Pliocene Italian specimens is illustrated by the myriad of varieties described by Sacco (1892b). In view of this, we include Pliocene records that might refer to either form in the chresonymy. We have excluded the lower Pleistocene North Sea Basin record given by Van Regteren Altena *et al.* (1964, pl. 21, fig. 202) as *T. (Pyrgiscus) crenata*, which has the characters of the broader Atlantic form. However, further assessment including protoconch measurements is necessary to see if the differences suggested by Peñas *et al.* (2009) hold true for stratigraphically older populations. In Assemblage I *Pyrgiscus rufus* has been found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper); North Sea Basin, Denmark (Sorgenfrei, 1958); Proto-Mediterranean (Tortonian and Messinian), Italy (Sacco, 1892b; Moroni, 1955). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920); Atlantic, NW France (Ceulemans *et al.*, 2018), Guadalquivir Basin, Spain (Landau *et al.*, 2011); western Mediterranean, northeastern Spain, (Martinell, 1982), Tunisia (Fekih, 1969); central Mediterranean, Italy (Sacco, 1892b; Pavia, 1976; Guioli *et al.*, 2009; Chirli & Micali, 2011). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892b; Malatesta, 1974; Marasti & Raffi, 1976; Cavallo & Repetto, 1992). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1920); central Mediterranean, Italy (Cerulli-Irelli, 1914; Gianolla *et al.*, 2010; Brunetti, 2011); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: English Channel, England (Harmer, 1920); western Mediterranean, Bal-

earic Islands (Cuerda Barceló, 1987). Present-day: Possibly restricted to Mediterranean (Peñas & Rolán, 1997; Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean (Öztürk & Bitlis Bakir, 2013), Atlantic forms may all represent *P. crenatus* (Peñas *et al.*, 2009).

Genus *Pyrgolidium* Monterosato, 1884

Type species (by original designation) – *Chemnitzia internodula* Wood, 1848, Pliocene, British Isles.

1884 *Pyrgolidium* Monterosato, p. 89.

Note – Species in this genus are characterised by their solid shell and broad rounded ribs crossed by a single cord placed about mid-whorl that distorts or constricts the ribs. In the European Miocene to present-day faunas it is represented by a single species *P. internodulum* (Wood, 1848) (*Odostomia rosea* Monterosato, 1877 is a synonym).

***Pyrgolidium internodulum* (Wood, 1848)**

Plate 64, figs 1-3

- *1848 *Chemnitzia internodula* Wood, p. 81, pl. 10 fig. 6.
- 1877 *Odostomia rosea* Monterosato, p. 38, pl. 3, fig. 1.
- 1878 *Turbonilla internodula* S. Wood – Nyst, pl. 6, fig. 3.
- 1882 *Turbonilla internodula* S. Wood – Nyst, p. 73.
- 1879 *Chemnitzia internodula* var. *ligata* Wood, p. 24, pl. 2, fig. 11.
- 1892a *Turbonilla (Pyrgolidium) internodula* (Wood) – Sacco, p. 84.
- 1892a *Turbonilla (Pyrgolidium) internodula* var. *miocenica* Sacco, p. 84, pl. 2, fig. 82.
- 1892a *Turbonilla (Pyrgolidium) internodula* var. *turrituloides* Sacco, p. 84, pl. 2, fig. 83.
- 1892a *Turbonilla (Pyrgolidium) internodula* var. *subanodulina* Sacco, p. 84, pl. 2, fig. 84.

- 1892a *Turbonilla (Pyrgolidium) internodula* var. *astensipupoidea* Sacco, p. 84, pl. 2, fig. 84bis.
- 1914 *Turbonilla (Pyrgolidium) internodula* (S. Wood) – Cerulli-Irelli, p. 451, pl. 55, figs 68, 69.
- 1920 *Turbonilla (Pyrgolidium) internodula* (S.V. Wood) – Harmer, p. 572, pl. 49, figs 33, 34.
- 1920 *Turbonilla (Pyrgolidium) internodula* var. *ligata* (J. Reeve [sic]) – Harmer, p. 573, pl. 49, fig. 35.
- 1920 *Turbonilla (Pyrgolidium) internodula* var. *acuminata* Harmer, p. 574, pl. 49, fig. 36.
- 1920 *Turbonilla (Pyrgolidium) internodula* var. *conica* Harmer, p. 574, pl. 49, figs 37, 38.
- 1920 *Turbonilla (Pyrgolidium) rosea* (Monterosato) – Harmer, p. 574, pl. 49, fig. 39.
- 1949a *Turbonilla (Pyrgolidium) internodula miocaenica* Sacco, 1892 – Glibert, p. 190, pl. 12, fig. 7.
- 1958 *Turbonilla (Pyrgolidium) internodula* f. *internodula* Wood – Glibert, p. 19, pl. 2, fig. 14a, b.
- 1958 *Turbonilla (Pyrgolidium) internodula* f. *acuminata* Harmer, 1920 – Glibert, p. 20, pl. 2, fig. 14c.
- 1958 *Turbonilla (Pyrgolidium) internodula* f. *harmeri* Glibert, p. 20, pl. 2, fig. 14d.
- 1964 *Turbonilla (Pyrgolidium) internodula* Wood, 1848 – Brébion, p. 293, pl. 7, fig. 18.
- 1964 *Turbonilla (Pyrgolidium) internodula* var. *miocaenica* Sacco, 1892 – Brébion, p. 294.
- 1964 *Turbonilla (Pyrgolidium) internodula* S.V. Wood – Van Registeren Altena *et al.*, p. 5, pl. 21, fig. 201.
- 1969 *Turbonilla (Pyrgolidium) internodula* (Wood.) – Fekih, p. 34, pl. 6, fig. 2.
- 1996 *Turbonilla internodula* (Woods [sic] S., 1848) – Peñas *et al.*, p. 62, figs 151.
- 1997 *Turbonilla (Pyrgolidium) internodula* (Wood, 1848) – Marquet, p. 109, pl. 10, fig. 4.
- 1997 *Turbonilla internodula* (S. Wood, 1848) – Peñas & Rolán, p. 46, figs 103-105.
- 1998 *Turbonilla (Pyrgolidium) internodula* (Wood, 1848) – Marquet, p. 202, fig. 174.
- 2001 *Turbonilla internodula* (Wood, 1848) – Silva, p. 571, pl. 26, figs 22, 23.
- 2011 *Turbonilla internodula* (Wood S, 1848) – Chirli & Micali, p. 81, pl. 29, figs 7-12 (*cum syn.*).
- 2011 *Turbonilla internodula* (Wood S, 1848) – Chirli & Linse, p. 206, pl. 81, fig. 1.
- 2014 *Pyrgolidium internodulum* (S. Wood, 1848) – Giannuzzi-Savelli *et al.*, p. 86, fig. 287, appendix p. 33, 81.

Material and dimensions – Maximum height 8.9 mm, width 1.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1073-1075 (3), NHMW 2016/0103/2068 (35), RGM.1348337 (3 + 2 fragments), RGM.1352703 (4), FVD (8), LC (45). **Sceaux-d'Anjou:** NHMW 2016/0103/1794 (6), RGM.1348592 (1 fragment), RGM.718050 (36).

Discussion – Glibert (1949a, p. 190) argued for the separation of the middle Miocene specimens from the Loire Basin as a chronosubspecies *Turbonilla (Pyrgolidium) internodula miocaenica* Sacco, 1892 based on morphometric data: narrower spire angle (21° vs 23°), taller spire whorls (H/W 50% vs 46%), fewer ribs (13-15 vs 18-20), that were wider spaced and less oblique (16° vs 22°) and the nodules formed where the centrally placed spiral cord crosses the ribs more accentuated. We are not sure how Glibert measured the spire angle, but it is measured here as the angle formed by the lines defined by the outermost points on both sides of the spire. In the Assemblage I material it is quite variable from 18.6°-25°. Again, with the spire whorls we are not sure which whorl he measured, but for the penultimate whorl the H/W ratio is 56-58%, which does not agree with either of Glibert's populations. Again we are unsure on which whorl Glibert counted the ribs, but there are 16-18 on the last whorl in the Assemblage I specimens. Glibert's measurement of the rib angle 'inclination des côtes axiales sur les sutures' is again unusual, and the whorl measured is again not stated. On the penultimate whorl, if a plumbline is dropped from the suture and the angle measured between the sutural angle and the rib angle, it is 70.1°-77.1° (if this is taken away from 90°, as Glibert must have done; 12.9°-19.9°), again quite variable. The rib count is slightly lower than that given by Chirli & Micali (2011, p. 81; 18-20). However, some specimens at hand from the North Sea Basin Pliocene also have as few as 14-16 ribs. We therefore

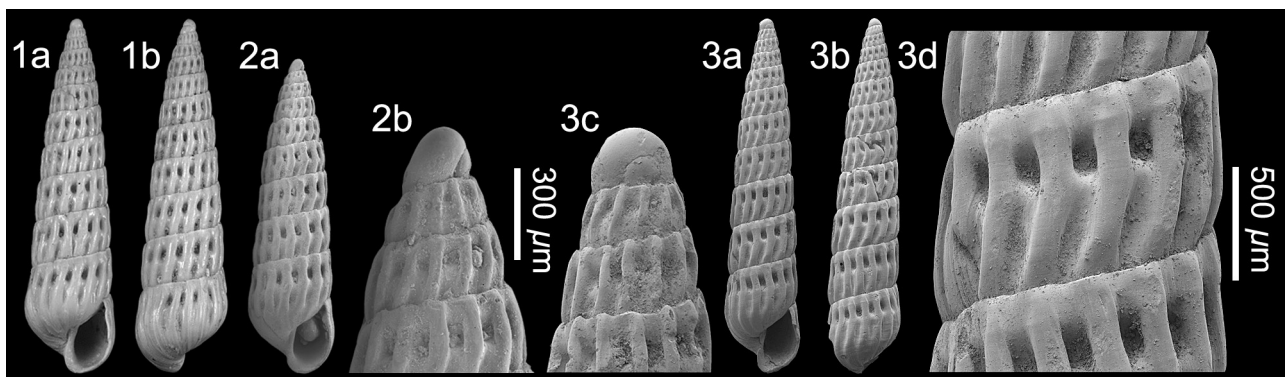


Plate 64. *Pyrgolidium internodulum* (Wood, 1848); 1. NHMW 2016/0103/1073, height 7.8 mm, width 1.8 mm; 2. NHMW 2016/0103/1074, height 5.5 mm, width 1.4 mm, 2b, detail of protoconch (SEM image); 3. NHMW 2016/0103/1075, height 6.7 mm, width 1.5 mm, 3c, detail of protoconch, 3d, detail of teleoconch sculpture penultimate whorl (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

consider there to be insufficient grounds to separate the Miocene form as a subspecies.

Pyrgolidium internodulum (Wood, 1848) had a wider geographic distribution in the fossil record than it has today, where it does not occur north of southern Portugal. This range contraction seems to have occurred relatively recently, as it was still present around the British Isles in upper Pleistocene deposits (Harmer, 1920).

Brébion (1964, p. 295) recorded this species from Assemblage I (Thorigné, St-Michel, Beaulieu), to which we add St-Clément-de-la-Place and Sceaux-d'Anjou, Assemblage II (Apigné), Assemblage III (Le Girondor, Palluau), to which we can add La Dixmérie (BL unpublished data), and Assemblage IV (Gourbesville).

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1949a). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Brébion, 1964); Proto-Mediterranean Sea: Po Basin, Italy (Sacco, 1892a). Lower Pliocene: North Sea Basin, Coralline Crag, England (Wood, 1848; Harmer, 1920), Kattendijk Formation, Belgium (Marquet, 1997, 1998); Atlantic, NW France (Brébion, 1964); central Mediterranean, Italy (Chirli & Micali, 2011), Tunisia (Fekih, 1969). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1848; Harmer, 1920), Oorderen and Kruisschans Sands, Belgium (Marquet, 1997, 1998); Atlantic, Mondego Basin, Portugal (2001); western Mediterranean, Estepona Basin, Spain (Landau & Micali, in prep.); central Mediterranean, Italy (Sacco, 1892a). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Lower Pleistocene: North Sea Basin, Netherlands (Van Regteren Altena *et al.*, 1964); central Mediterranean, Italy (Cerulli-Irelli, 1914); eastern Mediterranean, Rhodes (Chirli & Linse, 2011). Upper Pleistocene: North Sea Basin, British Isles (Harmer, 1920). Present-day: Atlantic, southern Portugal, West Africa, Morocco, Senegal south to Angola (Rolán, 2005), Mediterranean, mainly limited to the South West of Spain, adjacent to the Strait of Gibraltar (Peñas *et al.*, 1996) with occasional records in Sicily and Tyrrhenian Italian coasts (Peñas & Rolán, 2011; Giannuzzi-Savelli *et al.*, 2014).

Genus *Pyrgostylus* Monterosato, 1884

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

1884 *Pyrgostylus* Monterosato, p. 90.

Note – Turbonillids here included in the genus *Pyrgostylus* Monterosato, 1884 are similar to *Mormula* A. Adams, 1863 in having axial ribs, deeply incised spiral grooves, and irregular broad varices on the later teleoconch whorls. This genus has been synonymised by some authors (*e.g.* Glibert, 1949a), however, in *Mormula* the axials weaken gradually on the last whorl, whereas in *Pyrgostylus* they end abruptly at a well-developed basal disc and the base bears only spiral sculpture. Moreover, the shell is more

slender and less solid than *Mormula*.

***Pyrgostylus lanceae* (Libassi, 1859)**

Plate 65, figs 1-3

*1859 *Chemnitzia lanceae* Libassi, p. 21, fig. 6.

1966 *Turbonilla (Mormula) lanceae* (Libassi, 1859) – Moroni & Torre, p. 10, fig. 5 (*cum syn.*).

2011 *Turbonilla lanceae* (Libassi, 1859) – Chirli & Micali, p. 87, pl. 31, figs 1-6 (*cum syn.*).

2011 *Turbonilla lanceae* (Libassi, 1859) – Chirli & Linse, p. 208, pl. 82, fig. 2.

2013 *Turbonilla lanceae* (Libassi, 1859) – Landau *et al.*, p. 316, pl. 52, fig. 10 (*cum syn.*).

non 2018 *Mormula lanceae* (Libassi, 1859) – Brunetti & Cresti, p. 114, fig. 509.

Material and dimensions – Maximum height 9.4 mm, width 2.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1093 (1), NHMW 2016/0103/1100 (1), NHMW 2016/0103/1094 (40), RGM.1352705 (5), FVD (7), LC (12). **Sceaux-d'Anjou:** NHMW 2016/0103/2198 (1), NHMW 2016/0103/1114 (2), RGM.1348338 (3 + 7 fragments), RGM.1348617 (2 fragments), RGM.1352713 (1 fragment), RGM.718049 (2). **Renauleau:** NHMW 2016/0103/1351 (19), LC (15), FVD (11).

Discussion – *Pyrgostylus lanceae* (Libassi, 1859) is extremely similar to the Pliocene to Recent Mediterranean species *Pyrgostylus striatulus* (Linnaeus, 1758). Indeed, Micali (1994) suggested they were conspecific, with modifications occurring in protoconch size and shape since the Pliocene, suggesting a shortening of the planktotrophic stage. However, Chirli & Micali (2011) again separated the two species, and considered both to be present in upper Miocene and Pliocene deposits of Italy. *Pyrgostylus lanceae* differs from *P. striatulus* in having a taller protoconch, a broader shell, the spire whorls having a more drop-shaped profile, and the suture being more superficial and more inclined (Chirli & Micali, 2011, p. 88). *Pyrgiscus martae* (Peñas & Rolán, 1997), an extant species from West Africa, is extremely similar to *P. lanceae*, with a multispiral type A2 protoconch. Peñas & Rolán did not compare their West African taxon to *P. lanceae*, and we can find no clear separation between the two taxa, but refrain from synonymising them formally.

In Assemblage I *Pyrgostylus lanceae* has been found at St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Middle Miocene: northeastern Atlantic (Langhian): Loire Basin, France (Glibert, 1949a); Proto-Mediterranean (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: NW France (this paper); central Proto-Mediterranean Italy (Sacco, 1892a, b). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Ruiz Muñoz, 1997; Landau *et al.*, 2011); central Mediterranean, Italy (Chirli, 1989; Guioli *et al.*, 2009; Chirli & Micali, 2011), Tunisia (Fekih, 1969). Upper Pliocene: Atlantic, Mondego Basin, Portugal (NHMW collection)

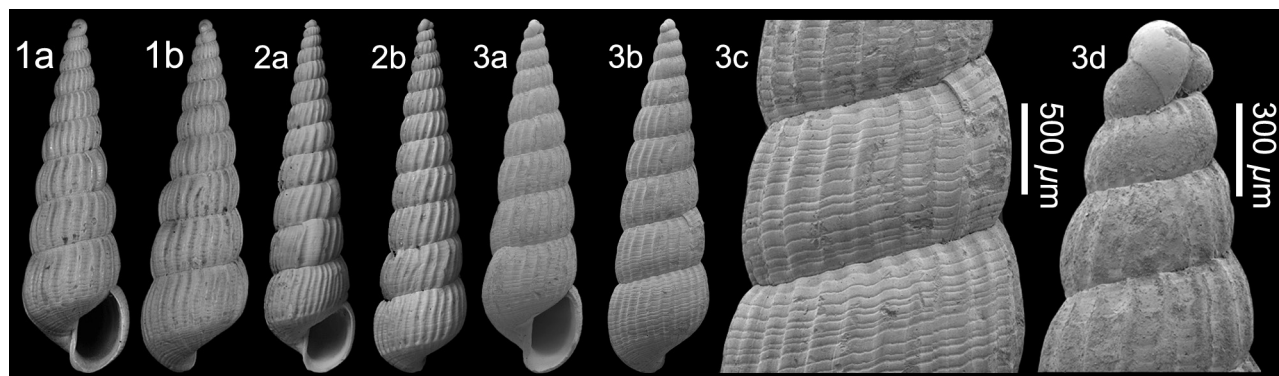


Plate 65. *Pyrgostylus lanceae* (Libassi, 1859); 1. NHMW 2016/0103/1093, height 7.5 mm, width 2.3 mm; 2. NHMW 2016/0103/1100, height 9.4 mm, width 2.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/2198, height 9.2 mm, width 2.2 mm, 3c, detail of teleoconch sculpture penultimate whorl, 3d, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

western Mediterranean, Estepona Basin (this paper); central Mediterranean, Italy (Sacco, 1892a, b; Marasti & Raffi, 1976; Chirli, 1989; Cavallo & Repetto, 1992; Bogi & Cauli, 1998; Sosso & dell'Angelo, 2010). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914); eastern Mediterranean (Chirli & Linse, 2011).

Genus '*Strioturbonilla*' Sacco, 1892 *sensu* Cossmann, 1921

Type species (by original designation) – *Odostomia sigmoidea* Monterosato, 1880, present-day, Tangier Bay, Atlantic Morocco.

1892a *Strioturbonilla* Sacco, p. 94.

Note – Sacco (1892a) chose *Odostomia sigmoidea* Monterosato, 1880 as type species for his genus *Strioturbonilla*, although he gave the author of the species as Jeffreys. Jeffreys (1884, p. 354) considered it a Monterosato manuscript name. In Sacco's description he characterised the subgenus as having an outline like *Turbonilla*, but with spiral striae present in interspaces and passing over the ribs, the ribs attenuated towards the base, no peribasal cord, and a convex base. He placed in this subgenus species like *Turbonilla* (*Strioturbonilla*) *alpina* Sacco, 1892 and *Turbonilla* (*Strioturbonilla*) *miocrassulata* Sacco, 1892, which are quite different from the type of the genus. In the selection of type of the genus Sacco was possibly misled by Jeffreys's drawing (1884, pl. 26, fig. 9), showing an outline like a *Turbonilla*, while *Odostomia sigmoidea* is quite different from a *Turbonilla*. It differs from the Italian Neogene species included in '*Strioturbonilla*' by Sacco in having a much thinner shell, with strongly convex whorls separated by a deep suture and strongly sinuous axial ribs. Indeed it bears more similarity to *Parthenina* or *Chrysallida*, where it has been placed by recent authors (Schander, 1994, fig. 2f; Penas *et al.*, 1996, fig. 17; Chirli & Micali, 2011, pl. 13, fig. 11-15 [as *Chrysallida* aff. *sigmoidea*]).

Dall & Bartsch (1904, p. 7) erroneously indicated *Turbonil-*

la (*Strioturbonilla*) *alpina* Sacco, 1892 as the type species. This was followed by Cossmann (1921, p. 281) and Wenz (1940, p. 870). Well aware of the discrepancy between the type species designed by Sacco, and the species included by him in '*Strioturbonilla*', we anyway prefer to use this genus in the sense of Cossmann (1921, p. 281). This group is characterised by rather solid turbonillid shells with strong axial ribs that do not persist onto the base, but do not end abruptly at a basal disc, as in members of the genus *Chemnitzia* d'Orbigny, 1840, and have very fine crowded spirals, more numerous and regular than in the genus *Pyrgiscus* Philippi, 1841, that continue over the base.

We do not know if the change of Sacco's type species suggested by Dall & Bartsch (1907, p. 495) was a *lapsus*, or the authors recognised that the species included by Sacco had little in common with *O. sigmoidea*, but it is inadmissible (ICZN, 1999, Art. 67.5). However, until a genetic phylogeny of the group is available, we are unwilling to erect more genus-group taxa. We therefore continue to use '*Strioturbonilla*' *sensu* Cossmann, 1921.

'*Strioturbonilla*' *miocrassulata* (Sacco, 1892)

Plate 66, figs 1-3

- *1892a *Turbonilla* (*Strioturbonilla*) *miocrassulata* Sacco, p. 95, pl. 2, fig. 113.
- 1949a *Turbonilla* (*Strioturbonilla*) *miocrassulata* Sacco, 1892 – Glibert, p. 191, pl. 11, fig. 17.
- 1964 *Turbonilla* (*Strioturbonilla*) *miocrassulata* Sacco, 1892 – Brébion, p. 297.
- 2013 *Turbonilla* *miocrassulata* Sacco, 1892 – Landau *et al.*, p. 317, pl. 52, fig. 11.

Material and dimensions – Maximum height 8.4 mm, width 2.3 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1101-1103 (3), NHMW 2016/0103/1104 (4), FVD (2), LC (3). **Sceaux-d'Anjou:** NHMW 2016/0103/1115 (5), RGM.718051 (29), RGM.1348607 (2), RGM.394067 (1). **Renauleau:** NHMW 2016/0103/1360 (1), LC (20), FVD (6). **Beugnon:** RGM.1352684 (2).

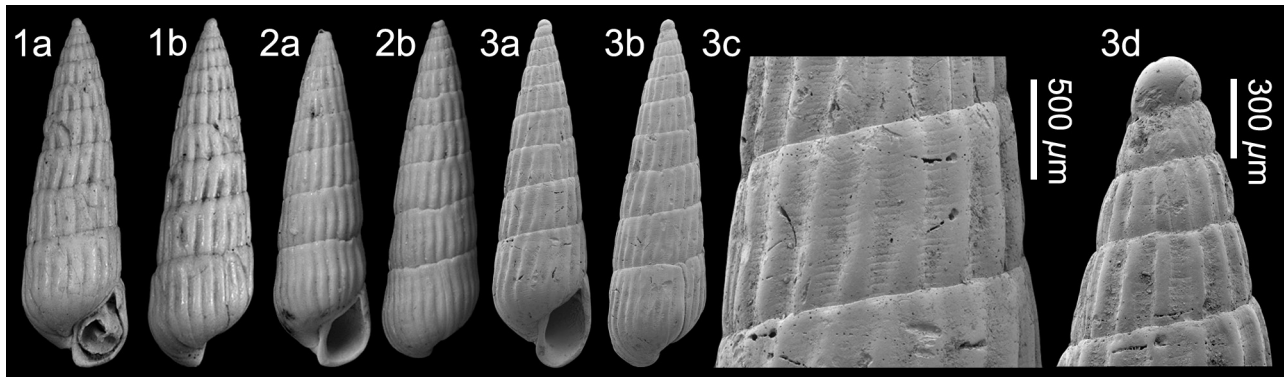


Plate 66. ‘*Strioturbonilla*’ *miocrassulata* (Sacco, 1892); 1. NHMW 2016/0103/1101, height 8.0 mm, width 2.3 mm; 2. NHMW 2016/0103/1102, height 8.4 mm, width 2.3 mm; 3. NHMW 2016/0103/1103, height 8.7 mm, width 2.4 mm, 3c, detail of teleoconch sculpture penultimate whorl, 3d, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – ‘*Strioturbonilla*’ *miocrassulata* (Sacco, 1892) is characterised by its solid conical to pupoid shell, with cyrtocooid profile abapically, type A1 tending to B protoconch, teleoconch composed of 8-9 straight-sided whorls, separated by a superficial linear suture. Sculpture consists of 17-22 rounded, weakly opisthocline axial ribs, roughly equal in width to their interspaces that weaken over the base, overrun by fine spiral sculpture that covers the entire whorl surface. The last whorl is strongly convex at the base, the aperture pyriform, the columella strongly thickened, short, bearing a small fold at its abapical end.

Three congeners occur in the Italian Pliocene; ‘*S.*’ *plicatulosenensis* (Sacco, 1892) (syntype figured in Ferrero Mortara *et al.*, 1984, pl. 13, fig. 1) is closely similar, but has a more regularly conical profile instead of a cyrtocooid early whorl profile seen in ‘*S.*’ *miocrassulata*, so that the last whorl is broader, and the initial whorls are taller. ‘*Strioturbonilla*’ *alpina* (Sacco, 1892) (holotype figured in Ferrero Mortara *et al.*, 1984, pl. 13, fig. 9) is based on an incomplete, poorly preserved shell. Nevertheless, it clearly differs from either of the above in being more slender with fewer, more elevated ribs. ‘*Strioturbonilla*’ *subalpina* (Sacco, 1892) (see Ferrero Mortara *et al.*, 1984, pl. 13, fig. 1; Chirli & Micali, pl. 38, figs 1-6) has convex whorls separated by a deeper suture, and an A2 helicoid protoconch.

The only extant species with this type of sculpture is ‘*Strioturbonilla*’ *multilirata* (Monterosato, 1875) from the present-day central and eastern Mediterranean and Italian upper Pliocene (Bongiardino & Micali, 2018, p. 104), but that species is smaller, composed of fewer whorls, with stronger ribs, and the last whorl is more slender and relatively taller.

In Assemblage I ‘*Strioturbonilla*’ *miocrassulata* is widespread, found at St-Clément-de-la-Place, Sceaux-d’Anjou, Renauleau and Beugnon.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949a). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964).

Genus *Sulcoturbonilla* Sacco, 1892

Type species (by original designation) – *Tornatella turricula* Eichwald, 1853 (= *Tornatella costellata* Dujardin, 1837), Miocene, Russia.

1892a *Sulcoturbonilla* Sacco, p. 92.

Note – Species in this genus are characterised by having well-developed axial ribs without spiral cords on the spire whorls, but strongly developed spiral sculpture over the base. (Dall & Bartsch, 1904, p. 7).

Sulcoturbonilla costellata (Dujardin, 1837)

Plate 67, figs 1, 2

- *1837 *Tornatella costellata* Dujardin, p. 282, pl. 19, fig. 25.
- 1853 *Tornatella turricula* Eichwald, p. 262, pl. 10, fig. 2.
- 1854 *Auricula Costulata* Millet, p. 154 (*nomen nudum*).
- 1854 *Melania Anaglypta* Millet, p. 154 (*nomen nudum*).
- 1865 *Turbonilla turricula* Eichw. – Hörnes, p. 501, pl. 43, fig. 31.
- 1865 *Auricula costulata* Millet, p. 579.
- 1865 *Melania anaglypta* Millet, p. 579.
- 1892a *Turbonilla* (*Sulcoturbonilla*) *turricula* (Eichw.) – Sacco, p. 92.
- 1892a *Turbonilla* (*Sulcoturbonilla*) *turricula* var. *conico-mutinensis* Sacco, p. 92, pl. 2, fig. 107.
- 1921 *Turbonilla* (*Sulcoturbonilla*) *Moulinsi* Fisch. – Cossmann, p. 283, pl. 6, figs 51-52.
- 1928 *Turbonilla* (*Sulcoturbonilla*) *turricula* Eichw. – Friedberg, p. 454, pl. 28, fig- 6.
- 1949a *Kleinella* (*Sulcoturbonilla*) *costellata* Dujardin, 1837 – Glibert, p. 183, pl. 12, fig. 2.
- 1964 *Turbonilla* (*Sulcoturbonilla*) *costellata* Dujardin, 1837 – Brébion, p. 297.
- 1966 *Turbonilla* (*Sulcoturbonilla*) *turricula* Eichwald – Kókay, p. 54, pl. 7, figs 2-4.

2011 *Turbonilla (Sulcoturbonilla) turricula* (Eichwald, 1853) – Katona *et al.*, p. 8, pl. 2, fig. 8.

Material and dimensions – Maximum height 12.3 mm, width 3.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1096-1098 (3), NHMW 2016/0103/1095 (50+), RGM.1348339 (1), RGM.1349148 (3), RGM.1352702 (3), FVD (16), LC (25). **Sceaux-d’Anjou:** NHMW 2016/0103/1795 (16), RGM.718032 (50+), RGM.1348299 (3), RGM.1348584 (3), RGM.1348606 (20), RGM.1348618 (1), RGM.1348783 (2), RGM.1352364 (7), RGM.1352532 (2), RGM.1352714 (1), FVD (13). **Renauleau:** NHMW 2016/0103/2060 (19), LC (49 + 15 fragments), FVD (29). **Beugnon:** RGM.1352426 (2), RGM.1352682 (3).

Discussion – *Sulcoturbonilla costellata* (Dujardin, 1837) differs from all Assemblage I turbonillids by the characters of the genus; strong opisthocline axial ribs with no spiral sculpture above the base and strong spiral cords over the base. The columella is straight with a small fold developed at its adapical end. The protoconch is very small, of type B. This species was widely distributed during the middle and late Miocene along the European Atlantic frontage, Proto-Mediterranean and Paratethys. *Sulcoturbonilla benoisti* (Cossmann & Peyrot, 1917) from the lower Miocene Burdigalian of the Aquitaine Basin differs mainly in having a regularly conical spire as opposed to distinctly scalate, as in *S. costellata*. The other differences mentioned by Cossmann & Peyrot (1917, p. 362); more inflated shell, shorter last whorl, less flexuous axial ribs and ribs not ending as abruptly at the base, do not seem to be consistent. Unfortunately, the protoconch is missing in the specimen figured on the MNHN website (<https://science.mnhn.fr/institution/mnhn/collection/f/item/j04512?listIndex=44&listCount=105>). Brébion (1964, p. 298) recorded this species from numerous Assemblage I localities (Renauleau, Sceaux-d’Anjou, Thorigné, St-Clément-de-la-Place, Les Pierres Blanches), to which we add Beugnon.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1949a); Paratethys, Austria (Hörnes, 1856), Hungary (Kókay, 1966), Poland (Fried-

berg, 1928), Romania (Katona *et al.*, 2011). Upper Miocene: Atlantic (Tortonian): NW France (Millet, 1854, 1865; Brébion, 1964); Proto-Mediterranean Sea: Po Basin, Italy (Sacco, 1892a).

Tribe Eulimellini Saurin, 1958
Genus *Bacteridium* Thiele, 1929

Type species (by monotypy) – *Eulimella praeclara* Thiele, 1925, present-day, Sumatra, Indonesia.

1925 *Bacteridium* Thiele, p. 236.

Note – *Bacteridium* species are characterised by their small, slender, smooth or finely striated shells, scalate spire, whorls separated by a strongly oblique suture and absence of columellar fold or umbilicus. No all recent authors have accepted the genus, which was synonymised with *Anisocycla* Monterosato, 1880 by Van Aartsen *et al.* (2000, p. 16).

***Bacteridium* sp.**
Plate 68, fig. 1

Material and dimensions – Height 2.2 mm, width 580 μ m. **St-Clément-de-la-Place:** NHMW 2016/0103/2163 (1), NHMW 2016/0103/2229 (1).

Discussion – Unfortunately this species is represented by only two specimens, both missing their apex, and therefore not suitable for description. It probably represents an undescribed species that differs from the present-day Mediterranean and West African *B. carinatum* (de Folin, 1870) in having a less scalate spire. In *B. carinatum* the spire whorls are sharply shouldered, delimiting a narrow subhorizontal sutural platform. It also differs in having spiral sculpture, absent in *B. carinatum*.

The genus is not speciose, with only four extant species known. *Bacteridium bermudense* (Dall & Bartsch, 1911) from present-day Bermuda does have spiral sculpture, but differs in having even more strongly shouldered

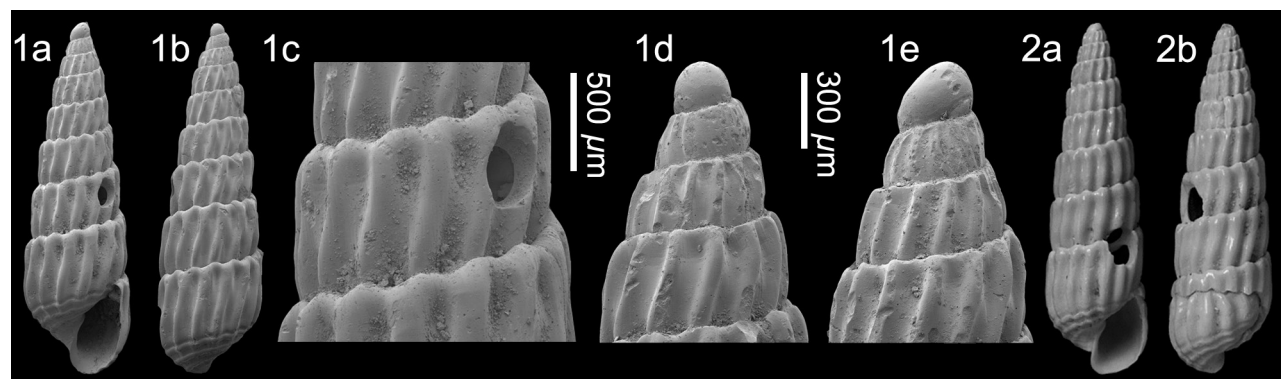


Plate 67. *Sulcoturbonilla costellata* (Dujardin, 1837); 1. NHMW 2016/0103/1096, height 9.2 mm, width 2.5 mm, 1c, detail of teleoconch sculpture penultimate whorl, 1d-e, detail of protoconch (SEM image); 2. NHMW 2016/0103/1098, height 8.2 mm, width 2.3 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

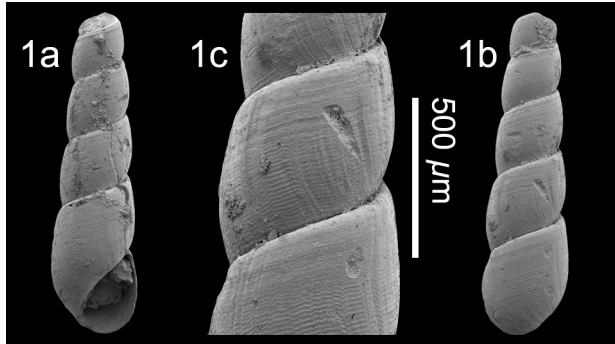


Plate 68. *Bacteridium* sp.; 1. NHMW 2016/0103/2163, height 2.2 mm, width 580 µm, 1c, detail of teleoconch sculpture penultimate whorl (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorls than *B. carinatum*. *Bacteridium resticulum* (Dall, 1889), also from the Caribbean, is very tall and slender. Like the French species it is less shouldered than its extant congeners, but it differs from the St-Clément-de-la-Place species in having more disjunct whorls separated by a deeper suture and lacking spiral sculpture. *Bacteridium vittatum* (A. Adams, 1861) from Japan is probably most similar to the French species in having weakly shouldered whorls and spiral sculpture. We await further material to formally describe this species.

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

Genus *Eulimella* Forbes & MacAndrew, 1846

Type species (by original designation) – *Eulima macandrei* Forbes, 1844 (= *Melania scillae* Scacchi, 1835), present-day, Europe.

1846 *Eulimella* Forbes & MacAndrew, p. 1027.

1861 *Aciculina* Deshayes, p. 530. Type species (by typification of replacement name [ICZN 1999, art.

79.2.3] *Belonidium* Cossmann, 1893, p. 350): *Aciculina gracilis* Deshayes, 1861, Eocene, France.

1880 *Anisocyclus* Monterosato, p. 72. Replacement name for *Aciculina* Deshayes, 1861 non H. & A. Adams, 1853. Type species (by typification of replaced name): *Aciculina gracilis* Deshayes, 1861, Eocene, France (by way of type species of *Belonidium*).

1892a *Ptycheulimella* Sacco, p. 59. Type species (by original designation): *Tornatella pyramidata* Deshayes, 1835, Pliocene: Greece.

1893c *Belonidium* Cossmann, p. 350. Type species (by original designation): *Aciculina gracilis* Deshayes, 1861, Eocene, France. *Nom. nov. pro Aciculina* Deshayes, 1861, non A. Adams, 1853 (Gastropoda: Nassariidae).

1959 *Instarella*, Laseron, p. 249, figs 211, 212. Type species (by original designation): *Instarella subcarina* Laseron, 1959, present-day, Northern Territory, Australia.

1959 *Zonella*, Laseron, p. 248, figs 208, 209. Type species (by original designation): *Odostomia amoebaea* Watson, 1886, present-day, Queensland, Australia.

Note – Species included in this genus have tall, slender shells, smooth, except for microscopic growth lines, without a columellar ‘tooth’ (Peñas & Rolán, 2016, p. 53).

***Eulimella cf. perspicua* (Cossmann & Peyrot, 1917)**

Plate 69, figs 1, 2

cf. *1917 *Anisocyclus perspicua* Cossmann & Peyrot, p. 384, pl. 9, figs 91-92.

Material and dimensions – Maximum height 4.1 mm, width 900 µm. **St-Clément-de-la-Place:** NHMW 2016/0103/2195-2196 (2), NHMW 2016/0103/2162 (15), FVD (2). **Sceaux-d’Anjou:** NHMW 2016/0103/2170 (1). **Renauveau:** NHMW 2016/0103/2206 (1).

Discussion – *Eulimella perspicua* (Cossmann & Peyrot, 1917) from the Atlantic lower Miocene Aquitanian and

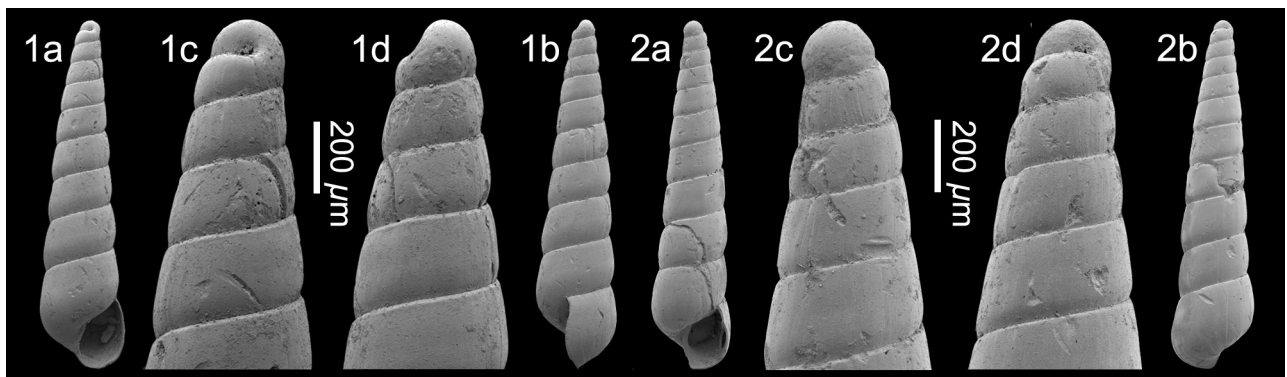


Plate 69. *Eulimella cf. perspicua* (Cossmann & Peyrot, 1917); 1. NHMW 2016/0103/2195, height 4.1 mm, width 900 µm, 1c-d, detail of protoconch; 2. NHMW 2016/0103/2196, height 4.0 mm, width 1.0 mm, 2c-d, detail of protoconch (SEM images). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Burdigalian of France is characterised by its tall slender shell, type A2 protoconch and smooth whorls that are slightly swollen just above the suture. The specimens from Assemblage I differ slightly in having the protoconch a little more tilted (Pl. 69, fig. 1d vs holotype figured at https://science.mnhn.fr/institution/mnhn/collection/item/j04520?lang=en_US). Its protoconch of type A2 is tilted perpendicular to shell teleoconch axis, while in the Assemblage I specimens it is inclined of about 135°, with the nucleus partially immersed in the first teleoconch.

Eulimella subalpina Sacco, 1892 (holotype figured in Ferrero Mortara *et al.*, 1984, pl. 11, fig. 12) from the Pliocene of Italy is also similar in teleoconch characters, but the profile of the early teleoconch whorls is cyrtocoid. Unfortunately, the protoconch of that species is not preserved. The specimen from Assemblage I also resembles *Eulimella (Eulimella) acicula* (Philippi, 1836) drawn in A.W. Janssen (1984, pl. 16, fig. 6a-d), but clearly differs in having a more inclined protoconch, with the nucleus much less exposed.

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

***Eulimella redoniana* nov. sp.**

Plate 70, figs 1, 2

Type material – Holotype NHMW 2016/0103/2168, height 6.6 mm, width 1.7 mm; paratype 1 NHMW 2016/0103/2169, height 5.2 mm, width 1.4 mm.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/2217 (1).

Etymology – Named after the historical name for these deposits, the Redonian. *Eulimella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Eulimella* species of small size, A1 protoconch tilted at about 120°, early profile cyrtocoid, straight-sided below, base not delimited, weak columellar fold.

Description – Shell small, slender, relatively elongate. Protoconch type A1, tilted at angle of about 120° to main shell axis. Teleoconch of 7-8 weakly convex to almost straight-sided whorls separated by impressed, linear suture. Early spire profile cyrtocoid, straight-sided below. Surface smooth, except for inconspicuous, slightly prosocline growth lines. Last whorl 36-40% of total height, regularly convex at periphery, base not delimited. Aperture 22% of total height, outer lip straight abapically, rounded adapically. Small columellar fold placed mid-aperture.

Discussion – The distinctive features of *Eulimella redoniana* nov. sp. are its type A1 protoconch and its profile, which is cyrtocoid for the early teleoconch whorls and straight-sided below. Some of the congeners from the Italian Pliocene illustrated by Chirli & Micali (2011) also have slightly cyrtocoid apices, like *Eulimella subcylindrata* Dunker in Wienkauff, 1862, but that species has an A2 type protoconch. Others have a distinctly cyrtocoid profile to the entire shell, like *E. laevissima* (Seguenza, 1876) and *E. pyramidata* (Deshayes, 1835), but these are far broader-shelled species. *Eulimella variabilis* de Folin, 1870 from present-day West Africa is somewhat similar and has a type A1 protoconch, but has fewer whorls and a lower last whorl. *Eulimella redoniana* has been found at St-Clément-de-la-Place and Sceaux-d’Anjou.

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

***Eulimella* cf. *roeri* (Pavia, 1976)**

Plate 71, figs 1, 2

cf. *1976 *Ebala (Ebalina) roeri* Pavia, p. 161, pl. 11, figs 11-13.

cf. 2011 *Eulimella roeri* (Pavia, 1976) – Chirli & Linse, p. 200, pl. 76, fig. 2.

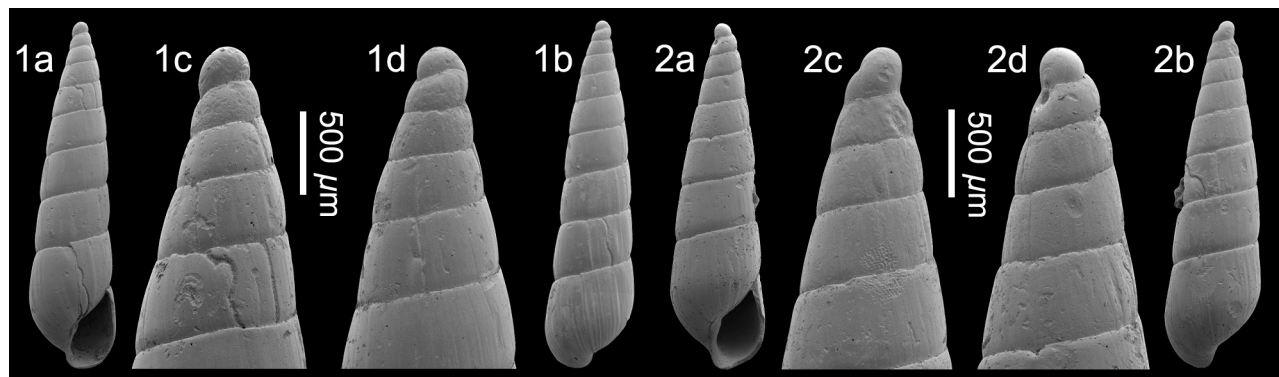


Plate 70. *Eulimella redoniana* nov. sp.; 1. **Holotype** NHMW 2016/0103/2168, height 6.6 mm, width 1.7 mm, 1c-d, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/2169, height 5.2 mm, width 1.4 mm, 2c-d, detail of protoconch (SEM images). La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

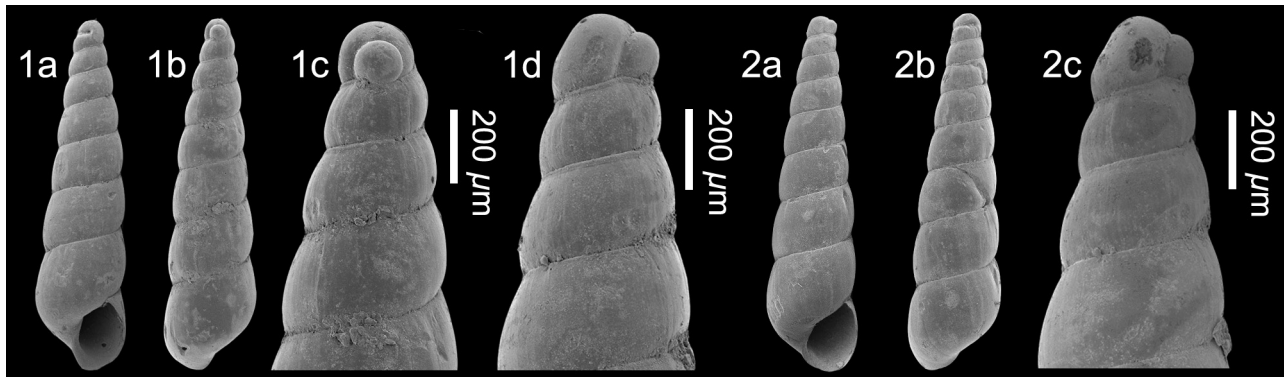


Plate 71. *Eulimella* cf. *roeri* (Pavia, 1976); 1. NHMW 2016/0103/2255, height 2.7 mm, width 680 μm , 1c-d, detail of protoconch; 2. NHMW 2016/0103/2256, height 2.9 mm, width 710 μm , 2c, detail of protoconch (SEM images). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Material and dimensions – Maximum height 1.5 mm, width 470 μm . **St-Clément-de-la-Place:** NHMW 2016/0103/2216 (5), NHMW 2016/0103/2255-2256 (2). **Sceaux-d’Anjou:** NHMW 2016/0103/2184 (1), LC (X), FVD (X).

Discussion – The shells illustrated here are very similar to the holotype of *Ebala* (*Ebalina*) *roeri* Pavia, 1976 from the lower Pliocene of Italy, with which they share the presence of a subsutural groove. The generic placement proposed by Pavia (1976) is considered incorrect, as species in the genus *Ebala* have a very characteristic elevate protoconch. The genus *Ebalina* Thiele, 1929 was erected for *Eulimella*-like species with a subsutural groove. Whilst placement in this genus is valid, the presence of a subsutural groove alone does not justify the use of a separate genus, especially as it is very weakly developed and does not alter the whorl profile. A subsutural groove is also seen in several other species placed in the genus *Eulimella*. Therefore we prefer to provisionally place this species in the genus *Eulimella*.

Compared to *E. roeri* from the lower Pliocene of Italy, the French specimens show a more protruding protoconch nucleus, deforming the first teleoconch whorl, while in the former this does not happen (Pavia, 1976, pl. 11, figs. 11d, 11e). It differs from *Eulimella pseudoanisocycloides* Sacco, 1892 in having a protoconch of 2-2.5 whorls exposed with a blunt apex, whereas *E. pseudoanisocycloides* has three whorls exposed with a more pointed apex (see Ferrero Mortara *et al.* (1984, pl. 11, fig. 13).

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

Eulimella semilaeve nov. sp.

Plate 72, figs 1, 2

?1958 *Eulimella concinna* Sorgenfrei (*partim*), p. 321, pl. 69, fig. 238b, not pl. 70, fig. 238.

?2010 *Eulimella* sp. 1 – Moths *et al.*, p. 87, fig. 48a.

Type material – Holotype NHMW 2016/0103/2012,

height 6.0 mm, width 1.2 mm, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/2161, height 4.3 mm, width 1.1 mm, **Sceaux-d’Anjou**.

Other material – **St-Clément-de-la-Place:** NHMW 2016/0103/2230 (6).

Etymology – Latin ‘*laevis*, -e, -ior’, meaning smooth, prefix semi-, meaning almost, reflecting subobsolete sculpture. *Eulimella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Eulimella* species with type A1 tending to B protoconch, frustate whorls, sculpture much reduced, visible only under magnification, flattened ribs separated by shallow grooves, one spiral groove placed two-thirds whorl height.

Description – Shell small, tall, slender, with sculpture much reduced, visible only under magnification. Protoconch type A1 tending to B, planispiral. Teleoconch of 6.5 frustate whorls (terminology adopted from Allmon, 1996; suture slightly below the convex periphery), weakly concave upper half and swollen lower third, separated by impressed suture, at 165° to main shell axis. Sculpture only visible under SEM imaging, consists of broad flattened ribs separated by faint, shallow grooves, one equally faint interrupted spiral groove runs at two-thirds whorl height. Last whorl 38% of total height, base rounded, not delimited. Aperture ovate. Columella twisted with moderately strong columellar fold at adapical end.

Discussion – *Eulimella semilaeve* nov. sp. is an unusual species, and is placed in the genus *Eulimella* Forbes & MacAndrew, 1846 despite the presence of extremely weak axial sculpture, and the presence of a columellar fold. It differs from all other Assemblage I eulimellids, in having weak ribs, only visible under SEM imaging. The

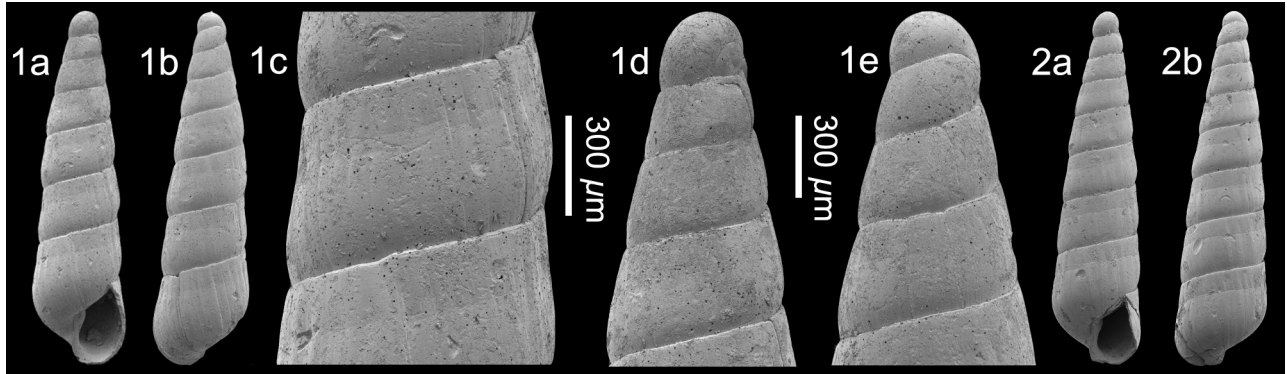


Plate 72. *Eulimella semilaeve* nov. sp.; 1. **Holotype** NHMW 2016/0103/2012, height 6.0 mm, width 1.2 mm, 1c, detail of teleoconch sculpture penultimate whorl, 1d-e, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place. 2. **Paratype 1** NHMW 2016/0103/2161, height 4.3 mm, width 1.1 mm (SEM images). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

small specimen of *Eulimella concinna* Sorgenfrei, 1958 (pl. 69, fig. 238b) from the lower Miocene Arnum Formation of Denmark and the specimen figured by Moths *et al.* (2010, fig. 48a) from coeval beds in Germany might be this species. The specimen figured by Sorgenfrei only has three teleoconch whorls, but they have the same whorl profile, with a single groove at about two-thirds whorl height, and the same protoconch type. The holotype of *E. concinna* (Sorgenfrei, 1958, pl. 70, fig. 238) is not this species.

Placement in the genus *Turbonilla* Risso, 1826 is also possible. *Turbonilla subacicula* d'Orbigny, 1852 from the Aquitanian lower Miocene of the Aquitaine Basin of France is also smooth at first glance, but has extremely fine and regular spiral sculpture (see syntype MNHN.A12712; <https://science.mnhn.fr/institution/mnhn/collection/f/item/a12712>). It differs clearly from *E. semilaeve* in whorl profile having lower, almost straight-sided whorls. Some of the extant species, such as *T. haullevillei* Dautzenberg, 1912 from West Africa also have reduced sculpture, but none as obsolete as in *E. semilaeve*.

This species has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – ?Lower Miocene: North Sea Basin, Arnum Formation, Denmark (Sorgenfrei, 1958), ?Germany (Moths *et al.*, 2010). Upper Miocene: Atlantic (Tortonian): NW France (this paper).

Eulimella ventricosa (Forbes, 1844)

Plate 73, fig. 1

- *1844 *Parthenia ventricosa* Forbes, p. 188.
- 1847 *Eulimella gracilis* Jeffreys, p. 311.
- 1850 *Eulimella affinis* Forbes & Hanley, p. 313.
- 1858 *Eulimella obeliscus* Jeffreys, p. 46.
- 1981 *Eulimella (E.) ventricosa* (Forbes) – Caldara *et al.*, p. 151, pl. 2, fig. 3.
- 1986 *Eulimella ventricosa* (Forbes, 1843 [sic]) – Fretter *et al.*, p. 627, figs 437, 438.

- 1988 *Eulimella ventricosa* (Forbes, 1843 [sic]) – Graham, p. 616, fig. 269.
- 1991 *Eulimella ventricosa* (Forbes, 1844) – Warén, p. 111, figs 37C-D, 38D.
- 1996 *Eulimella ventricosa* (Forbes, 1844) – Peñas *et al.*, p. 36, figs 72-73, 77.
- 2013 *Eulimella ventricosa* (Forbes, 1844) – Öztürk & Bitlis Bakir, p. 428, fig. 9.
- 2014 *Eulimella ventricosa* (Forbes, 1844) – Høisaeter, p. 60, figs 96, 101-102.
- 2014 *Eulimella ventricosa* (Forbes, 1844) – Giannuzzi-Savelli *et al.*, p. 88, figs 301-304, appendix p. 36, 83.
- 2018 *Eulimella ventricosa* (Forbes, 1844) – Brunetti & Cresti, p. 108, fig. 469.

Material and dimensions – Maximum height 1.8 mm, width 520 μm. **Sceaux-d'Anjou:** RGM.1352340 (1).

Discussion – This single juvenile specimen probably represents *Eulimella ventricosa* (Forbes, 1844). It is characterised by its type A1 protoconch, tending to B and teleoconch composed of up to ten strongly and regularly

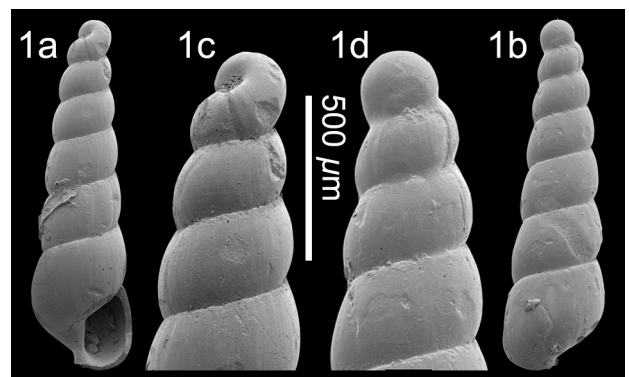


Plate 73. *Eulimella ventricosa* (Forbes, 1844); 1. RGM.1352340, height 1.8 mm, width 520 μm, 1c-d, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

convex whorls, smooth, with fine sinuous growth lines. It differs from *Eulimella perspicua* (Cossmann & Peyrot, 1917) in having more regularly convex whorls, and its type A1 protoconch.

In Assemblage I *Eulimella ventricosa* has so far only been found at Sceaux-d'Anjou.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Brunetti & Cresti, 2018). Lower Pleistocene: central Mediterranean, Italy (Seguenza, 1876; Micali & Villari, 1989; Caldara *et al.*, 1981; Di Geronimo *et al.*, 1982; Di Geronimo & La Perna, 1997; Gianolla *et al.*, 2010; Brunetti, 2011). Present-day: Eastern Atlantic from Norway (Warén, 1991; Høisaeter, 2014), Shetlands (Fretter *et al.*, 1986; Graham, 1988) to Canary Islands (Van Aartsen *et al.*, 2000), Madeira, Cape Verde Islands (Peñas & Rolán, 1997), Mediterranean (Peñas & Rolán, 1996; Giannuzzi-Savelli *et al.*, 2014), eastern Mediterranean, Turkey (Öztürk & Bitlis Bakir, 2013).

Family Amathinidae Ponder, 1987

Genus *Clathrella* Récluz, 1864

Type species (by monotypy) – *Nerita costata* Brocchi, 1814 (= *Fossarus clathratus* Philippi, 1844), Pliocene, Italy.

1864 *Clathrella* Récluz, p. 251.

1896 *Amathinoides* Sacco, p. 41. Type species (by original designation): *Nerita sulcosa* Brocchi, 1814, Pliocene, Italy.

Clathrella clathrata (Philippi 1844)

Plate 74, figs 1, 2

1814 *Nerita costata* Brocchi, 1814, p. 300, pl. 1, fig. 11 (junior homonym of *Nerita costata* Gmelin, 1791).

1828 *Turbo minutus* Michaud, p. 122, pl. unnumbered, figs 7-9 (junior homonym of *Turbo minutus* Brown, 1818).

*1844 *Fossarus clathratus* Philippi, p. 148, pl. 25, fig. 5.

1854 *Delphinula Costata* Millet, p. 157 (*nomen nudum*).

1865 *Delphinula costata* – Millet, p. 584.

1964 *Phasianema costata* Brocchi, 1814 – Brébion, p. 281.

2001b *Clathrella* sp. – Peñas & Rolán, p. 104, figs 4-7.

2013 *Clathrella clathrata* (Philippi 1844) – Landau *et al.*, p. 319, pl. 52, fig. 12 (*cum syn.*).

2014 *Clathrella clathrata* (Philippi 1844) – Brunetti, p. 74, unnumbered fig. bottom.

2014 *Clathrella clathrata* (Philippi 1844) – Giannuzzi-Savelli *et al.*, p. 92, figs 313-317, appendix p. 37, 85.

2018 *Clathrella clathrata* (Philippi 1844) – Ceulemans *et al.*, p. 138, pl. 8, figs 19, 20 (*cum syn.*).

2018 *Clathrella clathrata* (Philippi, 1844) – Brunetti & Cresti, p. 104, fig. 444.

Material and dimensions – Maximum height 8.2 mm, width 6.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1068-1069 (2), NHMW 2016/0103/1070 (50+), RGM.1352412 (26), FVD (25), LC (25). **Sceaux-d'Anjou**: NHMW 2016/0103/1072 (15), RGM.718056 (50+), RGM.739210 (1 + 1 juvenile), RGM.1348881 (2 + 2 juveniles), RGM.1352292 (1), RGM.1352359 (13 juveniles), RGM.1352528 (4), RGM.1352711 (1; monstrosity with bifid spiral cords), FVD (5). **Renaleau**: NHMW 2016/0103/1071 (3), LC (13 + 10 juveniles), FVD (8). **Beugnon**: RGM.1348482 (1), RGM.1352277 (3).

Discussion – We agree with Lozouet *et al.* (2001) that the French Atlantic early Miocene shells confused with *Clathrella clathrata* (Philippi, 1844) by many authors are not conspecific. The shell illustrated by Lozouet *et al.* (2001, pl. 36, fig. 5) differs in having only two elevated spiral cords on spire whorls, as opposed to three in *C. clathrata*, the cords on the last whorl are of subequal strength, whereas in *C. clathrata* the shoulder and peripheral cords are more prominent than the others, and the aperture is smaller and far less dilated than in *C. clathrata* (For further discussion see Landau *et al.*, 2013, p. 320). As with many other species from Assemblage I, the population is smaller-shelled than in most other assemblages, and as the shell enlarges the outer lip becomes more flared.

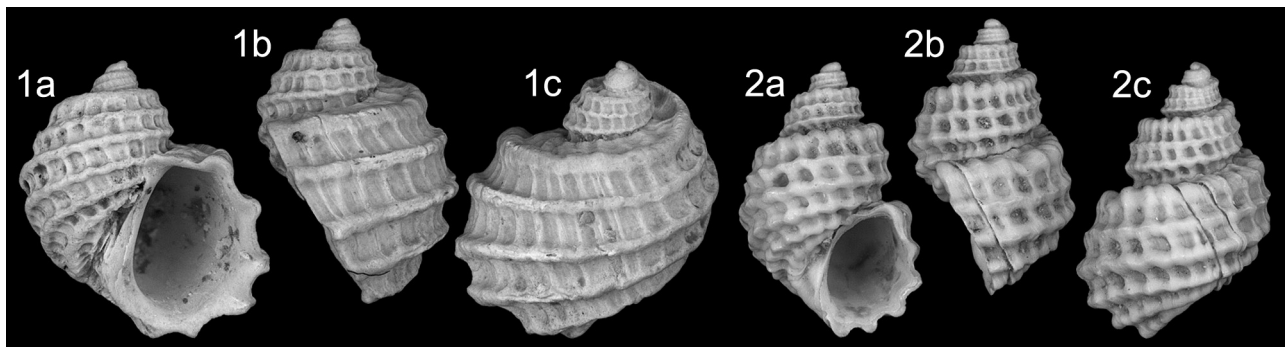


Plate 74. *Clathrella clathrata* (Philippi, 1844); 1. NHMW 2016/0103/1068, height 4.9 mm, width 3.9 mm; 2. NHMW 2016/0103/1069, height 4.2 mm, width 2.8 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Some of the smaller specimens resemble *C. microstoma* (Boettger, 1902) from the middle Miocene Paratethys of Romania. We have not seen that species, but it may just be a tall, slender, weakly sculptured subadult form of *C. clathrata*.

Millet (1865, p. 584) described this species as *Delphinula costata* (junior homonym of *D. costata* Danilo, 1856) from the Assemblage I locality of Sceaux-d'Anjou, to which Brébion (1964, p. 282) added Renauleau, St-Michel, Saint-Clément-de-la-Place, Les Pierres Blanches, and we add Beugnon, Assemblage III localities (La Dixmerie, Le Pigeon Blanc, Le Girondor, Palluau) and Assemblage IV localities (St-Jean-La-Poterie, Gourbesville).

Distribution – Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, (Cossmann & Peyrot, 1919), (Langhian): Loire Basin, France (Glibert, 1949a); Paratethys (Langhian-Serravallian): Poland (Friedberg, 1923; Bałuk, 1995), Vienna (Hörnes, 1856), Hungary (Strausz, 1962, 1966), Ukraine (Zelinskaya *et al.*, 1968), Slovakia (Švagrovský, 1960); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian): NW France (Millet, 1854, 1865; Brébion, 1964; Ceulemans *et al.*, 2018), (Tortonian): Algarve Basin, Portugal (Dollfus *et al.*, 1904). Lower Pliocene: Atlantic, NW France (Ceulemans *et al.*, 2018), Guadalquivir Basin, Spain (González Delgado, 1988; Ruiz Muñoz *et al.*, 1997; Landau *et al.*, 2011); western Mediterranean, Roussillon Basin, France (Fontannes, 1880); central Mediterranean, Italy (Sacco, 1896; Forli *et al.*, 1999; Chirli, 2008; Brunetti & Cresti, 2018); Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin (Landau & Micali, in prep.), central Mediterranean, Italy (Sacco, 1896; Caprotti, 1970, 1976; Cavallo & Repetto, 1992; Ragaini & Bernieri, 2007; Brunetti, 2014). Upper Pliocene-Pleistocene: Atlantic, northwestern France (Brébion, 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1914). Present-day: Mediterranean (Peñas *et al.*, 1996; Giannuzzi-Savelli *et al.*, 2014).

Clathrella semilaeve nov. sp.

Plate 75, figs 1-3

Type material – Holotype NHMW 2016/0103/1725, height 4.1 mm, width 2.3 mm; paratype 1 NHMW 2016/0103/1726, height 3.3 mm, width 2.0 mm (SEM image), **Renauleau**. Paratype 2 NHMW 2016/0103/1000, height 2.6 mm, width 1.6 mm; paratype 3 RGM.1352727, height 2.8 mm, **St-Clément-de-la-Place**.

Other material – Maximum height 4.1 mm, width 2.3. **St-Clément-de-la-Place**: NHMW 2016/0103/1767 (2), NHMW 2016/0103/1001 (50+), RGM.1352728 (2), RGM.1352729 (8), FVD (4), LC (2). **Renauleau**: NHMW 2016/0103/1738 (11), LC (7), FVD (3).

Etymology – Latin ‘*laevis*, -e, -ior’, meaning smooth, prefix semi-, meaning almost, reflecting subobsolete sculpture. *Clathrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathrella* species of small size, type B protoconch, 2.25 rapidly expanding teleoconch whorls with subobsolete spiral sculpture, axial sculpture absent, large aperture, small umbilical chink.

Description – Shell small, fusiform. Protoconch type B, initial whorls obscured by first teleoconch whorl. Teleoconch of 2.25 rapidly expanding convex whorls separated by impressed to narrowly canaliculated, strongly oblique suture. Sculpture reduced to irregular, subobsolete spiral cords and prominent axial growth lines and ridges. Last whorl about 85% of total height, narrow concave sub-sutural ramp, shoulder weakly angled, high-placed, delimited by weak cord, regularly convex below, groove delimiting base, weakly and irregularly spirally sculptured to almost completely smooth in some specimens, narrow umbilical chink. Aperture large, 52% of total height, ovate, outer lip regularly rounded, expanded abapically. Columella smooth, almost straight, tilted abaxially.

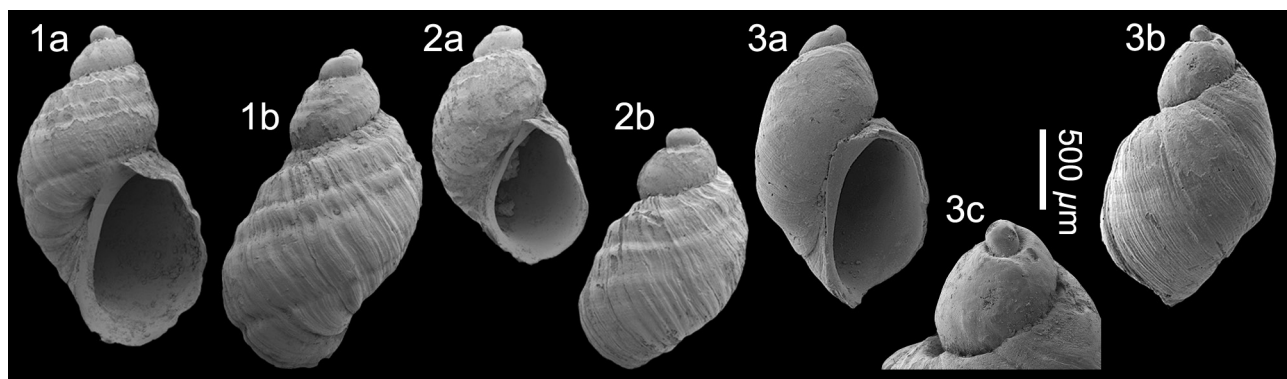


Plate 75. *Clathrella semilaeve* nov. sp.; 1. **Holotype** NHMW 2016/0103/1725, height 4.1 mm, width 2.3 mm; 2. **Paratype 1** NHMW 2016/0103/1726, height 3.3 mm, width 2.0 mm. Renauleau. 3. **Paratype 2** NHMW 2016/0103/1000, height 2.6 mm, width 1.6 mm (SEM images). Le Grand Chauverau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Clathrella semilaeve* nov. sp. is immediately separated from *Clathrella clathrata* (Philippi, 1844), with which it co-occurs in Assemblage I, by its more fusiform shape and much weaker sculpture. The sculpture in *C. semilaeve* is somewhat variable, although never stronger than that seen in the holotype (Pl. 75, fig. 1), and some specimens are almost completely smooth (Pl. 75, fig. 3). The Pliocene Mediterranean *Clathrella sulcosa* (Brocchi, 1814) and present-day *C. volumen* Peñas & Rolán, 2001 from West Africa both have a more capuliform shell than either of the other two congeners discussed above, with a much lower spire and strong spiral cords (8 in *C. sulcosa*; 12–16 in *C. volumen*). This species is uncommon in Assemblage I and found at Renauleau and St-Clément-de-la-Place.

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

Genus *Leucotina* A. Adams, 1860

Type species (by monotypy) – *Leucotina nipponensis* A. Adams, 1860, present-day, Japan Sea.

- 1860b *Leucotina* A. Adams, p. 406.
 1860b *Myonia* A. Adams, p. 406. Type species (by monotypy): *Myonia japonica* A. Adams, 1860, present-day, Japan Sea. Junior homonym of *Myonia* Dana, 1847 [Bivalvia].
 1895 *Adelactaeon* Cossmann, p. 54. Type species (by typification of replaced name): *Myonia japonica* A. Adams, 1860, present-day, Japan Sea. *Nom. nov. pro Myonia* A. Adams, 1860, *non* Dana, 1847 [Bivalvia], *non* Walker, 1854 [Lepidoptera].

Note – Ceulemans *et al.* (2018, p. 139) used the genus *Monotygmia* G.B. Sowerby II, 1839 (type species, *Monotygmia striata* Gray, 1847, by subsequent monotypy, present-day, Indo-West Pacific) for this group of species. However, following Peñas *et al.* (2014, p. 202) the genus *Leucotina* A. Adams, 1860 may be best for these more inflated amathiniids, whereas the taller turriculate species

are placed in *Monotygmia*. Van Aartsen & Hori (2006, p. 3) discussed the possible synonymy between these two genera.

Leucotina ivolasi (Mayer-Eymar, 1900)

Plate 76, figs 1, 2

- *1900 *Sigaretus Ivolasi* Mayer-Eymar in Ivolas & Peyrot, p. 152, pl. 2, fig. 34.
 1915 *Odontostomia (Noemia) Ivolasi* Mayer – de Morgan, p. 228, fig. 10.
 1949a *Kleinella (Leucotina) ivolasi* Mayer, 1900 – Gilbert, p. 180, pl. 11, fig. 20.
 1964 *Kleinella (Acteopyramis) nov. sp.* Brébion, p. 282, pl. 7, fig. 7.
 2018 *Monotygmia ivolasi* (Mayer-Eymar, 1900) – Ceulemans *et al.*, p. 139, pl. 9, figs 1, 2.

Material and dimensions – Maximum height 5.8 mm, width 2.8 mm. **St-Clément-de-la-Place:** RGM.1352707 (1). **Sceaux-d'Anjou:** NHMW 2016/0103/1117–1118 (2), NHMW 2016/0103/2061 (4), RGM.718207 (14), RGM.1348885 (1), FVD (2).

Discussion – *Leucotina ivolasi* (Mayer-Eymar, 1900) is characterised by its relatively tall slender shell for the genus and elevated spire; the last whorl is inflated but usually less so than that of its congeners. Having said this, the Assemblage I specimens are quite variable; some specimens are quite globose (Pl. 76, fig. 1), similar to the lower Pliocene Assemblage III specimens illustrated by Ceulemans *et al.* (2018, pl. 9, figs 1, 2) from Le Pigeon Blanc, whilst others are more fusiform (Pl. 76, fig. 2) resembling *Leucotina merignacensis* (Cossmann & Peyrot, 1917) described from the Atlantic lower Miocene Burdigalian of the Aquitaine Basin, France. However the two specimens figured here are extreme forms and intermediates occur. The group is today present along the coast of West Africa by three species *Leucotina puncturata* (Smith, 1872), *L. elongata* (Van Aartsen, Gittenberger & Goud, 1998) and *L. lilyae* (Van Aartsen, Gittenberger & Goud, 1998), differing from each other in details of profile and sculpture

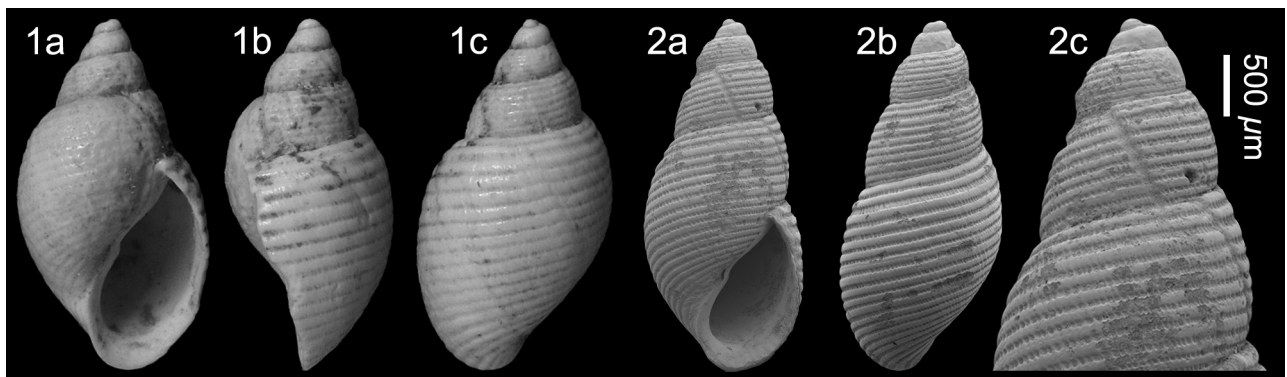


Plate 76. *Leucotina ivolasi* (Mayer-Eymar, 1900); 1. NHMW 2016/0103/1117, height 5.2 mm, width 2.4 mm (digital image); 2. NHMW 2016/0103/1118, height 5.8 mm, width 2.8 mm, 2c detail of teleoconch sculpture (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(see also Peñas *et al.*, 2014, fig. 33). However, if we consider the variability seen in the fossil specimens (Pl. 76, figs 1-2), originating from a single locality, we wonder if they might represent a single highly variable species. For further discussion see Ceulemans *et al.* (2018, p. 139). In Assemblage I *Leucotina ivolasi* has been found at St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Ivolas & Peyrot, 1900; de Morgan, 1915; Glibert, 1949a). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2018).

Discussion

In this paper we record 78 pyramidellid species (of which 15 are left in open nomenclature) representing 30 genera, 27 of those species are new: *Auristomia insulsa* nov. sp., *Megastomia pseudopolysarcula* nov. sp., *Menestho bertieae* nov. sp., *Odostomia fortistriata* nov. sp., *Odostomia robustissima* nov. sp., *Pseudoscilla breitenbergeri* nov. sp., *Ividella tuberculata* nov. sp., *Parthenina brebionii* nov. sp., *Parthenina chauvereauensis* nov. sp., *Parthenina clementiensis* nov. sp., *Parthenina lamellata* nov. sp., *Parthenina ligeriana* nov. sp., *Parthenina milleti* nov. sp., *Parthenina pouweri* nov. sp., *Parthenina redoniana* nov. sp., *Parthenina sceauxensis* nov. sp., *Parthenina tenuicostata* nov. sp., *Parthenina wesselinghi* nov. sp., *Pyrgulina cancellatissima* nov. sp., *Pyrgulina presselierensis* nov. sp., *Spiralinella pagoda* nov. sp., *Careliopsis gallica* nov. sp., *Chemnitzia miogallica* nov. sp., *Chemnitzia robusticostata* nov. sp., *Eulimella redoniana* nov. sp. *Eulimella semilaeve* nov. sp., and *Clathrella semilaeve* nov. sp.

Of the 78 pyramidellid species recorded here, 41 (52%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. This endemism is possibly falsely elevated by the number of species left in open nomenclature (15), which are considered to occur only in these assemblages. If we include the lower and middle Miocene, 54 (69%) are restricted to western France. Stratigraphically (see Fig. 1), 19 (24%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1952a). Twelve (15%) are also present in the Assemblage III (sensu Van Dingenen *et al.*, 2015) of northwestern France. Nine (possibly 10) are also found in the North Sea Basin Pliocene. Twenty-four (30%) are relatively cosmopolitan in the Miocene and/or Pliocene, found in the Atlantic and Mediterranean and 18 (23%) are still living in European Atlantic and/or Mediterranean waters. Endemism rates amongst poorly known groups, such as the pyramidellids, should be interpreted with caution, but the percentage found herein for the pyramidellids is not unlike that reported for other groups in these Assemblage I faunas [Part 1 (Patellogastropoda and Vetigastropoda) and Part 2 (Caenogastropoda) 63% (Landau *et al.*, 2017, 2018); Part 3 (Muricidae) 33% (Landau *et al.*,

2019a); Part 4 Neogastropoda 66% (Landau *et al.*, 2019b); Part 5 (Conoidea) 90 % (Landau *et al.*, 2020)].

This is an enormous increase in diversity compared to the ten species recorded by Brébion (1964). Of the ten Assemblage I species discussed by that author, all except one have been found. One specimen of *Euparthenia elegans* (Dollfus & Dautzenberg, 1886) was recorded from St-Michel by Brébion (1964, p. 284), and we have been unable to confirm this report. It therefore seems extremely uncommon in the upper Miocene, and is more abundant in the lower Pliocene Assemblage III deposits (Ceulemans *et al.*, 2018, p. 129). Brébion (1964, p. 293) also recorded without illustrating *Turbonilla elegantissima* var. *gastaldii* Semper, 1861 from numerous Assemblage I-IV deposits. This record no doubt refers to one or several of the members of the genus *Chemnitzia* discussed herein and in Ceulemans *et al.* (2018). As it was not figured this record is excluded.

Cossmann (1921) erected *Eulimella* (*Ptycheulimella*) *sacconi* for an incomplete specimen missing its apex from the “Redonien de la Loire-Inférieure” (Cossmann, 1921, p. 303, pl. 6, figs 97-98), without specifying the locality. He also did not give a description of the species, but incorporated the description into that of the subgenus *Ptycheulimella* Sacco, 1892. As the description is generic and the figure is very small, it is difficult to characterise this species. In any case, we have not found anything in Assemblage I that we would place in *Ptycheulimella*.

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

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For references see page 351

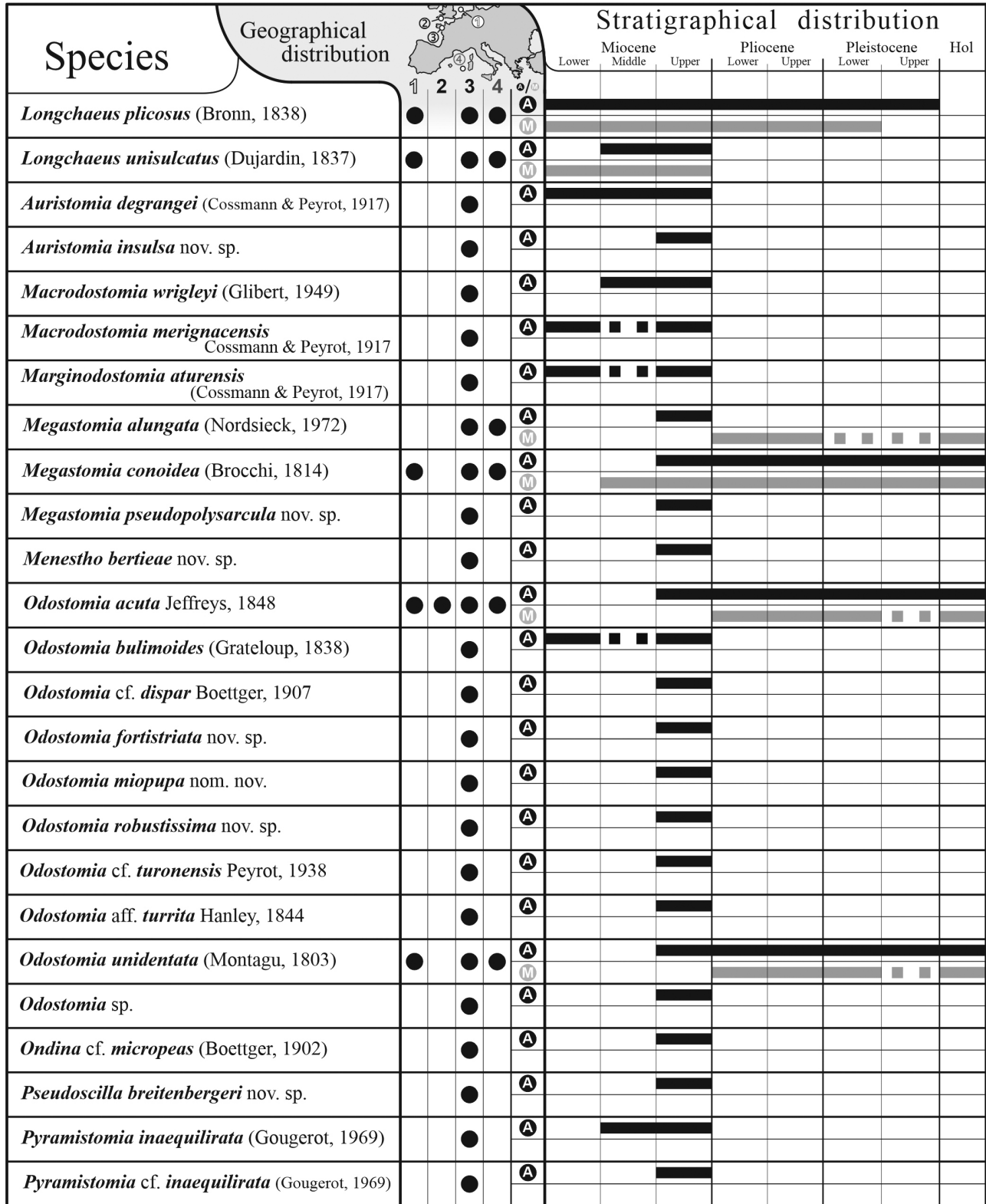


Figure 1. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black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

| Species | Geographical distribution | | | | | Stratigraphical distribution | | | | | | | | |
|---|---------------------------|---|---|---|-----|------------------------------|----------------|---------------|----------------|----------------|-------------------|-------------------|-----|---|
| | 1 | 2 | 3 | 4 | o/d | Miocene Lower | Miocene Middle | Miocene Upper | Pliocene Lower | Pliocene Upper | Pleistocene Lower | Pleistocene Upper | Hol | |
| <i>Tragula fenestrata</i> (Jeffreys, 1848) | | | ● | ● | A | | | | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Nisosyrnola concava</i> (Boettger, 1907) | | | ● | ● | A | | | ■ | | | | | | |
| <i>Syrnola turoniensis</i> (Glibert, 1949) | | | ● | | A | | | ■ | | | | | | |
| <i>Careliopsis gallica</i> nov. sp. | | | ● | | A | | | ■ | | | | | | |
| <i>Chemnitzia costellata</i> (Grateloup, 1828) | | | ● | | A | ■ | ■ | ■ | | | | | | |
| <i>Chemnitzia lactea</i> (Linnaeus, 1758) | ● | ● | ● | | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Chemnitzia miogallica</i> nov. sp. | | | ● | | A | | | ■ | | | | | | |
| <i>Chemnitzia</i> cf. <i>pseudoterebralis</i> (Sacco, 1892) | | | ● | | A | | | ■ | | | | | | |
| <i>Mormula catherinae</i> (Glibert, 1949) | | | ● | ● | A | | | ■ | | ■ | | | | |
| <i>Pyrgisculus jeffreysii</i> (Jeffreys, 1848) | | | ● | ● | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Pyrgiscus rufus</i> (Philippi, 1836) | ● | ● | ● | | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Pyrgolidium internodulum</i> (Wood, 1848) | ● | ● | ● | | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Pyrgostylus lanceae</i> (Libassi, 1859) | | | ● | ● | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ' <i>Strioturbonilla</i> ' <i>miocrassulata</i> (Sacco, 1892) | | | ● | | A | | | ■ | | | | | | |
| <i>Sulcoturbonilla costellata</i> (Dujardin, 1837) | | | ● | ● | A | | | ■ | | | | | | |
| <i>Bacteridium</i> sp. | | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella</i> cf. <i>perspicua</i> (Cossmann & Peyrot, 1917) | | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella</i> cf. <i>pseudoanisocycloides</i> Sacco, 1892 | | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella redoniana</i> nov. sp. | | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella</i> cf. <i>roeri</i> (Pavia, 1976) | | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella semilaeve</i> nov. sp. | ? | | ● | | A | | | ■ | | | | | | |
| <i>Eulimella ventricosa</i> (Forbes, 1844) | | | ● | ● | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Clathrella clathrata</i> (Philippi 1844) | | | ● | ● | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Clathrella semilaeve</i> nov. sp. | | | ● | | A | | | ■ | | | | | | |
| <i>Leucotina ivolasi</i> (Mayer-Eymar, 1900) | | | ● | | A | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |

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