

The upper Miocene gastropods of northwestern France, 1. Patellogastropoda and Vetigastropoda

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Seventy-six species are recorded of which 26 are new to science: *Diodora sancticlementensis* nov. sp., *Sinezona geigeri* nov. sp., *Anatoma redoniana* nov. sp., *Clanculus (Clanculus) brebioni* nov. sp., *Clanculus (Clanculopsis) sancticlementensis* nov. sp., *Clanculus (Clanculopsis) umbilicovadus* nov. sp., *Jujubinus coronatus* nov. sp., *Jujubinus redoniensis* nov. sp., *Jujubinus sceauxensis* nov. sp., *Gibbula brebioni* nov. sp., *Gibbula clanculiforma* nov. sp., *Gibbula conicomagus* nov. sp., *Gibbula marianae* nov. sp., *Phorcus gallicophorcus* nov. sp., *Calliostoma gibbuliforme* nov. sp., *Calliostoma lamellatum* nov. sp., *Calliostoma michaeli* nov. sp., *Calliostoma microgemmatum* nov. sp., *Calliostoma quaggoides* nov. sp., *Calliostoma presselierenense* nov. sp., *Calliostoma spinosum* nov. sp., *Calliostoma verrucosum* nov. sp., *Thysanodonta chauvereauiensis* nov. sp., *Pareuchelus dautzenbergi* nov. sp., *Dikoleps insula* nov. sp., *Lodderena redferni* nov. sp., *Parviturbo rubioi* nov. sp., *Pseudorbis beugnonensis* nov. sp., *Skenea minutocostata* nov. sp. and *Skenea wareni* nov. sp.

We highlight the first description of a member of the subfamily Thysanodontinae in the Europe faunas. Six are homonyms and receive replacement names: *Trochus heliciformis* Millet, 1865 is a junior homonym of *T. heliciformis* von Zieten, 1832, and is renamed *Calliostoma biangulatum* nov. nom. *Trochus millegranus* Millet, 1864, is a junior homonym of *T. millegranus* Philippi, 1836, and is renamed *Calliostoma milletigranum* nov. nom. *Trochus torulosus* Millet, 1865 is a junior homonym of *T. torulosus* Philippi, 1845, and is renamed *Calliostoma miotorulosum* nov. nom. *Trochus tumidus* Millet, 1865 is a junior homonym of *T. tumidus* Montagu, 1803, and is renamed *Calliostoma miotumidum* nov. nom. *Trochus echinatus* Millet, 1865 is placed in the genus *Calliostoma*, rendering *C. echinatum* Dall, 1881 a secondary homonym, which is renamed *C. caribbechinatum* nov. nom.

The following are new subjective synonyms: *Emarginula dujardini* Dollfus & Dautzenberg, 1886 is considered a junior subjective synonym of *Emarginula imbricata* Millet, 1865. *Gibbula (Colliculus) sosensis* Cossmann & Peyrot, 1917 is considered a junior subjective synonym of *Trochus insignis* Millet, 1854, *Monodonta (Oxysteles) amedei turoniensis* Glibert, 1949 is considered a junior subjective synonym of *Pitonellus trochiformis* Millet, 1865.

This is the most speciose European Neogene Vetigastropod assemblage known, with 31 different genera/subgenera represented. The fauna is highly endemic, with 63% of the species known only from the northwestern French Assemblage I localities. The generic composition is similar to that seen at these latitudes today; a few genera are extinct, such as *Lucapinella*, *Paroxysteles* and *Pareuchelus*. Few thermophilic elements are present. The composition of the assemblage represents a hard-bottomed littoral fauna.

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

Introduction

The rich fossil gastropod assemblages of northwestern France have been the object of study by our group for several years. To date only the lower Pliocene Assemblage III fauna (of Van Dingenen *et al.*, 2015) has been studied in part, and a systematic account of their content given by Van Dingenen *et al.* (2015; Nassariidae), Van Dingenen *et al.* (2016; Caenogastropoda), Ceulemans *et al.* (2016a; Patellogastropoda and Vetigastropoda), Ceulemans *et al.* (2016b; Muricidae) and Van Dingenen *et al.* (2017; Neo-

gastropoda, in part). Our aim is to mirror these papers with revisions of the equivalent taxonomic groups in the upper Miocene Tortonian Assemblage I deposits. In this paper we cover the same groups as those covered by Ceulemans *et al.* (2016a), the Patellogastropoda and Vetigastropoda. In order to avoid repetition of generic and species synonymies and discussions, we frequently refer back to that paper, which should be used in conjunction. It is with some trepidation that we commence the systematic taxonomic revision of the gastropods in what was previously known as the 'Redonien inférieur' (Bré-

bion, 1964) or ‘Redonien chaud’ (Lauriat-Rage, 1981), as this is the fourth attempt to do so (Landau *et al.*, 2016). Millet (1854, 1865) erected many new species described from material from northwestern France. He prepared four lithographed plates meant to accompany his ‘*Paléontologie de Maine-et-Loire*’ (Millet, 1854). However, these plates were never published, as he decided to prepare plates with photographed specimens. Millet’s plates were found by chance by Couffon (1909) and have subsequently been lost. Couffon (1915) was the next to attempt the task. He wrote ‘*Nous avons d’ailleurs entrepris une Iconographie du Miocène supérieur, en Anjou, qui ne comprendra moins de 40 planches, in 4°; les maquettes des première 25 planches sont déjà prêtes pour la phototypie et les événements actuels ont seuls empêché leur apparition*’. These ‘current events’ most likely refer to World War I, and this work was never completed. The third effort was that of Brébion (1964), who prepared his thesis on the ‘Redonian’ gastropods, describing and erecting many new species. Until now, this was the only work illustrating the fauna and has become the ‘bible’ of the ‘Redonian’. Unfortunately, Brébion never published his thesis and therefore all the taxa erected are *nomina nuda*. This is, therefore, the fourth attempt to produce an illustrated systematic account of the gastropods.

Geological setting

The localities studied herein of La Presselière (Sceaux-d’Anjou), Le Grand Chauvèreau (Saint-Clément-de-la-Place), Renauleau and Beugnon (Doué-en-Anjou) (Text-fig. 1) were included in the ‘Redonien’ of Brébion (1964) and are localities in the ‘Redonien chaud’ of Lauriat-Rage (1981) in the Maine-et-Loire department. The numerous problems surrounding the term ‘Redonien’ were highlighted by Van Dingenen *et al.* (2015), who concluded that it was best to restrict the term to the ‘Redonien Stratotypique’ of Néraudeau *et al.* (2003). Van Dingenen *et al.* (2015) recognised four major fossil assemblages in the post mid-Miocene of northwestern France, characterised by distinct gastropod faunas and designated them as Assemblages I – IV. Van Dingenen *et al.* (2015) correlated the stratigraphic sequences these assemblages occurred in with the upper Miocene to lower Pleistocene formations of Cornwall and East Anglia in England, and Belgium (2015, p. 78, fig. 2). The localities studied here are the Assemblage I localities of Van Dingenen *et al.* (2015).

Le Grand Chauvèreau (Saint-Clément-de-la-Place, Maine-et-Loire)

A deposit occurring along a 3 km wide irregular area, composed of ‘Redonian’ sands, marls and clays, ranging from La Poissardière in the NW to La Bellangerie in the SE. Most of it overlies the ‘Orthogneiss de Saint-Clément-de-la-Place’, a deposit outcropping along a 10 km long area oriented WNW-ESE. The most southern part overlies the ‘Granite de Bécon et de Saint-Lam-

bert-la-Potherie’, outcropping along a 9 km long and 2 km area E-W oriented. This granite intrudes the orthogneissic basement of Saint-Clément-de-la-Place. Multiple NNE-SSW oriented microgranite veins, up to 10 m in thickness, cut through both these geological units. At Le Grand Chauvèreau the ‘Chauvèreau-Naizance’ vein, in the form of solid rock and individual boulders, is exposed in a limited area on the shore of the pond, indirectly defining the pond contours. We can assume that this microgranite vein was part of the local Tortonian palaeogeography (Cavet *et al.*, 1976; Janjou *et al.*, 1998; and second author’s personal observations).

In this ‘Redonian’ deposit, several wide fossiliferous lenses are present, of which Le Grand Chauvèreau is the best known, consisting of fine sands and clayey sands with small to medium-sized pebbles. The fossiliferous layer occurs 3–4 m below the surface (depending on the location), approximately 1 m thick. Within this fossiliferous lense a 20–30 cm whitish homogeneous highly fossiliferous sandy layer occurs. Mollusc fossils are accompanied by enormous numbers of bryozoans, scattered corals and fish teeth. The molluscs at St-Clément-de-la-Place are the most diverse and best preserved. We therefore consider this the ‘type’ locality for Assemblage I. The gastropod fossils are almost all small in size, with very few shells attaining more than 20 mm in height. In contrast, the bivalve fossils show a much greater size range, with some relatively large specimens found with articulated valves, suggesting a low degree of post-mortem transport. Of note at St-Clément-de-la-Place is the assemblage of Polyplacophora (chitons), which is probably the most abundant and diverse in the European Neogene and will be described in a separate paper (Dell’Angelo *et al.* in prep.).

La Presselière (Sceaux-d’Anjou, Maine-et-Loire)

The famous 100 m wide fossiliferous outcrop is surrounded by colluvions and alluvial deposits, in the NW by Plio-Quaternary silt and residual (or reworked ?) sandy gravel formations (Brossé *et al.*, 1989).

The deposit consists of fine sands with small to medium-sized pebbles. The fossiliferous layer occurs 1–1.5 m below the surface, at some places showing a layer of clay. The section continues down for 1.5 m containing fossils which are frequently agglutinated to irregular sandy concretions, increasing in size towards the base. The assemblage is similar to that of St-Clément-de-la-Place, with small gastropod shells strongly predominant, but the fossils are somewhat worn, suggesting some degree of post-mortem transport.

Renauleau (Doué-en-Anjou, Maine-et-Loire)

The limited exposure at Renauleau and Beugnon (900 x 500 m) is located north of the village Brigné-sur-Layon. The site of Renauleau is located 60 m NE of the ‘Fontaine de Renauleau’. At this locality the Tortonian overlies the middle Cenomanian, represented by black clays. A pos-

sible source for the older Cretaceous reworked fossil brachiopods, oysters and rare shark teeth found mixed with the Miocene fossils is the upper Cenomanian 'Marnes à Ostracées', which occurs 250 m NE of the site (Blaise *et al.*, 1986).

The Tortonian deposits consist of fine sands and clayey sands, with numerous small to medium-sized pebbles and clay nodules. The fossiliferous layer occurs 6.5 m below the surface, approximately 3 m thick and covered by a 30-40 cm sandstone layer, gently dipping towards the south. In the upper part of this lense, white-bluish pockets with higher shell concentrations occur. At this deposit more fragments of larger shells such as muricids and coniids may be found, but invariably fragmented and showing signs of transport. In contrast large articulated bivalves occur in living position between 1.5 and 2 m below the sandstone. As with Sceaux-d'Anjou, the shells are usually somewhat worn.

Beugnon (Doué-en-Anjou, Maine-et-Loire)

The southern section of the Beugnon-Renauleau deposit overlies the 'Complexe de Saint-Georges-sur-Loire' (schist-sandstone and volcanic Upper Ordovician to Lower Devonian).

Named after the 'Fontaine du Beugnon' located 250 m SSW of the outcrop, the abandoned Beugnon quarry exposes at least 4 m of brownish consolidated calcareous beds, alternating with fine white sandy layers (Blaise *et*

al., 1986).

The gastropod assemblage in these sandy beds is similar to that of Renauleau, although some species are found in only one or other of the localities.

Rectifications/clarifications regarding the Beugnon-Renauleau area

1. Brébion used in his unpublished thesis the misspelled locality name 'Renauleau' instead of Renauleau. The spelling was probably adopted following Millet (1854), who also used the spelling 'Renauleau'. This spelling error has long been overlooked, although it might have been intentional. Consulting historical maps we have found that the map of Cassini, the first general map of the French territory, published from 1756 to 1815, uses the spelling 'Renauleau'. The 'Carte de l'état major', produced between 1817 and 1866 on the orders of Napoleon I, is the first using the modern spelling Renauleau. All subsequent maps and administrative entries to date retain this later spelling.

2. The first author has found during his work in the Naturalis collection, labels that indicate the location 'Brigneau'. Fortunately GPS coordinates were known. After these were plotted, it turned out that they correspond exactly to the site of Beugnon, named after the nearest landmark, the 'Fontaine du Beugnon'. The most plausible answer is that researchers who were unaware

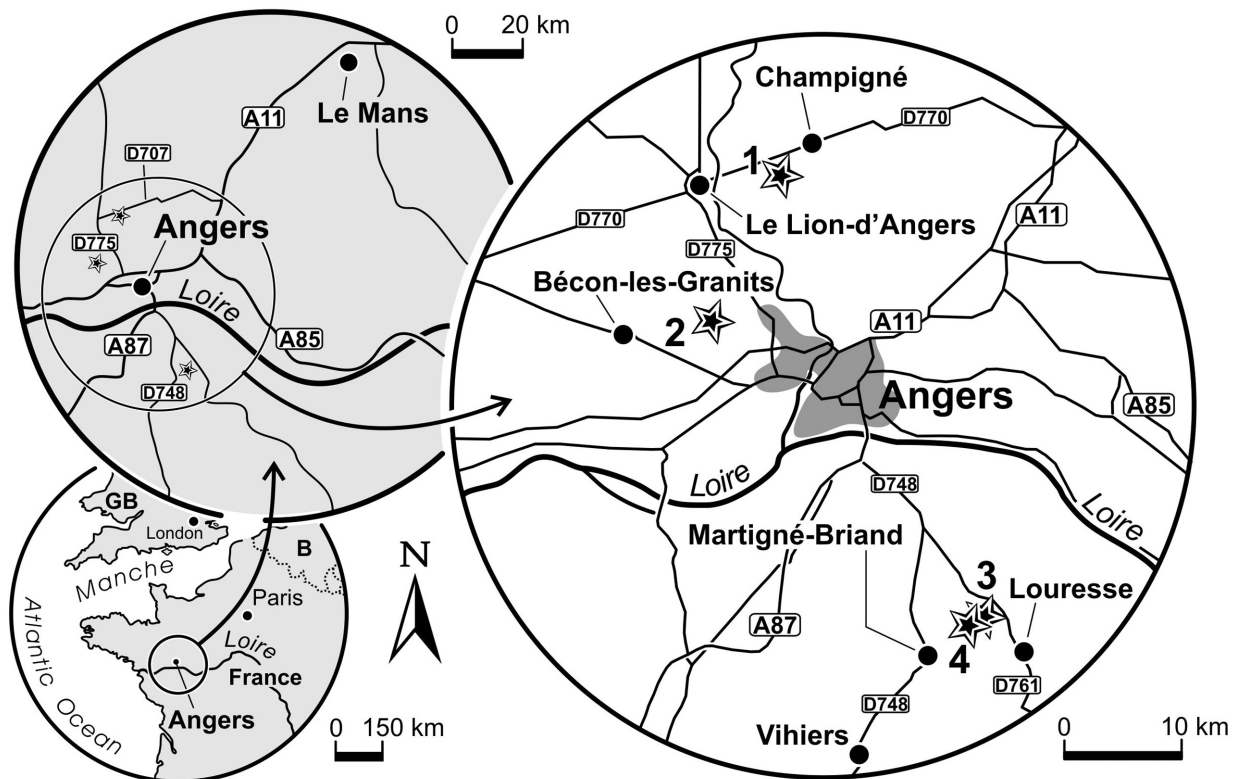


Figure 1. Geographic location of the localities sampled. 1. La Presselière, Sceaux-d'Anjou; 2. Le Grand Chauvère, St-Clément-de-la-Place; 3. Renauleau; 4. Beugnon, Maine-et-Loire, France.

of the fontaine, named the quarry after the nearest landmark known to them: Brigneau, a small suburb north of the village of Brigné-sur-Layon. To avoid confusion, we continue to use Beugnon.

3. The former commune of Brigné-sur-Layon was merged this year into the newly formed commune Doué-en-Anjou. In order to follow the current municipal administration we will from now on only refer to Doué-en-Anjou.

Other Assemblage I localities are:

- Thorigné-d'Anjou (Maine-et-Loire),
- Contigné (Maine-et-Loire),
- Les Pierres Blanches and St. Anne (Chalonnnes-sur-Loire, Maine-et-Loire),
- Saint-Michel-et-Chanveaux (Maine-et-Loire),
- Beaulieu (Mayenne) (Brébion, 1964, p. 15).

Material and methods

Large collections of northwestern French material are present in the Naturalis Biodiversity Center in Leiden (The Netherlands), the accumulation of several important collections collected by A.W. Janssen (1987) and kindly donated by W. Groeneveld (2004), C. Deerenberg (2010), F.A.D. van Nieulande (2012), H.P.J. Keukelaar (2015) and P. Hessel (2015). These were consulted and the material catalogued herein. We note that the locality given in the RGM collections of Brigneau or Brigné are more correctly here called Beugnon. These historical collections were augmented by new collections accumulated by the authors.

It is intended that this series of monographs be used in conjunction with those published by the authors in Cainozoic Research (*i.e.* Ceulemans *et al.*, 2016a, b; Van Dingenen *et al.*, 2015, 2016, 2017) describing the stratigraphically younger Assemblage III fauna of northwestern France. Where the generic synonymy and species chresonymy were covered in the Assemblage III series, they are not repeated here. In the chresonymy we have included the works of Millet (1854, 1864, 1865), but in most cases have excluded the records given by Couffon (*i.e.* 1909, 1915), as these are species lists without descriptions or illustrations and are not possible to verify. In the Assemblage III series we used Brébion's specimens as holotypes wherever possible. This has not been followed in this Assemblage I series for practical reasons. Almost all the species are small to minute. In order to describe them adequately we have chosen the best specimen as holotype, often selected from numerous specimens and almost invariably better preserved than the specimens figured by Brébion (1964) in his unpublished thesis, in which the specimens were photographed, but no light or scanning microscopy was performed.

Type material was deposited in the Muséum national d'Histoire naturelle, Paris (collection de Paléontologie), the Naturhistorisches Museum Wien, Vienna, Aus-

tria and the Naturalis Biodiversity Center, Leiden, The Netherlands. Further material is present in the personal collections of Luc Ceulemans, Rixensart (Belgium) and Frank Van Dingenen, Brecht (Belgium).

Abbreviations:

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

Systematic palaeontology

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

- 1758 *Patella* Linnaeus, p. 780. Type species (by subsequent designation, Fleming, 1818): *Patella vulgata* Linnaeus, 1758, present-day, Europe.

For generic synonymy see Ceulemans *et al.* (2016a, p. 53).

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

***Patella protea* Doderlein, 1862**

Plate 1, figs 1-3.

- 1854 *Patella Alternata* Millet, p. 166 (*nomen nudum* and junior homonym of *P. alternata* Say, 1826).
- *1862 *Patella protea* Doderlein, p. 98.
- 1865 *Patella alternata* Millet, p. 599 (junior homonym of *P. alternata* Say, 1826).
- 1896b *Patella protea* Dod. – Sacco, p. 23, pl. 2, figs 87-88.
- 1964 *Patella protea* Doderlein, 1862 – Brébion, p. 66, pl. 1, figs 13, 14.

Material and dimensions – Maximum diameter 12.6

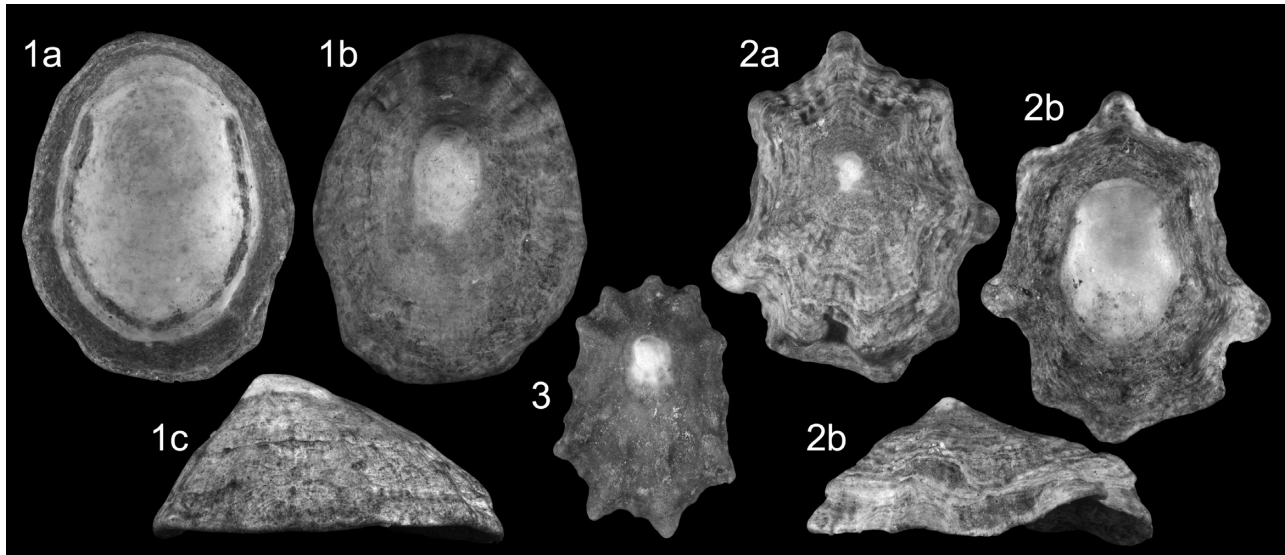


Plate 1. *Patella protea* Doderlein, 1862; 1. NHMW 2016/0103/0001, diameter 8.5 mm, height 4.1 mm. 2. NHMW 2016/0103/0002, diameter 7.0 mm, height 2.8 mm. 3. NHMW 2016/0103/0003, diameter 5.6 mm, height 1.9 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

mm; height 3.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0001-0003 (3), NHMW 2016/0103/0004 (50+), RGM.1309474 (50+), RGM.1309475 (6), RGM.1309493 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0645 (2), RGM.1348018 (1).

Discussion – Brébion (1964, pl. 1, figs 13, 14) illustrated a small patellid from Assemblage I localities (Sceaux-d'Anjou, St-Michel, Contigné) as *P. protea* Doderlein, 1862, which was originally described from the upper Miocene Tortonian of Italy and said to be common at Montegibbio. Numerous specimens at hand from the Assemblage I locality of St-Clément-de-la-Place resemble tiny specimens of *P. caerulea*, but differ in having an anterior primary rib placed at six o'clock, when the dorsum is viewed on its antero-posterior axis, posterior border placed at the top, whereas in *P. caerulea* the anterior ribs are placed at five o'clock and seven o'clock. They are also considerably smaller: according to Brébion 10-15 mm diameter vs. 20-50 mm diameter for present-day *P. caerulea*. The specimens at hand from St-Clément-de-la-Place are smaller, similar in size to specimens of *P. protea* from the type locality of Montegibbio (3-6.5 mm; Sacco, 1986, p. 23), with one exceptionally large specimen attaining 12.6 mm in maximum diameter.

Patella protea in the NW French Neogene is found in several Assemblage I localities. Millet (1854, p. 166; 1865, p. 599) recorded it from Sceaux-d'Anjou, Brébion (1964, p. 67) added St-Michel and Contigné, to which we add St-Clément-de-la-Place, the only locality in which it is abundant.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet; 1854, 1865; Brébion, 1964); Proto-Mediterranean, Italy (Doderlein, 1862; Sacco, 1896b).

Superfamily Lottioidea Gray, 1840

Family Lottiidae Gray, 1840

Genus *Tectura* Gray, 1847

- 1847b *Tectura* Gray, p. 158. Type species (by original designation): *Patella parva* da Costa, 1778 [= *Tectura virginea* (Müller, 1776)], present-day, British Isles.

***Tectura virginea* (Müller, 1776)**

Plate 2, figs 1-2.

- *1776 *Patella virginea* Müller, p. 43.
 1778 *Patella parva* da Costa, p. 7, pl. 8, fig. 11.
 1835 *Patella pulchella* Forbes, p. 591, fig. 61.
 1844 *Lottia unicolor* Forbes, p. 135.
 1848 *Tectura virginea* var. *conica* Jeffreys – Wood, p. 161, pl. 18, fig. 6c.
 1865 *Tectura virginea* var. *conica* Jeffreys, p. 249.
 1865 *Tectura virginea* var. *lactea* Jeffreys, p. 249.
 1896b *Tectura virginea* (Müll.) – Sacco, p. 19, pl. 2, figs 46-49.
 1896b *Tectura virginea* var. *parvoligustica* Sacco, p. 20, pl. 2, figs 50-52.
 1925 *Acmaea virginea* (Müller) – Harmer, p. 875, pl. 65, fig. 31.
 1925 *Acmaea virginea* var. *conica* S.V. Wood [sic] – Harmer, p. 876, pl. 65, fig. 32.
 1949 *Patelloidea* (*Tectura*) cf. *virginea* Müller, 1776 – Glibert, p. 31, pl. 1, fig. 14.
 1964 *Acmaea* (*Tectura*) cf. *virginea* Müller, 1776 – Brébion, p. 69.
 2003 *Acmaea* (*Tectura*) *virginea* (O.F. Müller, 1776) – Landau *et al.*, p. 8, pl. 5, fig. 3 (*cum syn.*).
 2004 *Tectura virginea* (Müller O.F., 1776) – Chirli, p. 20, pl. 7, figs 4-11.

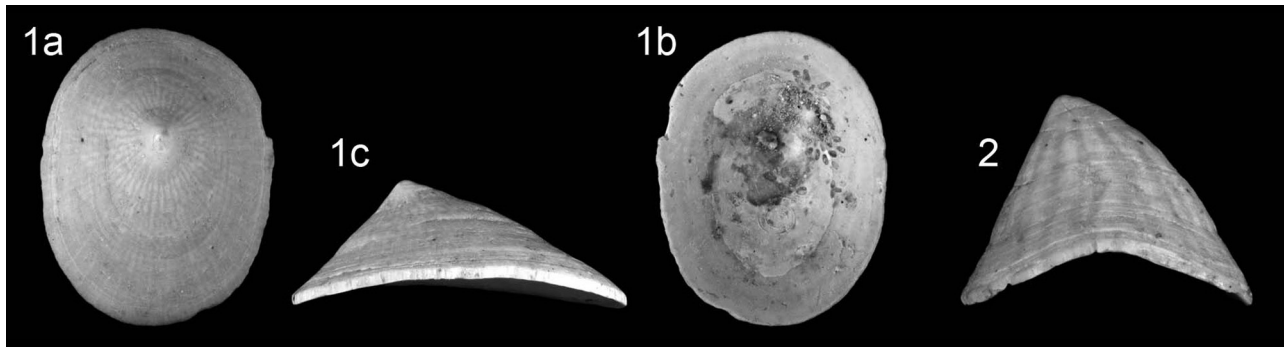


Plate 2. *Tectura virginea* (Müller, 1776); 1. NHMW 2016/0103/0005, diameter 7.5 mm, height 2.8 mm. 2. NHMW 2016/0103/0006, diameter 7.0 mm, height 2.8 mm. Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Material and dimensions – Maximum diameter 7.6 mm; height 3.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0005-0006 (2), NHMW 2016/0103/0007 (50+), RGM.1309477 (10), RGM.1309494 (50+), RGM.1309565 (15), RGM.1348012 (50+), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0009 (10), RGM.1309476 (10), RGM.1309502 (25), RGM.1309521 (7), RGM.1347948 (14), RGM.1348022 (11), LC (12), FVD (3). **Renauleau:** NHMW 2016/0103/0008 (16), LC (8), FVD (5). **Beugnon:** RGM.1309566 (1), LC (1).

Discussion – In the French Assemblage I localities *Tectura virginea* (Müller, 1776) is highly variable in height, with almost flat (Pl. 2, fig 1) and high arched (Pl. 2, fig. 2) specimens found together at St-Clément-de-la-Place, where this species is extremely abundant. Many shells retain their original colour pattern, similar to that seen in present-day specimens (see Fretter & Graham, 1976, p. 20, fig. 15), although their maximum diameter does not reach that recorded from the extant populations (10 mm; Fretter & Graham, 1976; Poppe & Goto, 1991). The smaller dimensions of the Assemblage I specimens compared to conspecific populations found in other strata is a recurrent theme we will encounter in this series.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, Coralline Crag, England (Harmer, 1925); central Mediterranean, Italy (Chirli, 2004), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Red Crag, England (S.V. Wood, 1848; Harmer, 1925), Mondego Basin, Portugal (Silva, 2001); western Mediterranean, Estepona Basin, S. Spain (Landau *et al.*, 2003); central Mediterranean, Italy (Sacco, 1896b). Pleistocene: Atlantic, England (Harmer, 1925); western Mediterranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1916; Ruggieri & Greco, 1965; Taviani *et al.*, 1998). Present-day: Atlantic, northern Scandinavia to Cape Verde Islands, 0-100m depth attached to hard substrates (Poppe & Goto, 1991), Mediterranean (Giannuzzi-Savelli *et al.*, 1994).

Subclass Vetigastropoda

Superfamily Fissurelloidea Fleming, 1822

Family Fissurellidae Fleming, 1822

Subfamily Emarginulinae Children, 1834

Tribe Diodorini Odhner, 1932

Genus *Diodora* Gray, 1821

- 1821 *Diodora* Gray, p. 233. Type species (by monotypy):
Patella apertura Montagu, 1803, present-day, British Isles.

For generic synonymy see Ceulemans *et al.* (2016a, p. 54).

Diodora graeca (Linnaeus, 1758)

Plate 3, figs 1-4

- *1758 *Patella graeca* Linnaeus, p. 784.
1854 *Fissurella Exorata* Millet, p. 166 (*nomen nudum*).
1854 *Fissurella Labiatoides* Millet, p. 166 (*nomen nudum*).
1864 *Fissurella labiatoides* Millet, p. 680, footnote 2.
1865 *Fissurella exorata* Millet, p. 598.
1964 *Diodora italica* Defrance, 1820 – Brébion, p. 62 [non *D. italica* (Defrance, 1820)].
1964 *Diodora apertura* Montagu, 1803 – Brébion, p. 63, pl. 1, fig. 2.
2016a *Diodora graeca* (Linné, 1758) – Ceulemans *et al.*, p. 54, pl. 1, figs 4, 5 (*cum syn.*).

Material and dimensions – Maximum diameter 28.5 mm; height 9.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0077-0078 (2), NHMW 2016/0103/0079 (5), RGM.1309481 (50+ juveniles), RGM.1309482 (12 subadult and juveniles), RGM.1309487 (5 adult and juveniles), RGM.1309492 (2), RGM.1309495 (8 subadult and juveniles), RGM.1309780 (7), RGM.1309781 (50+ subadult and juveniles), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0080 (9), RGM.1309478 (1 large adult), RGM.1309479 (20), RGM.1309480 (4), RGM.1309483 (50+ subadult and juveniles), RGM.1309484 (10 subadult and juveniles), RGM.1309485 (38), RGM.1309488 (1), RGM.1309491 (12), RGM.1309501 (35 subadult and

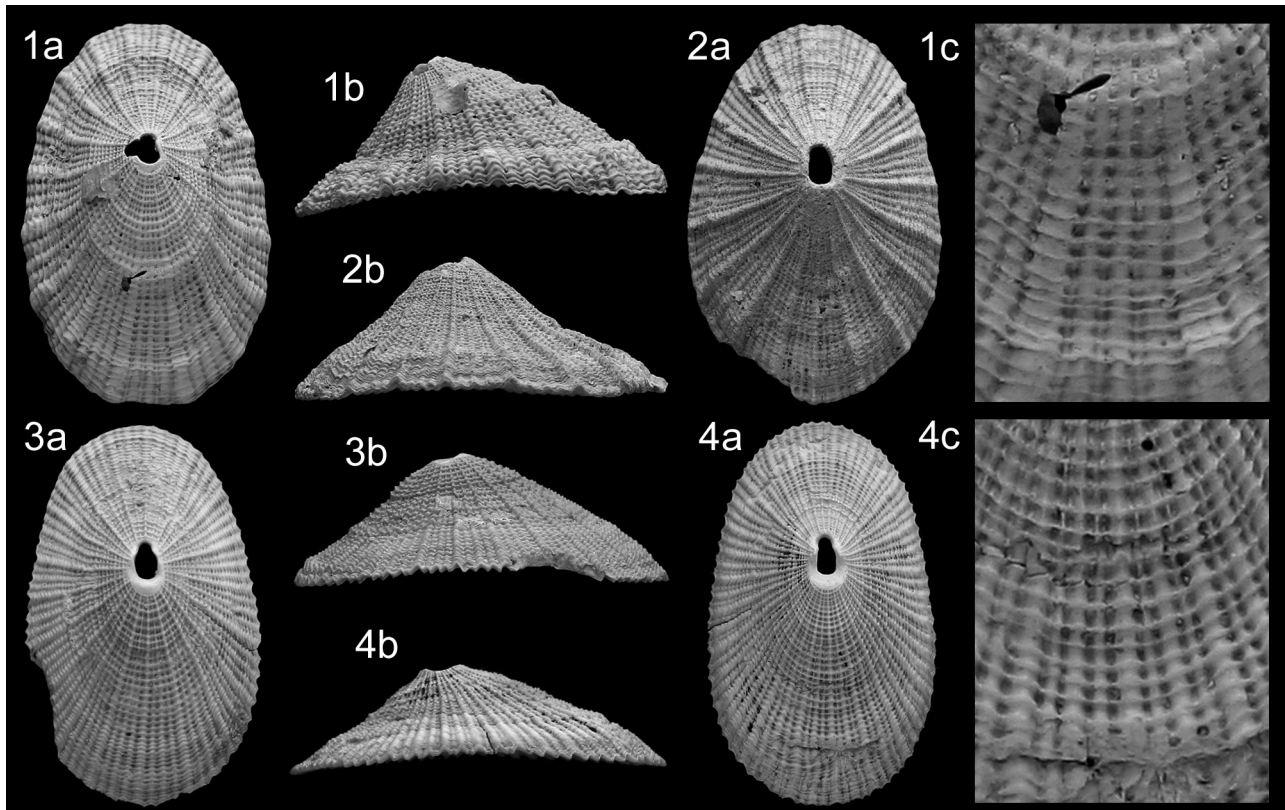


Plate 3. *Diodora graeca* (Linnaeus, 1758); 1. NHMW 2016/0103/0077, diameter 23.4 mm, height 9.0 mm; 2. NHMW 2016/0103/0078, diameter 24.1 mm, height 8.5 mm; 3. NHMW 2016/0103/0081, diameter 23.2 mm, height 8.0 mm; 4. NHMW 2016/0103/0081, diameter 26.1 mm, height 7.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

juveniles), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1438 (11), LC (50+), FVD (40). **Beugnon:** RGM.1309486 (25 subadult and juveniles), RGM.1309489 (7 subadult and juveniles), RGM.1309490 (22), RGM.1309495 (11), RGM.1309496 (5), LC (5), FVD (2).

Discussion – In the Assemblage I localities we encounter the same problem with *Diodora graeca* (Linnaeus, 1758) outlined by Ceulemans *et al.* (2016a, p. 55). Some specimens have more regular sculpture (Pl. 3, fig. 4) and had been described in the literature as *Diodora apertura* (Montagu, 1803), although intermediate specimens are also present (Pl. 3, fig. 3). We therefore continue to consider them as extreme forms of a single species. For discussion see Landau *et al.* (2003) and Ceulemans *et al.* (2016a, p. 55).

Brébion (1964, p. 65) reported this species (as *D. apertura*) in localities representing Assemblages II (Apigné, Le Temple du Cerisier, St-Jacques, Carcé), III (Le Pigeon Blanc, Le Girondor, La Gauvinière, Palluau, La Dixmérie) and IV (St-Jean-la-Poterie, Gourbesville). This is probably also the species recorded, but not illustrated, by Brébion (1964, p. 62) as *D. italica* (Defrance, 1820). Whilst the shell shape and relative smoothness of the sculpture are reminiscent of this species, the close-up of the sculpture (Pl. 3, fig. 4c) shows it to be that of *D. graeca*: strong primary cords with one medium-strength

secondary cord intercalated and one tertiary cord in each of the interspaces, as opposed to the alternating primary and secondary cords seen in *D. italica*. We therefore add the Assemblage I localities given by Millet (1854, 1864, 1965) and Brébion (1964) for this species (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place).

Distribution – Middle Miocene: Paratethys, Badenian, Poland (Bafuk, 1975); Hungary (Strausz, 1966). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1864; Brébion, 1964); Tethys, Tortonian: Po valley, Italy (Sacco, 1896b). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016a); Coralline Crag, England (Harmer, 1923), Luchtbal Formation, Belgium (Marquet & Landau, 2006); central Mediterranean, Italy (Chirli, 2004). Upper Pliocene: Red Crag, England (Harmer, 1923); western Mediterranean, Estepona, S. Spain (Landau *et al.*, 2003); France (Chirli & Richard, 2008); central Mediterranean, Italy (Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992). Pliocene (unspecified): central Mediterranean, Italy (Brambilla & Lualdi, 1988); Atlantic Morocco (Lecointre, 1952). Upper Pliocene-lower Pleistocene: Atlantic, NW France (Brébion, 1964); central Mediterranean, Italy (Cerullirelli, 1916; Malatesta, 1960). Pleistocene (unspecified): western Mediterranean, Balearic Islands, (Cuerda Bar-

celó, 1987); Atlantic, Morocco (Lecointre, 1952). Upper Pleistocene: England, Ireland (Harmer, 1923), The Netherlands (Wesselingh & Pouwer, 2011). Present-day: Atlantic British Isles to Canaries, Mediterranean and Black Sea, rocky shores under stones and rocks, especially where a little silt occurs, living near sponges, on which it feeds (Poppe & Goto, 1991).

***Diodora multifida* (Deshayes, 1830)**

Plate 4, fig. 1

- *1830 *Fissurella multifida* Deshayes, p. 136.
- 1830 *Fissurella mitis* Deshayes, p. 136.
- 1938 *Fissurella (Lucapina) mitis* Deshayes – Peyrot, p. 15, pl. 1, figs 10-12.
- 1849 *Diodora multifida* Deshayes, 1831 [*sic*] – Glibert, p. 28, pl. 1, fig. 12.
- 1964 *Diodora multifida* var. *mitis* Deshayes, 1832 [*sic*] – Brébion, p. 65.

Material and dimensions – Maximum diameter 17.9 mm; height 8.9 mm. **Sceaux-d’Anjou**: NHMW 2016/0103/0228 (1), NHMW 2016/0103/0229 (3), LC (8), FVD (8).

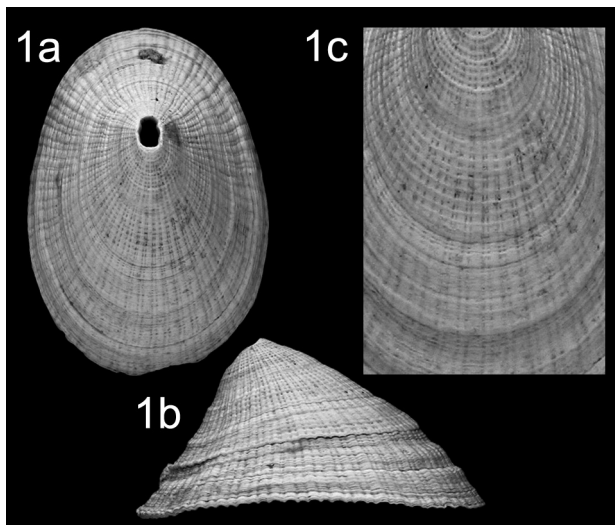


Plate 4. *Diodora multifida* (Deshayes, 1830); 1. NHMW 2016/0103/0228, diameter 17.9 mm, height 8.9 mm. La Presse-lière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – Both *Fissurella multifida* Deshayes, 1830 and *F. mitis* Deshayes, 1830 were described from middle or upper Miocene assemblages of northwestern France. We have scant material attributed to this species, so we accept Glibert’s (1949, p. 28) position in considering them extreme forms of a single species, the *mitis* form having finer sculpture in which the cords are all of roughly equal strength. A similar variability in sculpture occurs in many congeners (see *D. graeca* above). Having said that, material at hand from Sceaux-d’Anjou is all of the *mitis* variety. Apart from the finer sculpture, our specimens

also have a more convex anterior slope than the *multifida* form, also seen in Glibert’s figure (1949, pl. 1, fig. 12e).

Diodora multifida differs from *D. graeca* (Linnaeus, 1758) with which it co-occurs in being smaller shelled, in having a relatively more elevated dorsum and in having finer sculpture. *Diodora sancticlementensis* nov. sp., found so far only at St-Clément-de-la-Place where we have not found *D. multifida*, has a maximum size only one-third that of *D. multifida*, is more depressed, and has smooth axial ribs.

Brébion (1964, p. 66) only recorded this species from the upper Pliocene-Pleistocene Assemblage IV locality of Gourbesville. This is the first record in the Tortonian Assemblage I of northwestern France.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Diodora sancticlementensis* nov. sp.**

Plate 5, figs 1-4

Type material – Holotype MNHN.F.A57687, diameter 5.2 mm; height 2.0 mm; paratype 1 MNHN.F.A57688, diameter 6.9 mm; height 2.4 mm; paratype 2 NHMW 2016/0103/0083, diameter 5.8 mm; height 1.9 mm; paratype 3 NHMW 2016/0103/0084, diameter 6.4 mm; height 2.0 mm; paratype 4 RGM.1309498, height 1.9 mm, diameter 5.9 mm; paratype 5 RGM.1309499, height 1.6 mm, diameter 5.4 mm.

Other material – Maximum diameter 6.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0085 (50+), RGM.1309497 (50+), RGM.1309500 (25), RGM.1309523 (50+), LC (50+), FVD (50+).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Diodora* species of small size, low domed, sculptured by about 70 narrow, fine, smooth axial ribs of irregular strength, spiral sculpture inconspicuous.

Description – Shell small, patelliform, oval-elongated, relatively low, with apical aperture placed just posterior to mid length. Apical aperture ovate, thickened by callus on inner surface. Both shorter posterior and longer anterior slopes almost straight in profile. Sculpture of about 70 narrow axial ribs of irregular strength; in places of alternate strength, which are not interrupted by growth lines, resulting in almost smooth axial ribs.

Discussion – *Diodora sancticlementensis* nov. sp. is a

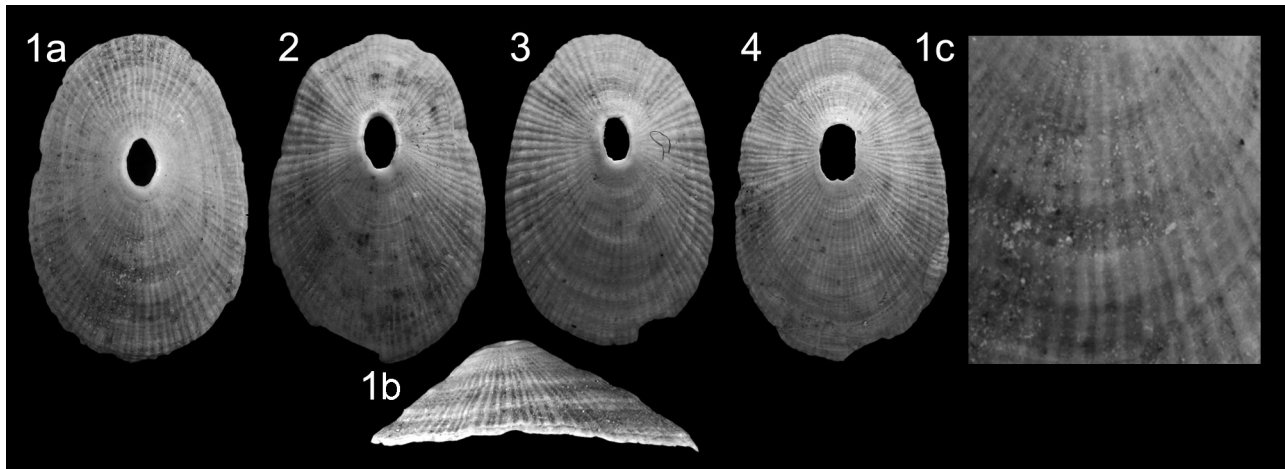


Plate 5. *Diodora sancticlementensis* nov. sp.; 1. **Holotype** MNHN.F.A57687, diameter 5.2 mm, height 2.0 mm; 2. **Paratype 1** MNHN.F.A57688, diameter 6.9 mm, height 2.4 mm; 3. **Paratype 2** NHMW 2016/0103/0083, diameter 5.8 mm, height 1.9 mm; 4. **Paratype 3** NHMW 2016/0103/0084, diameter 6.4 mm, height 2.0 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

distinctive species, characterised by its small size for the genus and sculpture of numerous, fine, smooth axial ribs. In some specimens the ribs are of alternate strength at the anterior and posterior margins and subequal on the lateral slopes (Pl. 5, fig. 3), but this feature is variable with some specimens having every 5th or 6th cord stronger (Pl. 5, fig. 2), or all cords subequal (Pl. 5, fig. 4). In most European *Diodora* species growth lines interrupt the axial ribs forming a cancellate or squamate surface sculpture. However, this is not the case in *Diodora sancticlementensis*, which has smooth ribs. We can find no other European fossil or present-day species with this type of sculpture. In this series covering the Assemblage I localities of northwestern France we are struck by the number of genera or species that have ‘dwarf’ forms in these deposits. *Diodora sancticlementensis* is a good example of this. At first it would seem that these shells represent juveniles. However, juvenile *Diodora* shells have an apical ‘beak’ on the dorsum at the anterior edge of the apical aperture, which disappears with maturity. Moreover, *D. sancticlementensis* is represented at St-Clément-de-la-Place by hundreds of individuals, none of which have a greater maximum diameter than 6.7 mm. This species is found only at the type locality.

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

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

- 1801 *Emarginula* Lamarck, p. 69. Type species (by monotypy): *Emarginula conica* Lamarck, 1801 [= *Emarginula fissura* (Linnaeus, 1758)], present-day, Europe.

For generic synonymy see Ceulemans *et al.* (2016a, p. 55).

Emarginula adriatica Costa, 1830

Plate 6, figs 1-2

- *1830 *Emarginula adriatica*, Costa, p. 11.
- 1854 *Emarginula Proclinata* Millet, p. 166 (*nomen nudum*).
- 1865 *Emarginula proclinata* Millet, p. 599.
- 1938 *Emarginula elongatoides* Peyrot, p. 18, pl. 1, figs 15, 16.
- 1949 *Emarginula clathrataeformis* Eichwald, 1830 – Glibert, p. 18, pl. 1, fig. 6 (?*non* Eichwald, 1830).
- 1964 *Emarginula clathrataeformis* Eichwald, 1830 – Brébion, p. 55 (?*non* Eichwald, 1830).
- 2003 *Emarginula adriatica* O.G. Costa, 1829 [*sic*] – Landau *et al.*, p. 19, pl. 3, figs 1-3 (*cum syn.*).

Material and dimensions – Maximum diameter 7.4 mm; height 3.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0095-0096 (2), NHMW 2016/0103/0097 (3), RGM.1309545 (2), RGM.1309612 (7), LC (6), FVD (7). **Sceaux-d’Anjou**: NHMW 2016/0103/0098 (18), RGM.1309607 (2), RGM.1309614 (5), RGM.1348015 (8), LC (2), FVD (15).

Discussion – *Emarginula adriatica* Costa, 1830 is variable in shape, with the apex more or less recurved and the axial sculpture stronger or equal in strength to the concentric ribs. Constant features are the oval-elongated shape and the papillae formed at the intersections of the sculpture. The nomenclature of this group is confused in the literature, making fossil records unreliable. Glibert (1949) illustrated shells we consider to be conspecific under the name *E. clathrataeformis* Eichwald, 1830. We are unsure if the Paratethyan shell is indeed conspecific, but the middle Miocene Loire Basin shells illustrated by Glibert are the same species as those figured here (Pl. 6, figs 1-2). Glibert described the characteristic tubercles formed at the sculptural intersections in his material:

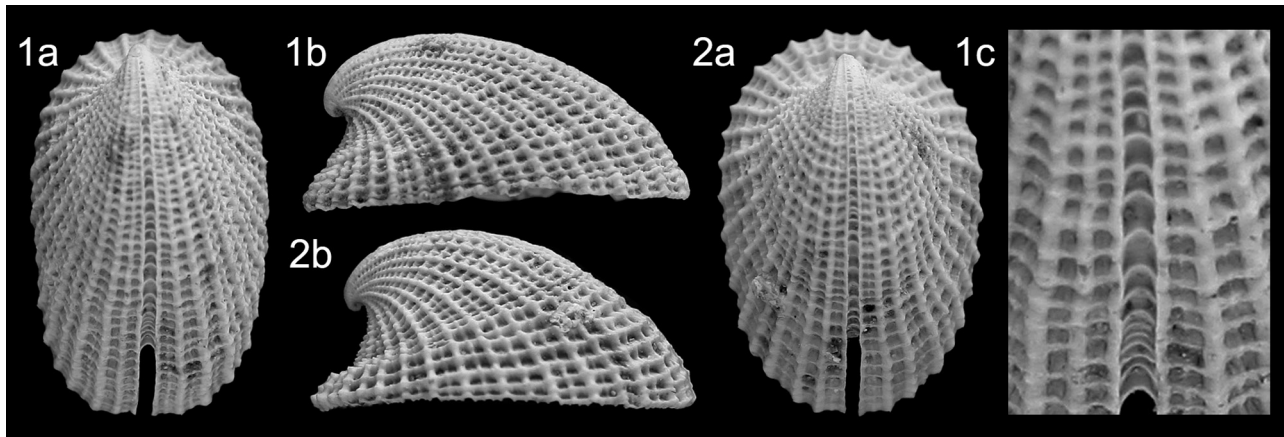


Plate 6. *Emarginula adriatica* Costa, 1830; 1. NHMW 2016/0103/0095, diameter 7.4 mm, height 3.2 mm; 2. NHMW 2016/0103/0096, diameter 7.4 mm, height 3.4 mm. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

'Les côtes principales sont également ornées d'une série de tubercules pointus rapprochés qui leur donnent une apparence dentelée' (1949, p. 19)'. We are unsure if the middle Miocene Paratethyan shell described by Eichwald (1830) is conspecific. If it were, *E. adriatica* might become a junior synonym of *E. clathrataeformis*, as Costa's work was not published before November 1830 and not 1829 as stated on the title page (Fasulo, 2013). The date of the front page of Eichwald's work is given as January 10th 1830, which means that the official version of the book was read by the censor in 1829. In the preface Eichwald dates his letter 23rd March 1830 and in the epilogue he refers to a paper published in May 1830, which he had just seen during the final phase of the book's preparation. Therefore a date before May/June 1830 is not possible, but we cannot get closer to a publication date. There is no further information on the library stamp of the copy at the NHMW (M. Harzhauser, personal communication June 2016).

Emarginula octaviana Coen, 1939, also found in the Assemblage I deposits, has a similarly elongated depressed shell with a strongly recurved apex and a reticulate sculpture, but in that species the lamellae on the selenizone, which are relatively coarser, are raised above the level of the reticulate sculpture.

Millet (1854) recorded this species from Assemblage I localities of Sceaux-d'Anjou and Thorigné, to which Brébion (1964, p. 55) added St-Clément-de-la-Place and Les Pierres Blanches.

Distribution – Middle Miocene: Atlantic, Loire Basin (Peyrot, 1938; Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854; Brébion 1964). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (Landau *et al.*, 2003). Pliocene (indeterminate): central Mediterranean, Italy (Piani, 1984). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1916; Borghi & Vecchi, 1998). Present-day: Atlantic coasts of Europe north to France, Morocco and Mediterranean, circalittoral, on corals from 20-400 m depth (Piani, 1984).

Emarginula imbricata Millet, 1865

Plate 7, figs 1-2

- 1854 *Emarginula Imbricata* Millet, p. 166 (*nomen nudum*).
- *1865 *Emarginula imbricata* Millet, p. 599.
- 1886 *Emarginula Dujardini* Dollfus & Dautzenberg, p. 142.
- 1964 *Emarginula dujardini* Dollfus & Dautzenberg – Brébion, p. 60, pl. 1, figs 10, 11.
- 2016a *Emarginula dujardini* Dollfus & Dautzenberg, 1886 – Ceulemans *et al.*, p. 56, pl. 2, fig. 1 (*cum syn.*).

Material and dimensions – Maximum diameter 20.2 mm, height 9.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0094 (1), RGM.1309503 (1), LC (3), FVD (8). **Sceaux-d'Anjou:** NHMW 2016/0103/1426 (1), LC (1), FVD (1). **Renauleau:** NHMW 2016/0103/1604 (1 fragment), LC (5), FVD (3). **Beugnon:** RGM.1309504 (1 fragment), RGM.1309505 (1 fragment).

Discussion – This is the largest emarginulid in the upper Miocene-Pleistocene northwestern French assemblages. When we recorded the species in the Assemblage III locality of Le Pigeon Blanc (Ceulemans *et al.*, 2016a), we failed to spot that *Emarginula dujardini* Dollfus & Dautzenberg, 1886 is a subjective junior synonym of *E. imbricata* Millet, 1865. The description given by Millet (1865, p. 599) that validated the earlier *nomen nudum* (Millet, 1854, p. 166) undoubtedly refers to this species 'Cette espèce, la plus grande de Maine-et-Loire, se distingue encore de celles-ci, en ce qu'elle présente à sa base plutôt un ovale qu'une ellipse, que son sommet, qui est à peine courbé, est placé aux deux tiers de la longueur totale de la coquille, que la fente marginale n'est pas suivie d'un canal et que toutes les stries ou très-petites côtes rayonnantes qui la couvrent sont imbriquées. Longueur: 13 millimètres; diamètre: 10 millimètres; hauteur: 8 millimètres. *Sc., Th., Ren.* (1865, p. 599)' This species has rarely been

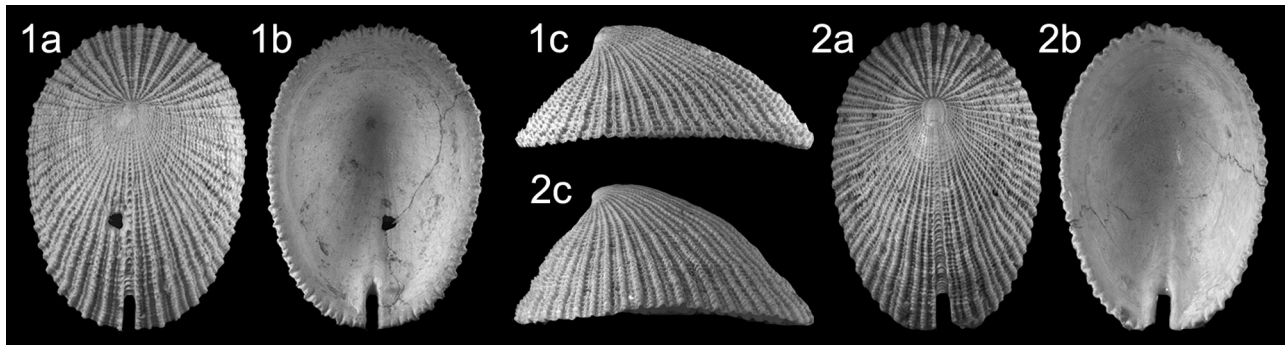


Plate 7. *Emarginula imbricata* Millet, 1865; 1. RGM.1309503, diameter 17.9 mm, height 7.0 mm. Le Grand Chauvreau, St-Clément-de-la-Place. 2. NHMW 2016/0103/1426, diameter 17.2 mm, height 8.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

recorded in the literature and we cannot therefore satisfy the requirements of Article 23.9.1.2 (ICZN 1999a) and consider Millet's name a *nomen oblitum*.

Emarginula imbricata is widespread, but always uncommon. Millet (1854, 1865) recorded it from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and Renauleau, to which Brébion (1964, p. 61) added St-Clément-de-la-Place and Chalonnès, Assemblage II (Apigné) and Assemblage III (Le Girondor, La Gauvinière); to which Ceulemans *et al.* (2016a) added Le Pigeon Blanc. For further discussion see Ceulemans *et al.* (2016a, p. 56).

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Dollfus & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1949). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.* 2016a).

Emarginula octaviana Coen, 1839

Plate 8, figs 1-2

- 1830 *Emarginula elongata*, Costa, p. 10 (*non* DeFrance, 1819; *non* G.B. Sowerby I, 1823; *non* Gray, 1825).

- *1839 *Emarginula octaviana* Coen, p. 71.
 1854 *Emarginula Ornata* Millet, p. 166 (*nomen nudum*).
 1865 *Emarginula ornata* Millet, p. 599.
 1949 *Emarginula elongata* Da Costa – Glibert, p. 20, pl. 1, fig. 9.
 2016a *Emarginula octaviana* Coen, 1839 – Ceulemans *et al.*, p. 57, pl. 2, fig. 3 (*cum syn.*).

Material and dimensions – Maximum diameter 12.8 mm; height 5.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0086-0087 (2), NHMW 2016/0103/0088 (29), RGM.1309605 (5), RGM.1309609 (20), RGM.1309613 (6), LC (11), FVD (10). **Sceaux-d'Anjou:** NHMW 2016/0103/0089 (30), RGM.1309604 (2), RGM.1309606 (20), RGM.1309608 (40), RGM.1309610 (9), RGM.1309615 (13), RGM.1309623 (6), RGM.1348016 (11), LC (18), FVD (50+). **Renauleau:** NHMW 2016/0103/1549 (7), LC (34), FVD (7). **Beugnon:** LC (3).

Discussion – The salient characters of this species were described by Glibert (1949, p. 20; as *E. elongata*): the low, elongated shell shape, coarse reticulate sculpture and most importantly the lamellae on the selenizone,

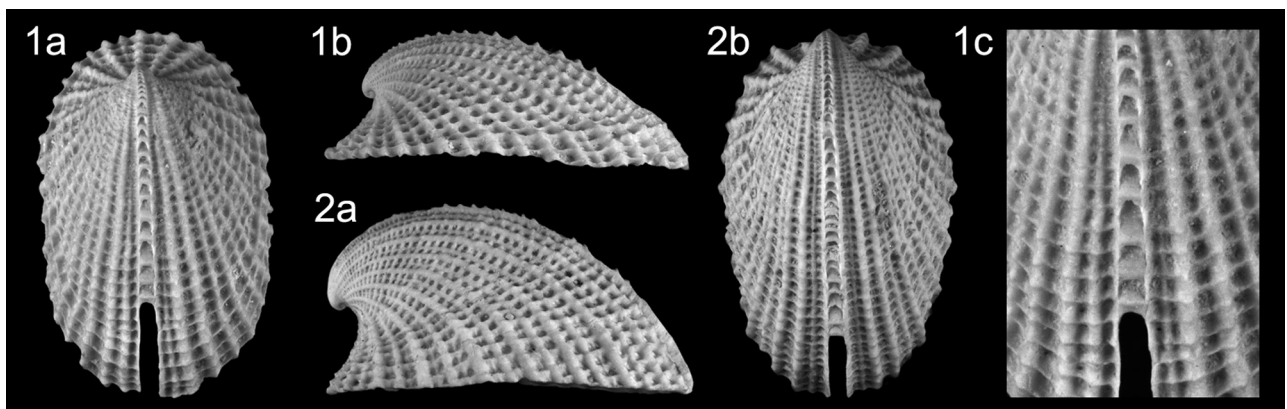


Plate 8. *Emarginula octaviana* Coen, 1839; 1. NHMW 2016/0103/0086, diameter 8.2 mm, height 3.1 mm; 2. NHMW 2016/0103/0087, diameter 9.3 mm, height 4.9 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

which are relatively coarse and raised above the level of the reticulate sculpture. The shell height is variable in the specimens from St-Clément-de-la-Place (Pl. 8, figs 1b, 2b). For further discussion see Ceulemans *et al.* (2016a, p. 58).

Millet (1854, 1865) recorded this species from Renauleau, Sceaux-d'Anjou, Thorigné and St-Clément-de-la-Place, to which Brébion (1964, p. 59; as *E. elongata*) added Chalonnès and a single specimen from Assemblage IV (Gourbesville). The maximum size of the specimens from Sceaux-d'Anjou is considerably greater than that of the specimens from St-Clément-de-la-Place (maximum diameter 12.7 mm vs. 9.3 mm). Ceulemans *et al.* (2016a, p. 57) added the Assemblage III locality of Le Pigeon Blanc.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.* 2016a). Upper Pliocene-lower Pleistocene: NW France (Brébion, 1964). Present-day: Atlantic Canaries, Portugal, Morocco and Mediterranean (Poppe & Goto, 1992).

Emarginula rosea Bell, 1824

Plate 9, figs 1-2

- *1824 *Emarginula rosea* Bell, p. 52, pl. 4, figs 1, 2.
- 1854 *Emarginula Rostrata* Millet, p. 166 (*nomen nudum*).
- 1865 *Emarginula rostrata* Millet, p. 599.
- 1923 *Emarginula rosea* T. Bell – Harmer, p. 779, pl. 62, fig. 10.
- 1949 *Emarginula conica* Lamarck, 1801 – Glibert, p. 17, pl. 1, fig. 3 [*non* Lamarck, 1801 = *E. fissura* (Linnaeus, 1758)].
- 1954 *Emarginula conica* Lamarck, 1801 – van Regteren Altena, p. 57, pl. 1, fig. 3 [*non* Lamarck, 1801 = *E. fissura* (Linnaeus, 1758)].
- 1964 *Emarginula reticulata* Sowerby, 1813 – Brébion (*partim*, Assemblage I specimens only), p. 55, pl. 1, fig. 5 (*non* Sowerby, 1813 = *E. fissura* (Linnaeus, 1758)].

us, 1758)].

- 1964 *Emarginula reticulata* var. *rosea* Bell, 1824 – Brébion, p. 57, pl. 1, fig. 6.
- 2003 *Emarginula rosea* Bell, 1824 – Landau *et al.*, p. 21, pl. 3, fig. 7 (*cum syn.*).
- 2011 *Emarginula rosea* Bell, 1824 – Wesselingh & Pouwer, p. 136, figs 21, 22.

Material and dimensions – Maximum diameter 7.5 mm; height 7.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0091-0092 (2), NHMW 2016/0103/0092 (50+), RGM.1309554 (1), RGM.1309611 (50+), RGM.1309620 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0093 (50+), RGM.1309557 (6), RGM.1309616 (9), RGM.1309619 (17), RGM.1309621 (1), RGM.1309622 (25), RGM.1348017 (21), LC (20), FVD (9). **Renauleau**: LC (4). **Beugnon**: LC (2).

Discussion – This group of emarginulids from the Miocene of northwestern France is problematic. Glibert (1949) described and illustrated specimens from the middle Miocene Loire Basin of France as *Emarginula reticulata* J. Sowerby, 1813 (= *E. fissura* Linnaeus, 1758). Brébion (1964) recorded *E. reticulata* and *E. rosea* Bell, 1824 from the 'Redonian' assemblages, and considered *rosea* a variety of *E. reticulata*. Ceulemans *et al.* (2016a) recognised *E. fissura* in the lower Pliocene Assemblage III deposit of Le Pigeon Blanc. *Emarginula rosea* is distinguished by its very elevated shell, usually smaller in size than *E. fissura*, coarse sculpture and the posterior position of the apex, which is slightly more recurved. The problem lies in the identification of the Assemblage I specimens. Some of the larger specimens are taller than they are broad, and are typical for *E. rosea*, whilst many of the smaller ones are lower and at first glance similar to *E. fissura*. However, examination of the numerous specimens at hand from St-Clément-de-la-Place and Sceaux-d'Anjou shows that the apex is always more posteriorly placed than it is in *E. fissura*. This is also true of the shell illustrated by Brébion (1964, pl. 1, fig. 5) from Beaulieu. Moreover, the size range of the Assemblage I shells is similar to that of *E. rosea*, *E. fissura* being twice as large or more. We therefore consider all the Assemblage I shells

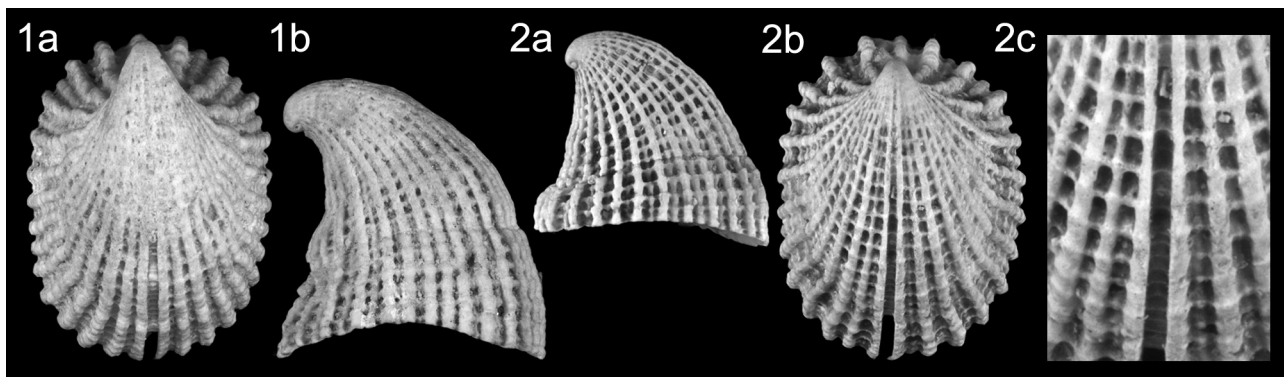


Plate 9. *Emarginula rosea* Bell, 1824; 1. NHMW 2016/0103/0090, diameter 5.2 mm, height 5.4 mm; 2. NHMW 2016/0103/0091, diameter 5.4 mm, height 4.5 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

seen *E. rosea* and therefore, *E. rostrata* Millet, 1865 is a junior subjective synonym of *E. rosea* rather than *E. reticulata*, as suggested by Brébion (1964, p. 56). It seems that the shell increases in height with growth, the tallest being the most gerontic (Pl. 9, fig. 1). The specimens from the middle Miocene Loire Basin described by Glibert (1949) as *E. reticulata* (= *E. fissura*) have a more centrally placed apex and do indeed seem to be that species. It seems, therefore, that both species were present in the middle-upper Miocene of northwestern France, and may have exploited different habitats as we have not found the two species together, although Fretter & Graham (1976, p. 10) suggested the two species shared a similar habitat today.

Emarginula rosea is the commonest emarginulid in the Assemblage I localities and, as discussed above, we consider the Assemblage I references to *E. reticulata* of Brébion (1964, p. 57) to be *E. rosea* (Renaudeau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu). The Assemblage II records need to be verified. Brébion (1964, p. 58) recorded *E. rosea* from the Assemblage III localities of Le Girondor, La Gauvinière and Palluau, although Ceulemans *et al.* (2016a) did not find it at Le Pigeon Blanc.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: North Sea Basin, Coralline Crag, England (Harmer, 1923), Kattendijk Formation, Belgium (Marquet, 1998); Atlantic, NW France (Brébion, 1964). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1923); western Mediterranean, Estepona Basin, S. Spain (Landau *et al.*, 2003), North Sea Basin (Marquet, 1995); central Mediterranean, Italy (Piani, 1984). Pliocene (indeterminate): North Sea Basin, The Netherlands (van Regteren Altena, 1954; Wesselingh & Pouwer, 2011). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1916). Upper Pleistocene: North Sea Basin, Netherlands (Wesselingh & Pouwer, 2011). Present-day: Atlantic coasts of Europe north to the British Isles and Mediterranean, 0-90 m (Piani, 1984).

Tribe Fissurellideini Pilsbry, 1890
Genus *Lucapinella* Pilsbry, 1890

Type species (by subsequent designation (Pilsbry, 1890) – *Clypidella callomarginata* Dall, 1871, present-day, California.

***Lucapinella clypeata* (Grateloup, 1828)**

Plate 10, figs 1-2

1828a *Fissurella depressa* Grateloup, p. 79, no. 9 [*non F. depressa* Lamarck, 1822 (= *F. crassa* Lamarck, 1822)].

*1828a *Fissurella clypeata* Grateloup, p. 79, no. 10.

2013 *Lucapinella clypeata* (Grateloup, 1828) – Landau *et al.*, p. 23, p. 1, fig. 1 (*cum syn.*).

Material and dimensions – Maximum diameter 4.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1626-1627 (2). **Sceaux-d'Anjou**: RGM.1348014 (1). **Renaudeau**: NHMW 2016/0103/1628 (5)

Discussion – Cossmann & Peyrot (1917) considered *Fissurella depressa* Grateloup, 1828 (*non* Lamarck, 1822, renamed *F. aquensis* by d'Orbigny, 1852) described from the early Oligocene Rupelian of Gaas, France, and specimens from the early Miocene Aquitanian-Burdigalian of the Aquitaine Basin, France, described as *Fissurella clypeata* Grateloup, 1828 to represent a single highly variable species. The specimens from the Assemblage I deposits are very small, but otherwise fit within the wide range of variability.

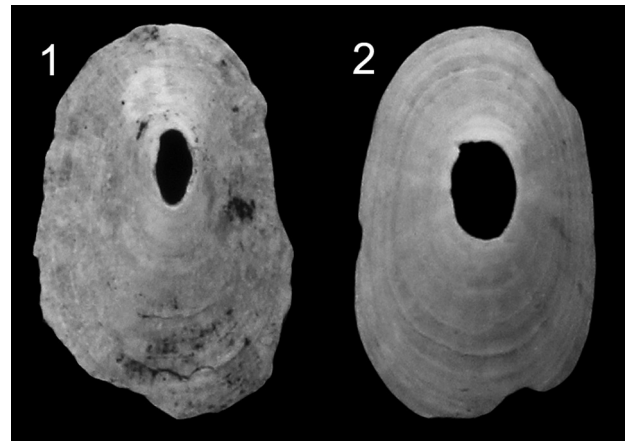


Plate 10. *Lucapinella clypeata* (Grateloup, 1828); 1. NHMW 2016/0103/1626, height 2.0 mm, length 4.6 mm; 2. NHMW 2016/0103/1627, height 1.9 mm, length 4.1 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Distribution – Lower Oligocene: Atlantic (Rupelian): Aquitaine Basin, France (Grateloup, 1828). Lower Miocene: Atlantic (Aquitanian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1917; Lozouet *et al.*, 2001a); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1896b). Middle Miocene: north-eastern Atlantic (Langhian): Aquitaine Basin, France (Cossmann & Peyrot, 1917), Loire Basin, France (Glibert, 1949); Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Hörnes, 1856), Poland (Bałuk, 1975), Hungary (Csepregy-Meznerics, 1954; Strausz, 1954, 1966), Bulgaria (Kojumdzieva & Strachimirov, 1960), Romania (Popa & Ianoliu, 2000), Bosnia (Atanacković, 1985); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Messinian): NW France (this paper); Proto-Mediterranean Sea (Tortonian): Po valley, Italy (Sacco, 1896b).

Superfamily Haliotoidea Rafinesque, 1815

Family Haliotidae Rafinesque, 1815

Genus *Haliotis* Linnaeus, 1758

Type species (by subsequent designation, de Montfort, 1810) – *Haliotis asinina* Linnaeus, 1758, present-day, Indo-Pacific.

- 1758 *Haliotis* Linnaeus, p. 779.
 1854 *Teinotis* H. Adams & A. Adams, p. 442. Type species (by subsequent designation, Fischer, 1885): *Haliotis asinina* Linnaeus, 1758, present-day, Indo-Pacific.
 1856 *Schismotis* Gray, p. 147. Type species (by monotypy): *Schismotis excisa* Gray, 1856, present-day, Australia.
 1885 *Tinotis* Fischer, p. 845. Incorrect subsequent spelling of *Teinotis*.
 1908 *Teinotus* Schepman, 1908. Incorrect subsequent spelling of *Teinotis*.
 1929 *Sanhaliotis* Iredale, p. 270. Type species (by original designation): *Haliotis varia* Linnaeus, 1758, present-day, Australia.
 1933 *Exohaliotis* Cotton & Godfrey, p. 16. Type species (by original designation): *Haliotis cyclobates* Péron, 1816, present-day, South Australia.
 1943 *Ovinotis* Cotton, p. 175, 179. Type species (by original designation): *Haliotis ovina* Gmelin, 1791, present-day, Indo-Pacific.
 1964 *Eurotis* Habe & Kosuge, p. 6. Type species (by original designation): *Haliotis tuberculatus* Linnaeus, 1758, present-day, Europe.
 1964 *Usahaliotis* Habe & Kosuge, p. 8. Type species (by original designation): *Haliotis cracherodii* Leach, 1814, present-day, north eastern Pacific.

***Haliotis* cf. *tuberculata coccinea* Reeve, 1846**

Plate 11, fig. 1

- cf. *1846 *Haliotis coccinea* Reeve, 1846, p. 55.
 cf. 1994 *Haliotis coccinea* Reeve, 1846 – Giannuzzi-Savelli *et al.*, p. 54, fig. 104.
 cf. 2000 *Haliotis tuberculata coccinea* Reeve, 1846 – Geiger & Poppe, p. 90, pl. 7.
 cf. 2002 *Haliotis tuberculata coccinea* Reeve, 1846 – Ávila *et al.*, p. 348, fig. 5.
 cf. 2012 *Haliotis tuberculata coccinea* Reeve, 1846 – Geiger & Owen, p. 135, pl. 69, figs 1-14.

Material and dimensions – Maximum diameter 16.8 mm (fragment). **St-Clément-de-la-Place**: NHMW 2016/0103/0147 (1), NHMW 2016/0103/0148 (26 fragments), RGM.1309555 (2 fragments), RGM.1309564 (3 fragments), LC (12 juveniles), FVD (1 fragment). **Renauleau**: NHMW 2016/0103/1439 (1 larger fragment), LC (1 juvenile).

Discussion – The genus is represented in the St-Clément-de-la-Place assemblage by a number of small specimens that we consider to be juvenile, as none of the tremata (respiratory openings) are open. They are sculptured by seven wavy narrow axial ribs between the suture and the tremata, narrower than their interspaces. The should-

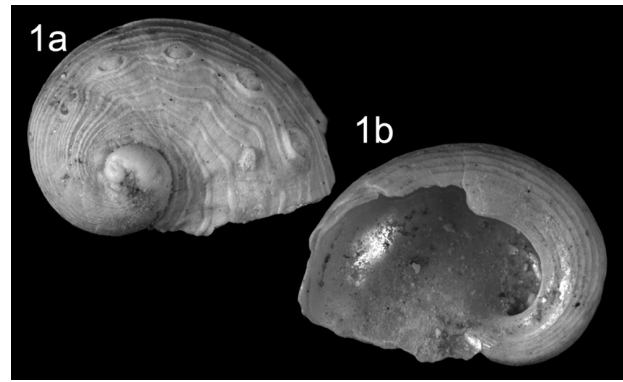


Plate 11. *Haliotis* cf. *tuberculata coccinea* Reeve, 1846; 1. NHMW 2016/0103/0147, diameter 3.0 mm x 2.1 mm. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

der rib is wider, splitting and surrounding the tremata. Three further ribs are placed between the shoulder and the sharp, elevated peripheral keel. The base bears eight regular ribs.

Similar axial sculpture composed of wavy ribs is present in juvenile shells of the present-day *Haliotis tuberculata coccinea* Reeve, 1846, but with slightly fewer cords (3-5 vs. 7). We therefore hesitate in considering the shells from St-Clément-de-la-Place conspecific with the present-day *H. t. coccinea*, but the two are nevertheless very similar. *Haliotis coccinea* is now considered a subspecies of *H. tuberculata* Linnaeus, 1758 (Geiger, 1998, p. 97; Geiger & Poppe, p. 90; Geiger & Owen, 2012, p. 135). Today this species has a more southern distribution, found in the Azores and Canary Islands. We have Pleistocene fossil specimens at hand from Santa Maria Island in the Azores (NHMW coll.; Ávila *et al.*, 2002).

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

Superfamily Scissurelloidea Gray, 1847

Note – For this section we have followed the terminology and descriptive terms adopted by Geiger (2012). We are greatly indebted to that author for his advice and guidance with this superfamily.

Family Scissurellidae Gray, 1847

Subfamily Scissurellinae Gray, 1847

Genus *Scissurella* d'Orbigny, 1824

Type species (by subsequent designation, Gray, 1847b) – *Scissurella laevigata* d'Orbigny, 1824 (= *S. costata* d'Orbigny, 1824), present-day, Mediterranean.

- 1824 *Scissurella* d'Orbigny, p. 341, 343.
 1856 *Schismope* Jeffreys, p. 321. Type species (by monotypy): *Scissurella striatula* Philippi, 1844,

- present-day, Italy.
- 1861 *Woodwardia* Crosse & Fischer, p. 160. Type species (by monotypy): *Scissurella elegans* d'Orbigny, 1824, Pliocene, Italy.
- 1998 *Maxwelliella* Bandel, p. 19. Type species (by original designation): *Scissurella annulata* Ravn, 1933, Paleocene, Denmark.
- 1998 *Reussella* Bandel, p. 44. Type species (by original designation): *Scissurella depressa* Reuss, 1860, Miocene, Bohemia. Junior homonym of *Reussella* Galloway, 1933 [Foraminifera].
- 1998 *Praescissurella* Lozouet, p. 66. Type species (by original designation): *Scissurella depontaillieri* Cossmann, 1879, Oligocene, France.

Scissurella transylvanica Reuss, 1860

Plate 12, fig. 1

- *1860 *Scissurella transylvanica* Reuss, p. 266, pl. 7, fig. 6.
- 2012 *Scissurella transylvanica* Reuss, 1860 – Geiger, p. 363, figs 259-263 (*cum syn.*).
- 2013 *Scissurella transylvanica* Reuss, 1860 – Landau *et al.*, p. 23, pl. 54, fig. 2 (*cum syn.*).

Material and dimensions – Maximum diameter 1.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1429 (3), RGM.1309568 (30). **Sceaux-d'Anjou**: RGM.1309575 (1), RGM.1309589 (1). **Renauleau**: NHMW 2016/0103/1429 (1), NHMW 2016/0103/1440 (10). **Beugnon**: RGM.1309552 (2).

Discussion – *Scissurella transylvanica* Reuss, 1860 is characterised by its strongly axially sculptured protoconch (Pl. 12, fig 1d) and strong, close-set axial ribs on the teleoconch. Little can be added to the excellent revision on the group by Geiger (2012), except to say that this occurrence in the Assemblage I deposits of NW France is the stratigraphically youngest for the species.

Distribution – Upper Oligocene: Aquitaine Basin, France (Bandel, 1998). Lower Miocene: northeastern Atlantic (Aquitanian): Aquitaine Basin, France (Benoist, 1875; Lozouet *et al.*, 2001). Middle Miocene: northeastern Atlantic (Langhian): Loire Basin, France (de Morgan, 1915); Paratethys (Langhian-Serravallian): Hungary (Kecskeméti

Körmendi, 1962; Kókay, 1966; Strausz, 1966), Poland (Friedberg, 1938; Bałuk, 1975), Romania (Reuss, 1860); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene (Tortonian): Atlantic, NW France (this paper).

Genus *Sinezona* Finlay, 1926

Type species (by original designation) – *Schismope brevis* Hedley, 1904, present-day, New Zealand.

- 1926 *Sinezona* Finlay, p. 341, 346.
- 1998 *Daizona* Bandel, p. 57. Type species (by original designation): *Sinezona doliolum* Herbert, 1986, present-day, South Africa.
- 1998 *Ariella* Bandel, p. 63. Type species (by original designation): *Ariella haliotimorpha* Bandel, 1998, Oligocene, France.

Sinezona geigeri nov. sp.

Plate 13, fig. 1

Type material – Holotype MNHN.F.A57395, diameter 0.9 mm; height 0.75 mm; paratype 1 NHMW 2016/0103/0010; paratype 2 NHMW 2016/0103/0011; paratype 3 NHMW 2016/0103/0011; paratype 4 RGM.1309567.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/1394 (1).

Etymology – Named after Daniel L. Geiger, curator at the Santa Barbara Museum of Natural History, California, USA in recognition of his enormous contribution to the knowledge of the superfamily Scissurelloidea. *Sinezona* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Sinezona* species of small size, with no axial sculpture on shoulder of teleoconch II, base with seven raised ribs that end abruptly at edge of base and deep umbilicus bordered by raised funiculus.

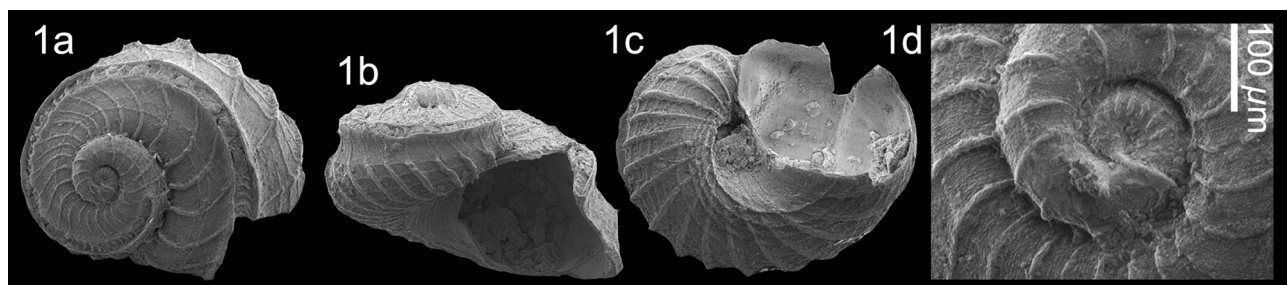


Plate 12. *Scissurella transylvanica* Reuss, 1860; 1. NHMW 2016/0103/1429, diameter 1.4 mm; 1d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

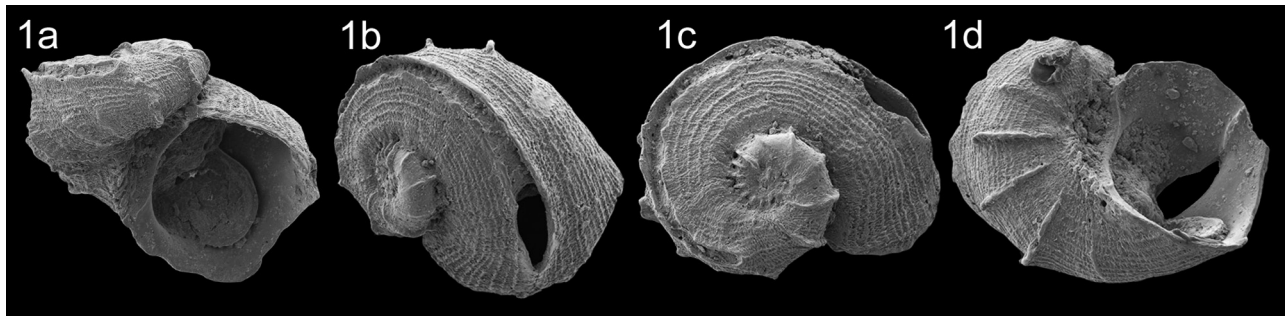


Plate 13. *Sinezona geigeri* nov. sp.; 1. **Holotype** MNHN.F.A57395, diameter 0.9 mm, height 0.75 mm (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell minute, depressed trochiform. Protoconch of 1.25 whorls, bearing strong axial sculpture on the outer half of the whorl, not connecting to embryonic cap. Teleoconch I of 0.65 whorl, bearing six strong, widely spaced axial ribs, no spiral in position of selenizone. Teleoconch II of 0.7 whorl, suture little impressed, spiral sculpture above selenizone starting with three cords, increasing abapically to eleven at outer lip; cords of irregular strength and position. Last whorl below selenizone straight-sided to weakly concave, bearing irregular fine cords. Base convex, with seven sharp, elevated ribs, which start abruptly at the edge of base. Selenizone just below apex of shell, slit closed to form triangular oblong foramen, keels moderately elevated. Umbilicus open, deep, bordered by elevated funiculus.

Discussion – *Sinezona geigeri* nov. sp. is separated from most of its European congeners by the absence of axial sculpture on the shoulder. There are relatively few eastern Atlantic congeners with which it can be compared. The Mediterranean and West African Pliocene to present-day *Sinezona cingulata* (O.G. Costa, 1861) has far denser axial sculpture on the protoconch and axial sculpture that extends between the sutures on teleoconch II. *Sinezona semicostata* Burnay & Rolán, 1990 from the Canary and Cape Verde Islands has a strongly depressed shell and strong axial sculpture. *Sinezona terquemi* (Deshayes, 1865) from the lower Miocene Aquitaine Basin of France has dense axial sculpture, weak spiral sculpture restricted to the ad-umbilical quarter of the base, and a broad umbilicus that is not delimited by a funiculus.

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

Family Anatomidae McLean, 1989
Genus *Anatoma* Woodward, 1859

Type species (by monotypy) – *Scissurella crispata* Fleming, 1828, present-day, British Isles.

- 1859 *Anatoma* Woodward, p. 204.
- 1877 *Schizotrochus* Monterosato, p. 416. Type species (by monotypy): *Scissurella crispata* Fleming,

1828, present-day, British Isles. Objective synonym.

- 1998 *Hainella* Bandel, p. 36. Type species (by original designation): *Scissurella euglypta* Pelseneer, 1903, present-day, Antarctic.
- 1998 *Thielella* Bandel, p. 35. Type species (by original designation): *Scissurella amoena* Thiele, 1912, present-day, Antarctic.
- 1998 *Pagodella* Bandel, p. 2 (*nomen nudum*).

***Anatoma redoniana* nov. sp.**

Plate 14, fig. 1

Type material – Holotype NHMW 2016/0103/1470, diameter 1.4 mm, height 0.9 mm, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/1624, diameter 1.2 mm, height 0.7 mm, **Renauleau**.

Other material – **Renauleau**: NHMW 2016/0103/1625 (2 fragments).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Anatoma* species of small size, low-turreted to flat dorsum, with protoconch bearing flocculent sculpture, teleoconch with narrow sutsel, slightly narrower than selenizone, sculptured by fine, close-set sinuous axial ribs on both dorsum and venter, no spiral sculpture, keeled base.

Description – Shell small, somewhat turreted to flat dorsum. Protoconch of 1.75 whorls, sculpture flocculent, no varix. Teleoconch I of 0.5 whorl bearing close-set, sinuous axials. Teleoconch II of one whorl, suture moderately impressed, sutsel (portion of the base between the suture and the lower keel of the selenizone above it; Geiger, 2012) slightly narrower than selenizone. Shoulder bear-

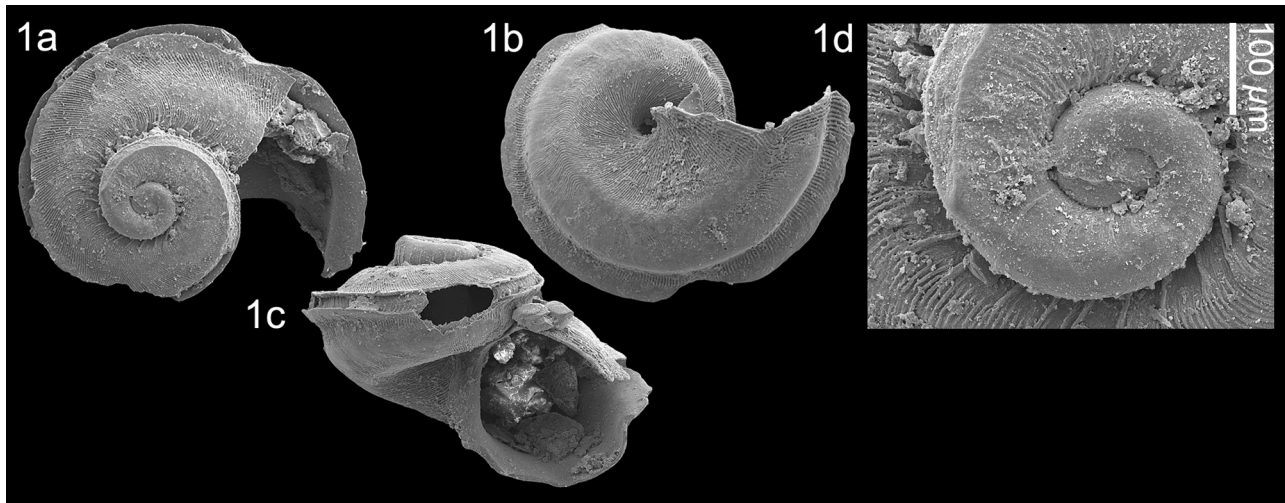


Plate 14. *Anatoma redoniana* nov. sp.; 1. **Holotype** NHMW 2016/0103/1470, diameter 1.4 mm; height 0.9 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ing numerous close-set, sinuous axial ribs. Spiral sculpture absent. Base not constricted below selenizone, moderately strongly keeled mid-base, with similar pattern of sinuous axials. Umbilicus open, deep, continuously sloping from base; funiculus curved away from apertural margin. Selenizone at periphery; lunules distinct; keels strong, elevated, external surface with many strong axial lines; slit open. Aperture subquadrate, somewhat flared, particularly towards umbilicus, where apertural margin fuses with funiculus.

Discussion – Despite being represented by scant material, *Anatoma redoniana* nov. sp. is so unlike its European congeners that it merits description. The most salient characters of this new species are the dense sinuous axial sculpture covering both the dorsum and the venter and the keeled base. We note that the spire in all three specimens from Renauleau is completely flat and not slightly elevated as seen in the holotype (Pl. 14, fig. 1c), but the rest of the characters and sculpture are like that of the holotype from St-Clément-de-la-Place. *Anatoma umbilicata* (Jeffreys, 1883), with which it is most similar in the European faunas differs in having far less dense axial sculpture and in not having a keeled base. The shells identified as *A. umbilicata* by Landau *et al.* (2003) from the lower upper Pliocene of Estepona, southern Spain are not this species, but *Anatoma eximia* (Seguenza, 1880), which has a more turreted shell shape, much wider sutsel at any given whorl count and the selenizone is placed higher on the whorl (Geiger, 2012, p. 1123). *Anatoma crispata* (Fleming, 1828) has a more globose shell with fine axial and spiral sculpture and a wider sutsel. The most similar species in shape and sculpture is *A. aupouria* (Powell, 1937) from present-day New Zealand, but this species differs in having a few spiral cords at the shoulder and within the umbilicus.

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

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

1810 *Clanculus* de Montfort, p. 191. Type species (by original designation): *Trochus pharaonius* Linnaeus, 1758, present-day, Red Sea.

For generic synonymy see Ceulemans *et al.* (2016a).

Note – In this section we follow the terminology of Herbert (1993). The works of Chirli (2004) and Spadini (2006) showed the Mediterranean Pliocene *Clanculus* fauna was far more diverse than previously thought. Until now only one species, *Clanculus (Clanculopsis) baccatus* (Defrance, 1824) was known from the middle and upper Miocene of northwestern France. In this work we show this also to be an underestimate of *Clanculus* diversity at the time.

***Clanculus (s.s.) brebioni* nov. sp.**

Plate 15, fig. 1; Plate 16, figs 1-2

Type material – Holotype NHMW 2016/0103/0246, height 11.9 mm, width 12.3 mm; paratype 1 NHMW 2016/0103/0246, height 10.4 mm, width 11.1 mm; paratype 2 MNHN.F.A66713, height 10.5 mm, width 11.4 mm (incomplete); paratype 3 MNHN.F.A66714, height 9.4 mm, width 9.5 mm (incomplete).

Other material – **St-Clément-de-la-Place:** LC (1), FVD (1).

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

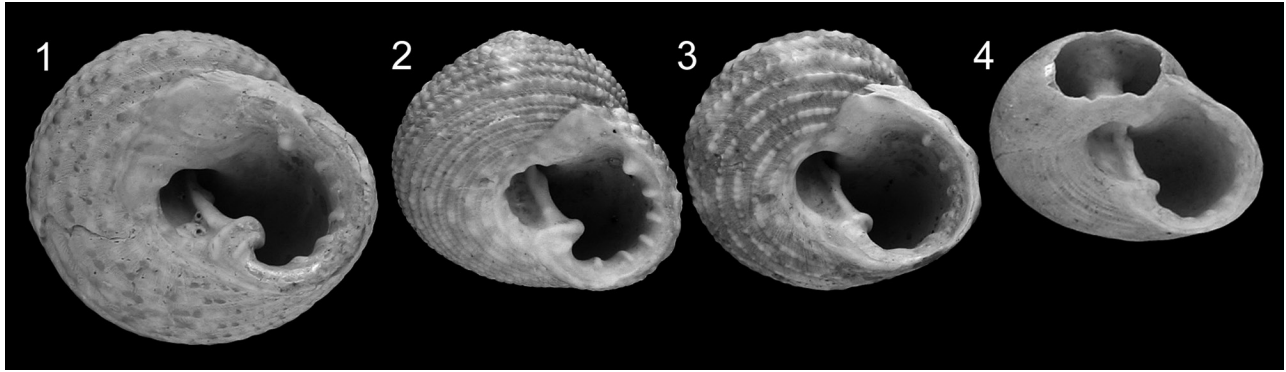


Plate 15. 1. *Clanculus (s.s.) brebioni* nov. sp., **holotype** NHMW 2016/0103/0246, height 11.9 mm, width 12.3 mm. Le Grand Chauvère, St-Clément-de-la-Place. 2. *Clanculus (Clanculopsis) baccatus* (Defrance, 1824), NHMW 2016/0103/0239, height 7.5 mm, width 7.9 mm. Renauleau. 3. *Clanculus (Clanculopsis) sancticlementensis* nov. sp., **holotype** MNHN.F.A57700, height 8.9 mm, width 9.0 mm. Le Grand Chauvère, St-Clément-de-la-Place. 4. *Clanculus (Clanculopsis) umbilicovadus* nov. sp., **holotype** NHMW 2016/0103/0248, height 4.1 mm, width 5.1 mm. Le Grand Chauvère, St-Clément-de-la-Place. All: Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clanculus (s.s.)* species of medium size, with moderately elevated conical spire, bearing reticulated sculpture on first two teleoconch whorls, axial sculpture that weakens abapically, so that sculpture on last two whorls of low beaded cords, four primary cords on last whorl with single smooth or beaded secondary cord in each interspace, surface covered in extremely fine, close-set axial growth lines and spiral threads forming tiny rows of dots in interspaces, and strong apertural dentition.

Description – Shell medium size for genus, solid, trochiform, with a moderately elevated conical spire. Protoconch not preserved. Teleoconch of five whorls, with periphery at abapical suture. Suture impressed. First teleoconch whorl with two low spiral cords. On second

whorl a third cord develops below adapical suture. Narrow, close-set, prosocline ribs, visible in interspaces between cords, forming reticulated sculpture with small, low, rounded tubercles at intersections. Abapically axial sculpture weakens and disappears; spiral cords remain low, bearing small beads. Last whorl bearing four rows of primary beads, with a single secondary cord in interspaces, developed to a varying degree; in holotype only secondary cord between 3rd and 4th primaries beaded, in paratype all secondary cords beaded. Surface covered in extremely fine and close-set prosocline growth lines. Fine spiral threads in interspaces between primary and secondary spiral sculpture interrupted by growth lines forming tiny spiral rows of dots. Base weakly convex, bearing 6-7 beaded cords, equal in strength and spacing. Umbilicus deep, surrounded by inductural callus, periumbilical edge smooth bearing stout, irregular umbilical dentition. Mature apertural dentition moderately strongly developed; anal tooth stout, six labial ridges; upper columellar tooth stout; bifid lower columellar tooth. Columella between upper and lower teeth smooth. Parietal callus

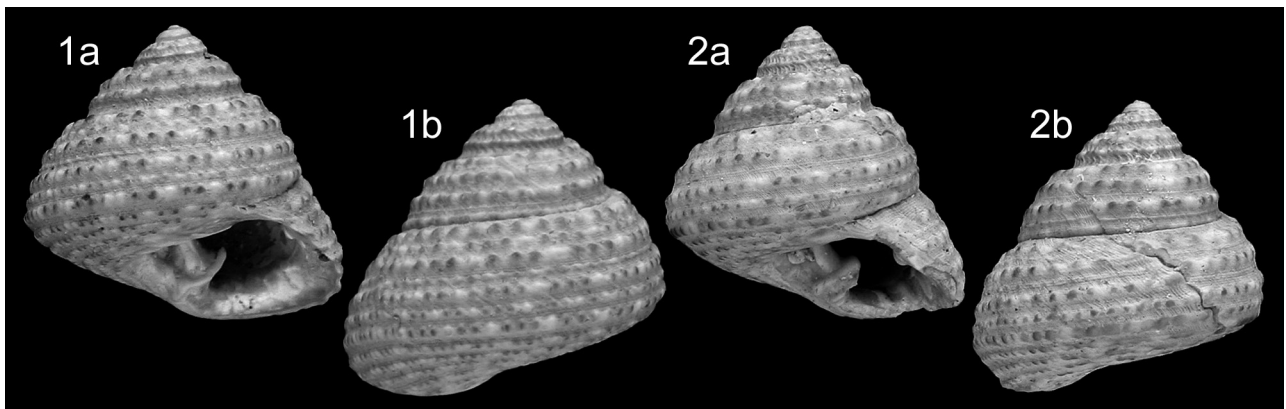


Plate 16. *Clanculus (s.s.) brebioni* nov. sp.; 1. **Paratype 1** NHMW 2016/0103/0246, height 10.4 mm, width 11.1 mm; 2. **Holotype** NHMW 2016/0103/0246, height 11.9 mm, width 12.3 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

moderately developed, bearing 3-4 parietal ridges. Colour pattern of interrupted vertical flammules, dark dots on many beads.

Discussion – *Clanculus (s.s.) brebioni* nov. sp. is the largest shelled and most solid *Clanculus* species in the Assemblage I fauna. We have attributed it to *Clanculus (s.s.)*, as the holotype has a bifid lower columellar tooth. We note that the paratype appears to have a single lower columellar tooth, but this may be artefact, as the labial ridges on the abapical half of the inside of the aperture are abraded, the abraded area extending to the abapical portion of the lower columellar tooth. Although *C. (s.s.) brebioni* has the same number of primary cords as *Clanculus (Clanculopsis) sancticlementensis* nov. sp., in the latter the reticulated early sculpture persists further along the teleoconch, the suture is canaliculated, the cords are raised and the beading is more prominent. There are also separated by the subgeneric character of the lower columellar tooth; bifid in *Clanculus (s.s.)*, simple in *C. (Clanculopsis)*. They also seem to have a different colour pattern, with dark dots on many of the beads in *C. (s.s.) brebioni*.

This new species is more closely similar to *C. (s.s.) bonfittoi* Chirli, 2004 from the Italian Pliocene, but that species is smaller shelled (maximum height 7.7 mm, width 7.4 mm; Spadini, 2006), and the spiral sculpture forms far more prominent beads; the beads in *C. (s.s.) brebioni* are rather subdued for the genus and the adapically beaded cord placed close below the suture is more strongly leading to a canaliculated suture, as in *C. (C.) sancticlementensis*, but not in *C. (s.s.) brebioni*. The Pliocene to present day European *C. (s.s.) corallinus* (Gmelin, 1791) differs in having more numerous beaded cords. The numerous present-day Eastern Atlantic species revised by Rubio & Rolán (2002) all differ in having more numerous beaded cords of roughly equal strength on the last whorl, rather than four primary cords above the basal cord, with secondaries intercalated, as seen in *C. (s.s.) brebioni*.

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

Subgenus *Clanculopsis* Monterosato, 1880

- 1880 *Clanculopsis* Monterosato, p. 222. Type species (by subsequent designation, Sacco, 1896a, p. 21): *Trochus cruciatus* Linnaeus, 1758, present-day, Mediterranean.

***Clanculus (Clanculopsis) baccatus* (Defrance, 1824)**

Plate 15, fig. 2; Plate 17, figs 1-2

- *1824 *Monodonta baccata* Defrance, 1824, p. 475.
 1854 *Monodonta Baccata* Defr. – Millet, p. 157.
 1964 *Clanculus baccatus* (Defrance, 1824) – Brébion, p. 122.
 2016a *Clanculus (Clanculopsis) baccatus* (Defrance, 1824) – Ceulemans *et al.*, p. 58, pl. 2, fig. 4 (*cum syn.*).

Material and dimensions – Maximum height 11.0 mm, width 10.9 mm. **St-Clément-de-la-Place**: RGM.1309556 (17), LC (5), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0242 (25), RGM.1309543 (10 +15 juveniles), RGM.1309544 (50+), RGM.1309550 (15), RGM.1309573 (22), RGM.1309580 (23 adults and subadults), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0239-0240 (2), NHMW 2016/0103/0241 (27), LC (50+), FVD (50+). **Beugnon**: RGM.1309541 (2), RGM.1309542 (8 + 10 juveniles), RGM.1309563 (17), RGM.1309594 (5), RGM.1309743 (4), FVD (1).

Discussion – *Clanculus (Clanculopsis) baccatus* (Defrance, 1824) differs from the Pliocene to present-day *C. (s.s.) corallinus* (Gmelin, 1791) by the presence of a single lower columellar tooth; in *C. (s.s.) corallinus* the lower columellar tooth is bifid. The specimens of *C. (C.) baccatus* from Assemblage I have a second columellar tooth below the strong single tooth, but it is far less strongly developed than in *C. corallinus*. *Clanculus (C.) baccatus* has six subequal primary beaded cords on the last whorl above the base, plus a well-developed secondary cord between the adapical cord and the second cord, which is almost equal in strength to the primary cords. The specimens of *C. (C.) baccatus* from the Assemblage I localities are small compared to those of the middle Miocene Loire Basin of France (maximum height 10.9;

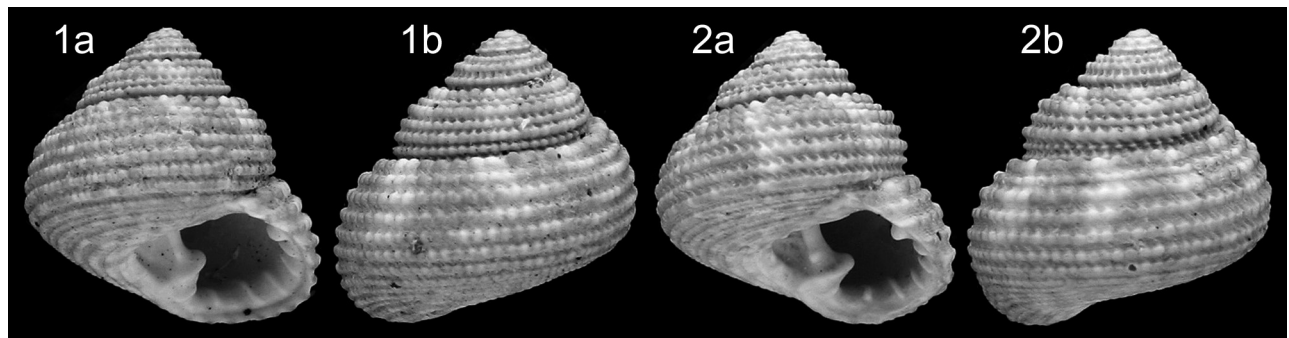


Plate 17. *Clanculus (Clanculopsis) baccatus* (Defrance, 1824); 1. NHMW 2016/0103/0239, height 7.5 mm, width 7.9 mm; 2. NHMW 2016/0103/0240, height 7.7 mm, width 7.8 mm. Renauleau, Maine-et-Loire, France, Tortonian, upper Miocene.

Glibert, 1949, p. 67) and slightly higher-spired than those from the lower Pliocene Assemblage III locality of Le Pigeon Blanc, which are wider and more depressed (Ceulemans *et al.*, 2016a, pl. 2, fig. 4). *Clanculus* (*C.*) *baccatus* has six subequal primary beaded cords on the last whorl above the base, plus a well-developed secondary cord between the adapical cord and the second cord.

Millet (1854) recorded this species from Assemblage I localities of Sceaux-d'Anjou, Thorigné, Renauleau, Saint-Michel and St-Clément-de-la-Place. Brébion (1964) recorded this species from numerous localities, representing Assemblage I, III and IV. However, this is the only *Clanculus* species he recorded from the French 'Redonian', which is shown here to be incorrect. Therefore, his records must be verified.

For further discussion see Ceulemans *et al.* (2016a, p. 58).

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016a). Upper Pliocene-lower Pleistocene: Atlantic, NW France (Brébion, 1964).

***Clanculus* (*Clanculopsis*) *sancticlementensis* nov. sp.**

Plate 15, fig. 3; Plate 18, figs 1-4

Type material – Holotype MNHN.F.A57700, height 8.9 mm, width 9.0 mm; paratype 1 MNHN.F.A57700, height 8.5 mm, width 8.5 mm; paratype 2 MNHN.F.A57701, height 9.6 mm, width 9.2 mm; paratype 3 NHMW 2016/0103/0244, height 8.1 mm, width 8.2 mm; paratype

4 RGM.1309546, height 8.7, width, 8.4 mm; paratype 5 RGM.1309547, height 86.5, width, 7.1 mm, paratype 6 RGM.1309548, height 6.6, width, 7.0 mm.

Other material – Maximum height 9.5 mm, width 9.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0245 (47), RGM.1309549 (25 juveniles), LC (50+), FVD (50+).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clanculus* (*Clanculopsis*) species of medium size, with moderately elevated conical spire, bearing four primary spiral cords on last whorl, crossed by narrow, close-set axial ribs, visible in interspaces, small tubercles developed at intersections and moderately weak apertural dentition.

Description – Shell medium size for subgenus, solid, trochiform, with moderately elevated conical spire. Protoconch consists of 1.5 smooth, convex whorls. Teleoconch of four whorls, with periphery at abapical suture. Suture impressed, canaliculate. First teleoconch whorl with two elevated spiral cords. On second whorl a third cord develops below adapical suture, gaining in strength. Third whorl with three subequal spiral cords, fourth cord develops above abapical suture. About 28 narrow prosocline ribs, elevated in interspaces between cords, forming small

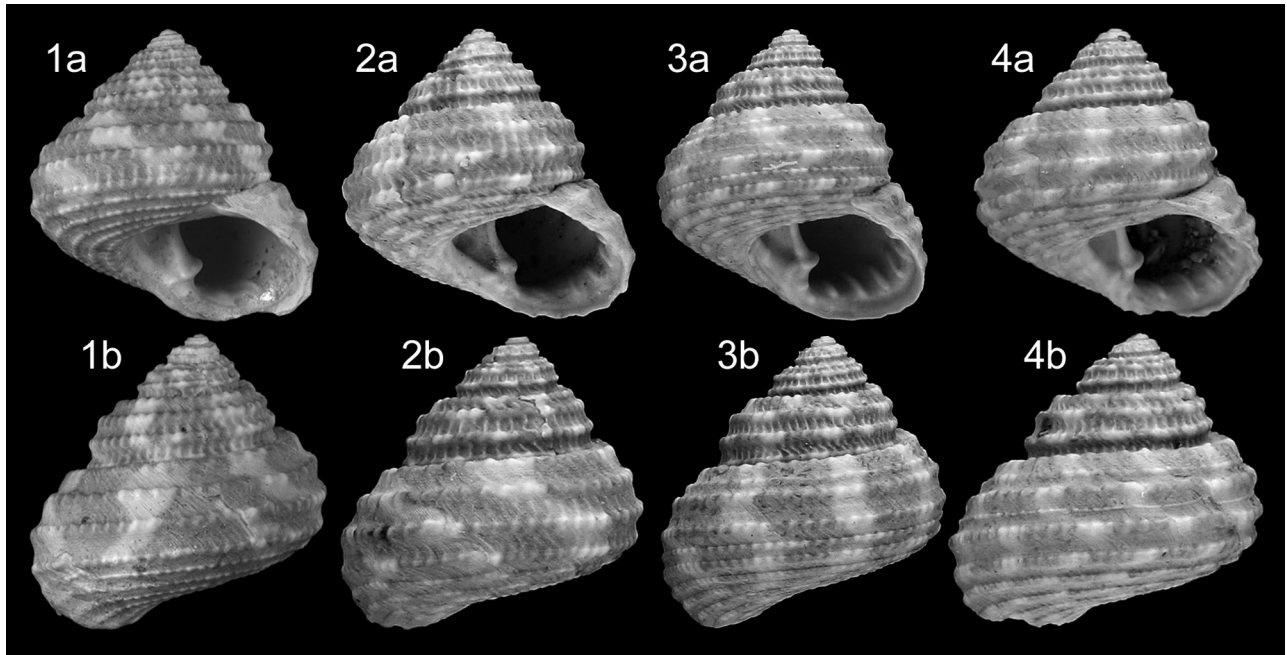


Plate 18. *Clanculus* (*Clanculopsis*) *sancticlementensis* nov. sp.; 1. **Holotype** MNHN.F.A57700, height 8.9 mm, width 9.0 mm; 2. **Paratype 1** MNHN.F.A57700, height 8.5 mm, width 8.5 mm; 3. **Paratype 2** MNHN.F.A57701, height 9.6 mm, width 9.2 mm; 4. **Paratype 3** NHMW 2016/0103/0244, height 8.1 mm, width 8.2 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

rounded tubercles at intersections. Last whorl convex, bearing four primary cords, with secondary cords developed in some of the interspaces, in some specimens. Base weakly convex, bearing six smooth to beaded cords, equal in strength and spacing. Umbilicus deep, surrounded by inductural callus, periumbilical edge smooth in most specimens; bearing weak umbilical dentition in some specimens. Mature apertural dentition moderately weakly developed; anal tooth only slightly stronger than labial ridges; upper columellar tooth small, simple; single lower columellar tooth, with one or two small tubercles below. Columella between upper and lower teeth smooth. Parietal callus moderately developed, smooth or bearing 1-2 parietal ridges. Colour pattern of interrupted vertical flammules is preserved in most specimens.

Discussion – This new species is unequivocally placed in the subgenus *Clanculopsis* Monterosato, 1880, characterised by its single lower columellar tooth. It is with surprise that we note that the vast majority of *Clanculus* (*Clanculopsis*) specimens from St-Clément-de-la-Place are not conspecific with those found in Renauleau and Sceaux-d'Anjou, but belong to a distinct species; *Clanculus* (*Clanculopsis*) *sancticlementensis* nov. sp. It differs from *Clanculus* (*Clanculopsis*) *baccatus* (Defrance, 1824) in having only four primary spiral cords on the last teleoconch whorl, whereas *C. (C.) baccatus* (Defrance, 1824) has six. Moreover, the mature apertural dentition, even in the shells in which it is most strongly developed, is always weaker than in *C. (C.) baccatus*. The sculpture in *C. (C.) sancticlementensis* is similar to that of *C. (s.s.) bonfittoi* Chirli, 2004 from the Italian Pliocene, but that species has a bifid lower columellar tooth and therefore belongs within *Clanculus* (*s.s.*). The numerous present-day Eastern Atlantic species revised by Rubio & Rolán (2002) all differ in having more numerous beaded cords of roughly equal strength on the last whorl, rather than four strong primary cords above the basal cord seen in *C. (C.) sancticlementensis*.

We have so far only found *C. (C.) sancticlementensis* at St-Clément-de-la-Place.

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

***Clanculus* (*Clanculopsis*) *umbilicovadus* nov. sp.**

Plate 15, fig. 4; Plate 19, fig. 1

Type material – Holotype NHMW 2016/0103/0248, height 4.1 mm, width 5.1 mm.

Other material – Known only from holotype.

Etymology – Compound name from Latin ‘*umbilicus*’, meaning navel and ‘*vadus, -a, -um*’, adjective meaning shallow, describing the shallow umbilicus for the genus. *Clanculus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clanculus* (*Clanculopsis*) species of small size, with depressed trochiform shell shape, sculpture composed of poorly developed narrow spiral cords and crowded, strongly prosocline axial growth lines, shallow, smooth-edged umbilicus, and weak apertural dentition.

Description – Shell small for subgenus, of medium thickness, depressed trochiform, with low spire. Protoconch consists of 1.5 smooth, convex whorls. Teleoconch of three depressed whorls, with periphery at abapical suture. Suture impressed, linear. First teleoconch whorl bearing two low, narrow spiral cords. Abapically spiral sculpture weakens further, four subobsolete cords on penultimate whorl. Axial sculpture of very fine, close-set, strongly prosocline growth lines covers entire shell. Last whorl strongly convex, bearing four narrow, poorly developed primary spiral cords, with even weaker secondary and tertiary cords developed in interspaces. Base weakly convex, bearing 11 smooth cords of irregular strength and position, with secondaries developed in some interspaces. Umbilicus shallow, surrounded by inductural callus, periumbilical edge smooth, devoid of umbilical dentition. Apertural dentition (?mature) weakly developed; anal tooth equal in strength to labial ridges; upper columellar tooth small, simple; single lower columellar tooth. Columella between upper and lower teeth smooth. Parietal callus thickened, smooth.

Discussion – Although represented by a single incom-

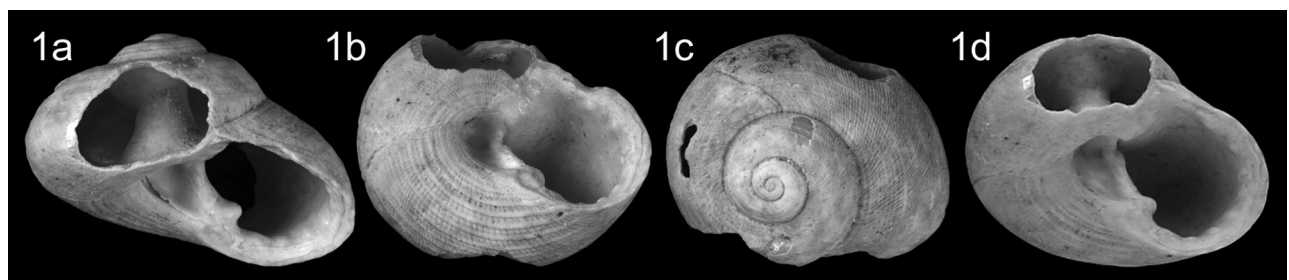


Plate 19. *Clanculus* (*Clanculopsis*) *umbilicovadus* nov. sp.; 1. **Holotype** NHMW 2016/0103/0248, height 4.1 mm, width 5.1 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

plete specimen, *Clanculus (Clanculopsis) umbilicovadus* nov. sp. is unlike any of its European Eastern Atlantic or Mediterranean fossil to present-day congeners in having a shallow umbilicus. It is also the most weakly sculptured of its congeners. The Pliocene to present-day *C. jus-sieui* (Payraudeau, 1826) is most similar in having weak sculpture and weak apertural dentition, but differs in having a deep umbilicus.

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

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

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

1884a *Jujubinus* Monterosato, p. 109

(For generic synonymy see Ceulemans *et al.*, 2016a, p. 59).

***Jujubinus coronatus* nov. sp.**
Plate 20, figs 1-3

Type material – Holotype MNHN.F.A57695, height 4.3 mm, width 3.9 mm; paratype 1 NHMW 2016/0103/0189, height 4.8 mm, width 4.3 mm; paratype 2 NHMW

2016/0103/0190, height 4.6 mm, width 3.9 mm; paratype 3 NHMW 2016/0103/0191, height 4.7 mm, width 3.9 mm; paratype 4 NHMW 2016/0103/0192 (juvenile).

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/0193 (21), LC (17), FVD (15).

Etymology – Latin ‘*coronatus*’, meaning crowned, referring to the prominently beaded adapical cord. *Jujubinus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Jujubinus* species of small size, with cyrtconoid spire, sculptured by spiral cords, adapical cord coarsely beaded giving whorls coronate appearance, and peripheral cord on last whorl stronger, every fourth bead further strengthened to give periphery crenulated appearance, intermediate cords narrow, non-beaded or 1-2 cords adjacent to sutures finely beaded.

Description – Shell small, of medium thickness, conical, with moderately high cyrtconoid spire, flattened base. Protoconch paucispiral, composed of 1.3 smooth whorls (dp = 320 µm, dn = 135 µm). Teleoconch consisting of about five straight-sided to weakly concave whorls, with periphery at abapical suture. Suture linear, impressed. Sculpture on spire whorls of one coarsely beaded broader adapical cord placed immediately below suture, giving whorls coronate appearance. Below lie narrow subequal

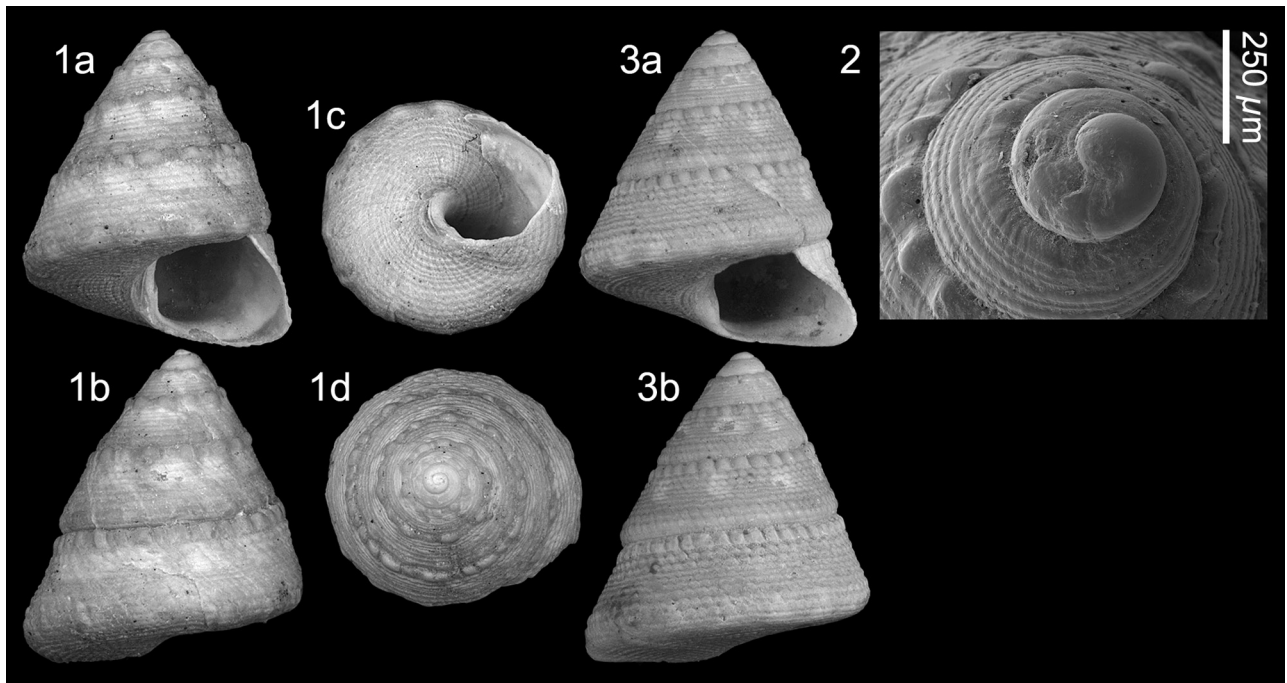


Plate 20. *Jujubinus coronatus* nov. sp.; 1. **Holotype** MNHN.F.A57695, height 4.3 mm, width 3.9 mm; 2. **Paratype 4** NHMW 2016/0103/0192, detail of protoconch (SEM image); 3. **Paratype 1** NHMW 2016/0103/0189, height 4.8 mm, width 4.3 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cords separated by narrow grooves, six on penultimate whorl; cords non-beaded or 1-2 cords closest to sutures finely-beaded. Last whorl with coronate subsutural cord, 6-8 narrow cords below, the abapical two cords strengthened to form peripheral band delimiting base and become beaded, every fourth bead further strengthened to give periphery crenulated appearance. Base imperforate, flattened, bearing about 14 concentric cords interrupted by prosocline axial growth lines. Aperture tangential; peristome discontinuous, outer lip not thickened, angled at periphery, smooth within. Columella straight, bearing a weak denticle mid-columella. Colour pattern is preserved, consisting of whitish blotches placed below the coronate adapical cord and mid-whorl (Pl. 20, fig. 3), in some specimens coalescent to form almost continuous white band (Pl. 20, fig. 1) and white blotches at periphery of last whorl coinciding with crenulations.

Discussion – This species is placed in the genus *Jujubinus* Monterosato, 1884 based on its smooth paucispiral protoconch (Pl. 20, fig. 2) and the presence of a small columellar tooth. *Jujubinus coronatus* nov. sp. is separated from all of its European Miocene to present-day congeners by the character of its coronate spire whorls. A swollen or beaded abapical cord is not uncommonly developed in members of this genus [*i.e.* the present day *J. montagui* (W. Wood, 1828); *J. exasperatus* (Pennant, 1777); *J. striatus* (Linnaeus, 1758)], but we can find no other congener with a beaded adapical cord. The most similar species is *Jujubinus redoniensis* nov. sp., from the same assemblage, which also has a beaded adapical cord; for comparison see under that species.

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

***Jujubinus* aff. *exasperatus* (Pennant, 1777)**

Plate 21, figs 1-4

- aff.*1777 *Trochus exasperatus* Pennant, p. 126.
 aff. 1923 *Trochus (Calliostoma) exasperatus* (Pennant) – Harmer, p. 723, pl. 58, fig. 18.
 1964 *Calliostoma* cf. *exasperatum* Pennant, 1777 – Brébion, p. 77.
 aff. 2003 *Jujubinus exasperatus* (Pennant, 1777) – Landau *et al.*, p. 42, pl. 9, fig. 6.
 aff. 2004 *Jujubinus exasperatus* (Pennant, 1777) – Chirli, p. 79, pl. 32, figs 10-12, pl. 33, figs 1-3 (?non fig 4).

Material and dimensions – **St-Clément-de-la-Place:** Maximum height 6.3 mm, width 4.8 mm. NHMW 2016/0103/0234-0237 (4), NHMW 2016/0103/0238 (25), LC (20), FVD (17). **Sceaux-d’Anjou:** RGM.1309732 (2).

Discussion – We echo Brébion’s (1964, p. 77) problem in the identification and placement of this small species. Whilst Brébion is correct in saying that the apertural characters are not those of *Jujubinus* Monterosato, 1884 – *i.e.*, that they lack the columellar fold or swelling – some of our specimens do have a weak swelling mid-columella, or just below (Pl. 21, fig. 1a). We note that the other small *Jujubinus* species from the Assemblage I localities also have the columellar swelling poorly developed; *i.e.*, *J. coronatus* nov. sp. and *J. redoniensis* nov. sp. More importantly, the paucispiral protoconch (Pl. 21, fig. 4) lacks the honeycomb surface sculpture that is so characteristic to the genus *Calliostoma* Swainson, 1840. Therefore placement in *Jujubinus* is more appropriate. *Jujubinus* aff. *exasperatus* is smaller shelled than the Pliocene to present day *J. exasperatus* (maximum height 6.3 mm vs. 9-15 mm for present-day specimens; Gianuzzi-Savelli *et al.*, 2004). Both the adapical and abapi-

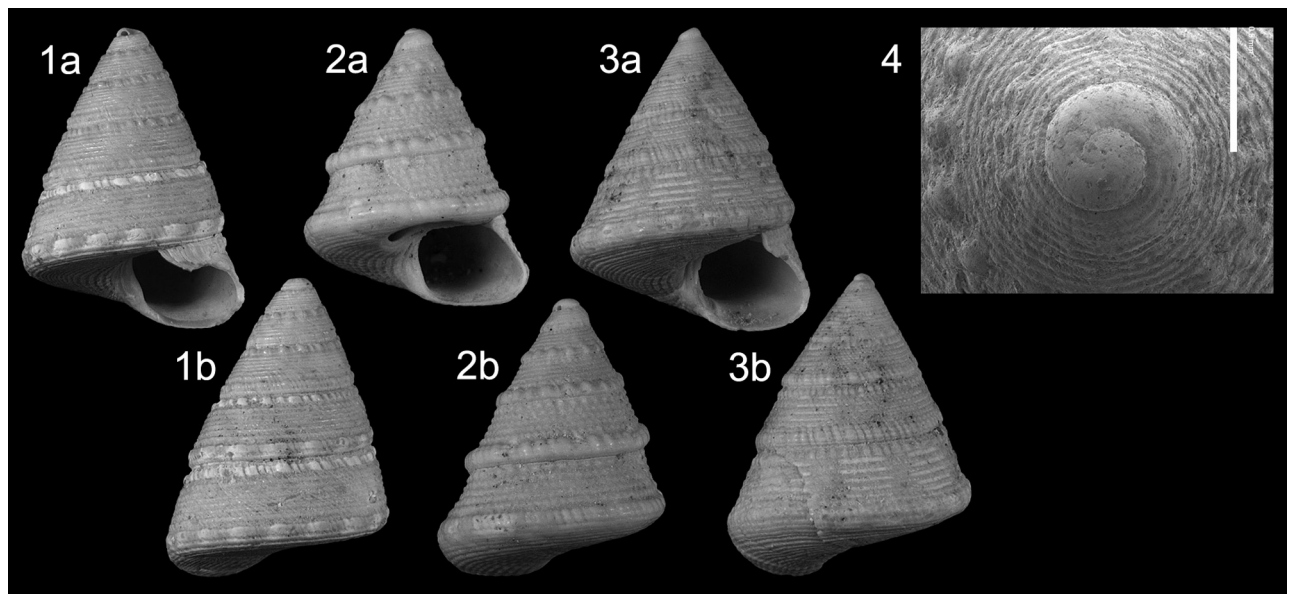


Plate 21. *Jujubinus* aff. *exasperatus* (Pennant, 1777); 1. NHMW 2016/0103/0234, height 6.0 mm; 2. NHMW 2016/0103/0235, height 4.9 mm; 3. NHMW 2016/0103/0236, height 5.3 mm; 4. NHMW 2016/0103/0237, detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cal cords are beaded, the abapical more strongly so, in some specimens leading to a crenulated periphery to the last whorl. The cords between these are smooth to finely beaded. This type of sculpture could fit within the enormous sculptural variability seen in the present-day specimens (Giannuzzi-Savelli *et al.*, 2004, figs 289-302). Some colour pattern is preserved in the fossil material, with white blotches present at the periphery, but this is not an uncommon colour pattern in *Jujubinus* species and not helpful as a specific character. Indeed the intraspecific colour pattern in *J. exasperatus* itself is highly variable (Giannuzzi-Savelli *et al.*, 2004, figs 289-302).

However, we doubt they are conspecific. The Assemblage I specimens are smaller, a feature common to many Assemblage I taxa and we hesitate to use that on its own to differentiate species, but they also have the columellar swelling far less well developed and the crenulation of the periphery of the last whorl is a feature we have not seen in *J. exasperatus*. Nevertheless, we refrain from erecting a new taxon based on this material.

Brébion (1964, p. 78) recorded this species from Assemblage I localities of Renauleau and Sceaux-d'Anjou, to which we add St-Clément-de-la-Place.

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

***Jujubinus proximus* (Millet, 1865)**

Plate 22, figs 1-3

1854 *Trochus Proximus* Millet, p. 157 (*nomen nudum*).

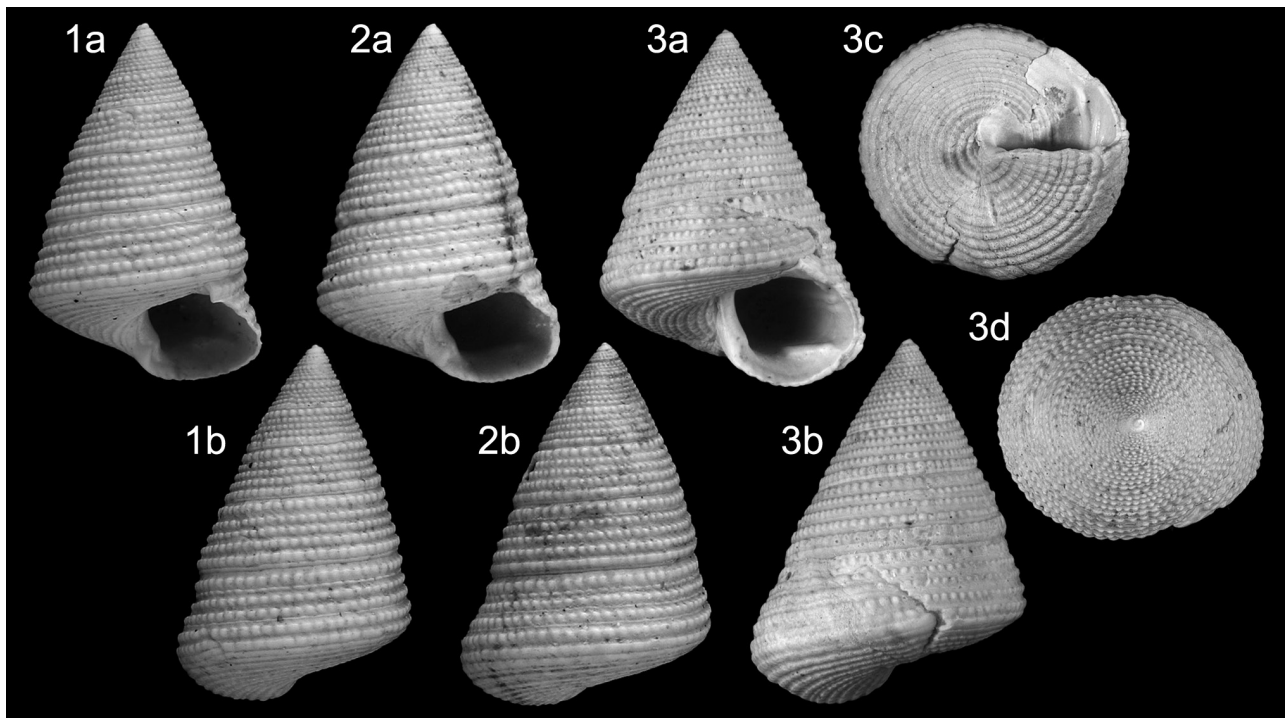


Plate 22. *Jujubinus proximus* (Millet, 1865); 1. NHMW 2016/0103/0154, height 10.0 mm, diameter 6.5 mm; 2. NHMW 2016/0103/0155, height 10.1 mm, width 6.1 mm. Le Renauleau. 3. NHMW 2016/0103/0149, height 10.1 mm, width 7.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*1865 *Trochus proximus* Millet, p. 582.

1964 *Calliostoma proximum* Millet 1854 [*sic*] – Brébion, p. 93, pl. 2, fig. 15.

Type material – Syntypes: Thorigné, Sceaux-d'Anjou and Renauleau, Musée d'Angers, France (*vide* Brébion, 1964, p. 93).

Material and dimensions – Maximum height 21.1 mm; width 15.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0149 (1), NHMW 2016/0103/0151 (40), RGM.1309674 (3), RGM.1309760 (6), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0153 (50+), RGM.1309650 (18), RGM.1309695 (9), RGM.1309714 (13), RGM.1309725 (26), RGM.1309774 (27), RGM.1309779 (20), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/0154-0155 (2), NHMW 2016/0103/0152 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1309676 (5), LC (4), FVD (1).

Original description – ‘*Trochus proximus*, Millet. Coq. en cône assez allongé, composée de 8-10 tours de spire aplatis, chacun d’eux recouvert par quatre filets légèrement perlés, dont celui de la base et celui du sommet sont plus gros et séparés par la suture. Dessous à peine concave, couvert de stries non perlées. Hauteur: 15-16 millimètres; diamètre à la base: 12 millimètres. Th., Sc, Ren. (Millet, 1865, p. 582)’

Revised description – Shell of medium size and thickness, with high regularly conical spire. Protoconch paucispiral, surface smooth. Teleoconch consisting of about seven weakly convex to straight-sided whorls, with pe-

riphery just above abapical suture. Suture linear, superficial. Sculpture of five beaded cords of subequal strength, with a secondary beaded cord between cords 1 and 2 on the last whorl in some specimens. Last whorl roundly angled at periphery. Base not sharply delimited, bearing about 12 similarly beaded, occasionally smooth cords. Aperture tangential; peristome discontinuous, outer lip not thickened, rounded at periphery, bearing an internal ridge bordering the broad, shallow, rounded siphonal canal. Columella sloping abaxially, bearing a weak columellar tooth.

Discussion – As *Jujubinus proximus* (Millet, 1865) is one of the most abundant *Jujubinus* species in the Assemblage I fauna and the original description is incorrect in certain details, we offer a revised description. The most important error in Millet's text is in describing four cords per whorl, whereas, as commented by Brébion in his revised description (1964, p. 93), it has five. Both Millet and Brébion described the basal cords as smooth, but in some specimens they are weakly beaded (Pl. 22, fig. 3c).

This species could be confused with *Calliostoma deshayesi* (Mayer, 1862), described from the older middle Miocene deposits of the Loire basin. They share the same tall conical shell shape (Pl. 22, figs 1, 2), although the apical angle can vary slightly and seems slightly wider on average than the Loire Basin shell, with some considerably broader shells also present (Pl. 22, fig. 3). However, the Assemblage I species differs in having five beaded spiral cords as opposed to the four described by Glibert (1949, p. 42) for the Loire Basin specimens, the base has more numerous concentric cords and the columella slopes abaxially, whereas in *C. deshayesi* it is almost vertical. Most importantly, the Assemblage I species does not belong within the genus *Calliostoma*, as it has a smooth and not honeycomb-sculptured protoconch and the apertural characters; columellar tooth and internal ridge bordering the siphonal canal, are characters we associate with the genus *Jujubinus*. We have not seen specimens of *C. deshayesi* from the Loire Basin and Glibert gives no description of the protoconch, but based on the shell illustrated, placement in the genus *Calliostoma* is probably correct.

Jujubinus proximus is abundant and the largest *Jujubinus* species in the Assemblage I deposits. It is particularly common at Renauleau, where it reaches a greater maximum size than at the other localities. There is some considerable degree of intraspecific variability in slenderness and basal angulation. The presence of five primary cords per whorl is consistent, although an occasional spiral thread is intercalated in the interspaces; these secondary cords gaining in strength in gerontic specimens and almost equal to the primary cords. In the very occasional specimen the spiral cords are weakly beaded or almost smooth.

Millet (1854, 1865) and Brébion (1964, p. 31) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d'Anjou and Thorigné.

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

Jujubinus cf. *proximus* (Millet, 1865)

Plate 23, fig. 1

cf.*1865 *Trochus proximus* Millet, p. 582.

Material and dimensions – NHMW 2016/0103/0194, height 14.6 mm, width 9.5 mm, Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France.

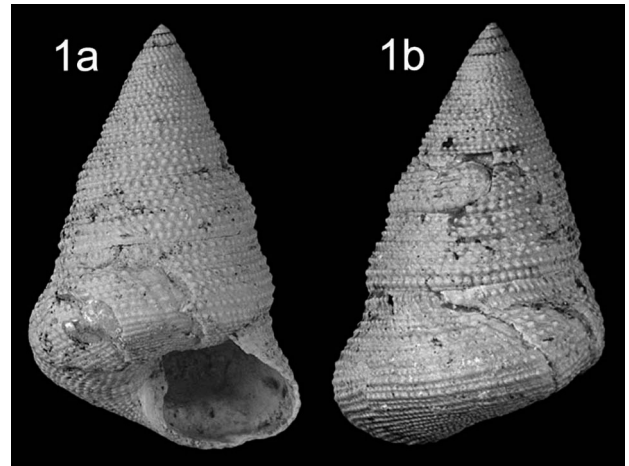


Plate 23. *Jujubinus* cf. *proximus* (Millet, 1865); 1. NHMW 2016/0103/0194, height 14.6 mm, width 9.5 mm; Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell of medium size and thickness, with high conical spire. Protoconch paucispiral, surface abraded. Teleoconch consisting of about eight weakly convex whorls, with periphery just above abapical suture. Suture linear, superficial. Sculpture of finely beaded cords of irregular strength, with an occasional secondary beaded cord intercalated, 6-7 primary cords on penultimate whorl. Last whorl slightly concave abapically, swollen and rounded at periphery. Base not sharply delimited, bearing similar beaded sculpture. Aperture tangential; peristome discontinuous, outer lip not thickened, rounded at periphery, bearing an internal ridge bordering the broad, shallow, rounded siphonal canal. Columella deeply excavated in mid-portion, bearing single, prominent, basal columellar tooth.

Discussion – The shape is closely similar to that of the largest specimens of *Jujubinus proximus* (Millet, 1865), except that the last whorl is somewhat swollen abapically, but this might be due to abnormal repair from crab attack (Pl. 23, fig. 1b). The first two whorls have five primary spiral cords, like *J. proximus*, but a secondary cord appears on the third whorl that gains in strength to become equal to the primary cords and further cords appear abapically. On later whorls the cords are subsequently narrower and more crowded than in *J. proximus*. The columellar tooth is strongly developed and the siphonal canal prominently ridged within the aperture, both more strongly developed than usual for *J. proximus*. We have insufficient material

to conclude whether this is an abnormal specimen of *J. proximus* or a distinct species.

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

***Jujubinus redoniensis* nov. sp.**

Plate 24, figs 1-2

1964 *Calliostoma couffoni* Brébion, p. 90, pl. 2, fig. 11 (*nomen nudum*).

Type material – Holotype MNHN.F.A57696, height 4.8 mm, width 3.6 mm; paratype 1 MNHN.F.A57697, height 4.8 mm, width 3.6 mm; paratype 2 NHMW 2016/0103/0205, height 5.0 mm, width 3.8 mm; paratype 3 NHMW 2016/0103/0206, height 4.8 mm, width 3.4 mm; paratype 4 NHMW 2016/0103/0207 (juvenile); paratype 5 RGM.1309667, height 5.6 mm, width 4.4 mm; paratype 6 RGM.1309668, height 6.5 mm, width 4.3 mm; paratype 7 NHMW 2016/0103/0254, height 7.8 mm, width 6.2 mm; paratype 8 NHMW 2016/0103/0255, height 7.0 mm, width 5.7 mm.

Other material – Maximum height 6.1 mm, width 4.5 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/0208 (35), RGM.1309669 (6); LC (20), FVD (26).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Jujubinus* species of small size, with a regularly conical shell shape, finely reticulated sculpture on the first two teleoconch whorls, later whorls bearing a single beaded adapical cord, smooth cords below, abapical cord more strongly developed, a flattened base bearing eight irregular cords, and a very weak columellar swelling.

Description – Shell small, of medium thickness, with tall regularly conical spire. Protoconch paucispiral, composed of 1.5 smooth whorls. Teleoconch consisting of about five straight-sided whorls, with periphery at abapical suture. Suture linear, impressed. Sculpture on first teleoconch whorls consists of two spiral cords, three on second whorl, crossed by narrow prosocline axial ribs, forming reticulated surface sculpture with small tubercles developed at intersections. On third whorl axial ribs disappear, sculpture consisting of a beaded adapical cord, beads close-set and of medium strength, cords below smooth, rounded, three on third whorl, four on penultimate, the abapical cord more strongly developed. Last whorl with beaded adapical cord, three cords below to roundly angular periphery, formed by two stronger cords. Base flattened, imperforate, bearing eight cords of irregular strength, tending to be subobsolete mid-base and stronger towards centre. Aperture tangential; peristome discontinuous, outer lip not thickened, angled at periphery, smooth within. Columella straight, bearing very weak thickening mid-columella.

Discussion – *Jujubinus redoniensis* nov. sp. belongs to a group of small *Jujubinus* species present in the Assemblage I deposits with weak columellar dentition for the genus. This species is characterised by its crowded narrow cords, beaded on early whorls, smooth, except for the adapical cord, on later whorls, and its swollen abapical cord. The regularly conical shell shape is constant, although the apical angle is slightly broader in some specimens and the usually acute angle at the base is slightly more rounded in some specimens. It is most similar to *J. coronatus* nov. sp. (see above) in having a beaded adapical cord, but differs in 1) having a regularly conical instead of cyrtocoid spire, 2) having finely reticulated sculpture on the first two teleoconch whorls, 3) although both have a beaded adapical cord, the beads in *J. coronatus* are stronger and more widely spaced, 4) the spiral cords below are less numerous, broader, stronger and rounded in *J. redoniensis* and 5) in having fewer basal cords.

Jujubinus aff. *exasperatus* (Pennant, 1777) differs in having the ad- and abapical cords more strongly beaded, which persists onto the late adult whorls and having fewer

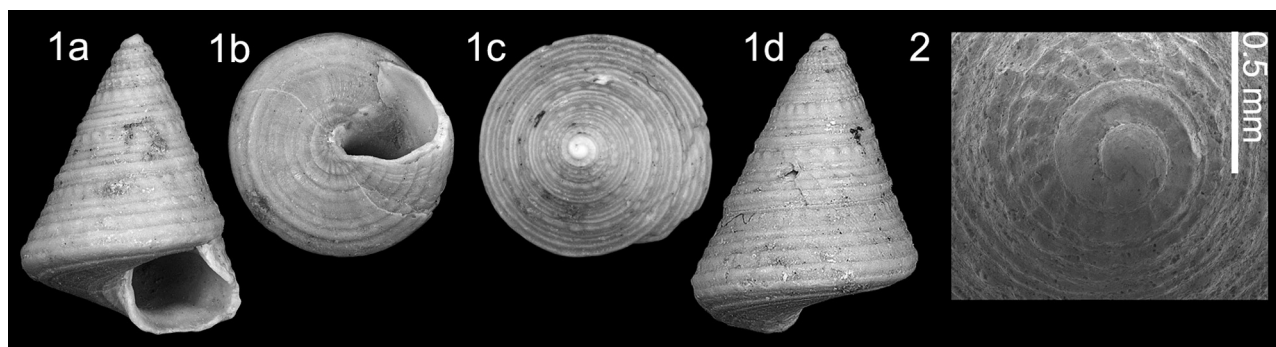


Plate 24. *Jujubinus redoniensis* nov. sp.; 1. **Holotype** MNHN.F.A57696, height 4.8 mm, width 3.6 mm; 2. **Paratype 4** NHMW 2016/0103/0207, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cords that are again wider than their interspaces. *Jujubinus striatus* (Linnaeus, 1758) has fewer cords, again wider than their interspaces. *Jujubinus sceauxensis* nov. sp. differs in having finely beaded sculpture.

Brébion (1964, p. 90) recorded this species from several Assemblage I localities (Sceaux-d'Anjou, Renauleau, St-Clément-de-la-Place).

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

***Jujubinus sceauxensis* nov. sp.**

Plate 25, figs 1-3

1964 *Jujubinus* (*Strigosella*) *andegavensis* Brébion, p. 121, pl. 3, fig. 13 (*nomen nudum*).

Type material – Holotype NHMW 2016/0103/0676, height 4.0 mm, width 4.0 mm; paratype 1 NHMW 2016/0103/0197, height 7.7 mm, width 6.1 mm; paratype 2 NHMW 2016/0103/0669, height 6.5 mm, width 6.5 mm; paratype 3 NHMW 2016/0103/0671, height 5.1 mm, width 5.3 mm; paratype 4 NHMW 2016/0103/0200, height 6.7 mm, width 6.3 mm; paratype 5 RGM.1309653, height 7.4 mm, width 6.0 mm; paratype 6 RGM.1309654, height 7.6 mm, width 6.4 mm; paratype 7 RGM.1309720, height 7.3 mm, width 6.3 mm; paratype 8 MNHN.F.A57937, height 6.7 mm, width 5.9 mm; paratype 9 MNHN.F.A57938, height 4.9 mm, width 4.8 mm.

Other material – **St-Clément-de-la-Place**: LC (2), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0204 (9), NHMW 2016/0103/0687 (6), RGM.1309655 (1), RGM.1309687 (4), RGM.1309713 (2), RGM.1309716 (1), RGM.1309721 (6), RGM.1309729 (4), RGM.1309769 (9), RGM.1348009 (2), FVD (6).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Jujubinus* species of small size, with pointed apex, low cyrtoconoid spire, sculptured by nine beaded spiral cords of equal strength, sharply angled last whorl, flattened base bearing 14 cords and narrow, shallow umbilicus.

Description – Shell small, solid, with pointed apex and moderately low cyrtoconoid spire. Protoconch paucispiral; surface abraded, but seemingly smooth. Teleoconch consisting of five straight-sided whorls, with periphery at abapical suture. Suture linear, superficial. Sculpture consists of about nine, narrow, close-set, beaded spiral cords of equal strength. Last whorl sharply angled at base. Base flattened, bearing about 14 concentric cords interrupted by prosocline axial growth lines, with a shallow, narrow,

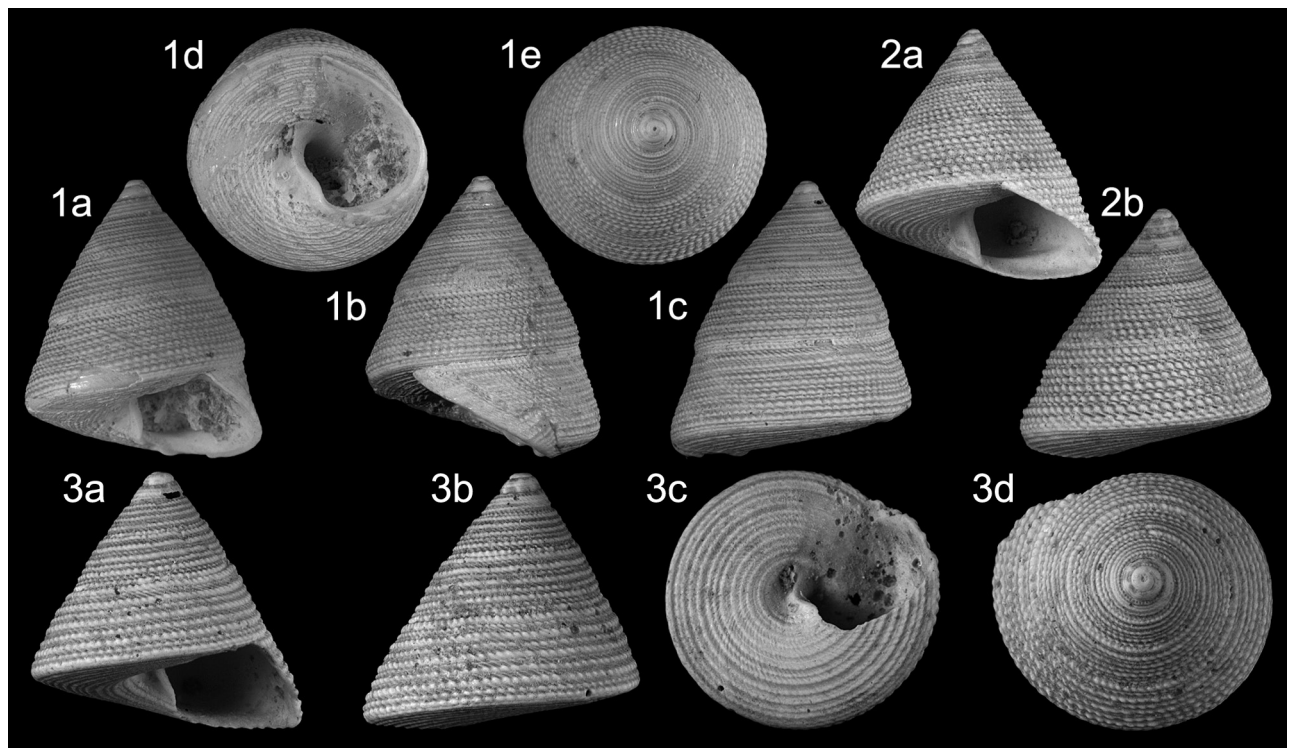


Plate 25. *Jujubinus sceauxensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/0676, height 4.0 mm, width 4.0 mm; 2. **Paratype 1** NHMW 2016/0103/0197, height 7.7 mm, width 6.1 mm; 3. **Paratype 2** NHMW 2016/0103/0669, height 6.5 mm, width 6.5 mm; 4. **Paratype 3** NHMW 2016/0103/0671, height 5.1 mm, width 5.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

smooth umbilicus. Aperture strongly tangential; peristome discontinuous, outer lip not thickened, angled at periphery, smooth within. Columella oblique, bearing a broad thickening below mid-columella.

Discussion – *Jujubinus sceauxensis* nov. sp. is a very peculiar little species. The finely beaded sculpture makes it superficially similar to some of the finely beaded calliostomiids found in the Assemblage I deposits of NW France, like *Calliostoma gratiosum* (Millet, 1865) and *C. microgemmatum* nov. sp., but the apertural characters show it to be a canthariid rather than a calliostomiid. The protoconch is abraded in all specimens, but seems to be smooth, devoid of the typical honeycomb pattern seen in *Calliostoma* species. There is no European fossil or extant species with which this new species can be usefully compared.

Brébion (1964, p. 122) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and Renauleau. Despite intensive collecting at Renauleau, we have only found it at St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Jujubinus striatus* (Linnaeus, 1758)**

Plate 26, figs 1-2

*1758 *Trochus striatus* Linnaeus, p. 759.

2016a *Jujubinus striatus* (Linnaeus, 1758) – Ceulemans *et al.*, p. 62, pl. 4, fig. 5 (*cum syn.*).

Material and dimensions – **St-Clément-de-la-Place**: Maximum height 6.1 mm, width 5.1 mm. NHMW 2016/0103/0127-0129 (3), NHMW 2016/0103/0130 (17), LC (15), FVD (15).

Discussion – Like the specimens from the Assemblage III locality of Le Pigeon Blanc, the specimens of *Jujubinus striatus* (Linnaeus, 1758) from St-Clément-de-la-Place are small compared to those found in European seas today (7-13 mm in height; Giannuzzi-Savelli *et al.*, 1994, figs 303-314). Colour pattern is preserved in some speci-

mens consisting of darker dots at the suture and vertical flammules, also seen in some present day specimens (*i.e.* Giannuzzi-Savelli *et al.*, 1994, fig. 311). The whorl coiling is somewhat disjunct in some specimens as seen in the series illustrated (Pl. 26, fig. 1). As far as we are aware, this is the stratigraphically oldest record for the species. For further discussion see Ceulemans *et al.* (2016a, p. 6).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Ceulemans *et al.*, 2016a), Guadalquivir Basin, S. Spain (Landau *et al.*, 2011); western Mediterranean, NE Spain (Martinell, 1978); central Mediterranean, Italy (Chirli, 2004). Upper Pliocene: Atlantic, Red Crag, England (Harmer, 1923); western Mediterranean, Estepona, S. Spain (Landau *et al.*, 2003); central Mediterranean, Italy (Spadini, 1986; Cavallo & Repetto, 1992). Pleistocene: Atlantic, Britain (Harmer, 1923); The Netherlands (Pouwer & Wesselingh, 2012); western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Italy (Malatesta, 1960; Taviani *et al.*, 1998). Present-day: Atlantic, Isle of Man to Canaries, Madeira, Azores and Mediterranean, from the extreme low tide to 200m deep on seaweeds and small stones (Poppe & Goto, 1991).

Genus *Colliculus* Monterosato, 1888

1888 *Colliculus* Monterosato, p. 171. Type species (subsequent designation, Bucquoy, Dautzenberg & Dollfus, 1898, p. 773): *Trochus adansonii* Payraud, 1826, present-day, Mediterranean.

For generic synonymy see Ceulemans *et al.* (2016a).

Note – We follow Lozouet *et al.* (2001, p. 18) in giving full genus rank to *Colliculus* Monterosato, 1888. For further discussion see Ceulemans *et al.* (2016a).

***Colliculus biangulatus* (Eichwald, 1830)**

Plate 27, fig. 1

*1830 *Trochus biangulus* Eichwald, p. 221.

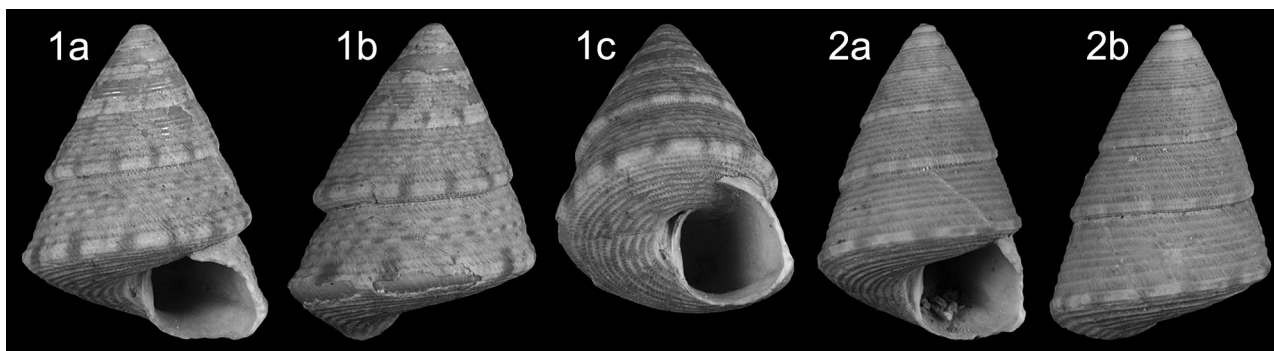


Plate 26. *Jujubinus striatus* (Linnaeus, 1758); 1. NHMW 2016/0103/0127, height 5.5 mm, width 4.3 mm; 2. NHMW 2016/0103/0128, height 5.5 mm, width 3.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

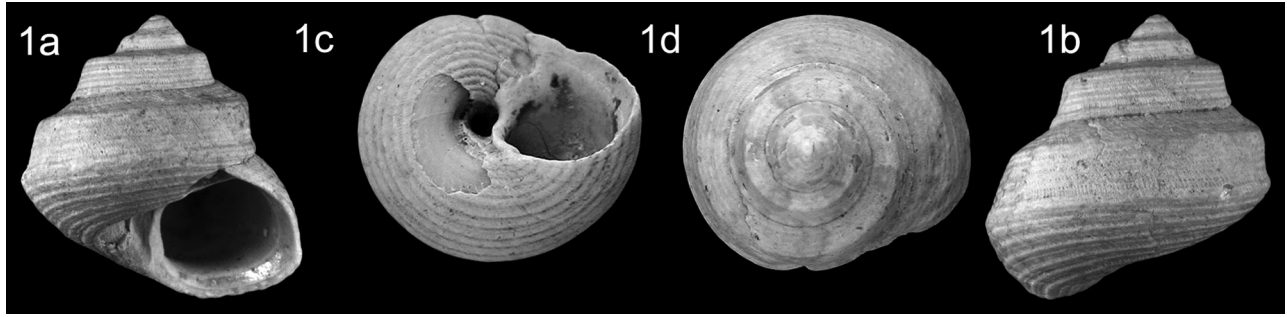


Plate 27. *Colliculus biangulatus* (Eichwald, 1830); 1. NHMW 2016/0103/0037, height 5.7 mm, width 5.5 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- 1856 *Trochus biangulus* Eichw. – Hörnes, p. 460, pl. 45, fig. 15.
 non 1917 *Gibbula (Colliculus) biangulata* (Eichwald) – Cossmann & Peyrot, p. 124, pl. 4, figs 20-22 [= *Colliculus aquitanicus* (Cossmann & Peyrot, 1917)].
 1928 *Gibbula biangulata* Eichw. – Friedberg, p. 486, pl. 30, fig. 20.
 1949 *Gibbula biangulata* Eichwald, 1830 – Glibert, p. 58, pl. 3, fig. 8.
 1964 *Gibbula (Colliculus) biangulata* Eichwald, 1830 – Brébion, p. 105.
 1966 *Gibbula biangulata* Eichwald, 1830 – Strausz (?partim), p. 35, pl. 52, figs 21-23 (?pl. 53, figs 1-3).
 1975 *Gibbula (Gibbula) cf. varia* (Linnaeus) – Bałuk, p. 35, pl. 3, fig. 1.
 1975 *Gibbula (Gibbula) cf. varia* (Linnaeus, 1766 [sic]) – Bałuk, p. 35, pl. 3, fig. 1.
 2006 *Gibbula (Gibbula) varia* (Linnaeus, 1766 [sic]) – Bałuk, p. 35, pl. 3, fig. 1 [non *Gibbula varia* (Linnaeus, 1758)].

Material and dimensions – Maximum height 8.4 mm, width 7.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0036 (1), NHMW 2016/0103/0037 (50+), RGM.1309524 (50+), RGM.1309532 (30), RGM.1309591 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou:** NHMW 2016/0103/0038 (8), RGM.1309509 (5), LC (2), FVD (13). **Renaleau:** NHMW 2016/0103/0117 (50+), LC (50+), FVD (50+). **Beugnon:** RGM.1309533 (1), RGM.1309742 (20), FVD (1).

Discussion – *Colliculus biangulatus* (Eichwald, 1830), which is widespread in the middle and upper Miocene NW French assemblages, is most like the older Atlantic lower Miocene *C. aquitanicus* (Cossmann & Peyrot, 1917) from the Aquitaine Basin of France, but lower-spired and more strongly biangular than the Aquitanian species, with narrower and more numerous spiral cords between the angulations.

Brébion (1964, p. 106) recorded this species from numerous Assemblage I deposits (Sceaux-d'Anjou, St-Michel, Les Pierres Blanches, Thorigné, St-Clément-de-la-Place).

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949); Paratethys, Austria (Hörnes, 1856), Hungary (Strausz, 1966), Poland (Friedberg, 1928; Bałuk, 1975, 2006). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

***Colliculus insignis* (Millet, 1854)**

Plate 28, fig. 1

- *1854 *Trochus Insignis* Millet, p. 156.
 1865 *Trochus insignis* Millet – Millet, p. 582.
 1917 *Gibbula (Colliculus) sosensis* Cossmann & Peyrot, p. 127, pl. 4, figs 33-36.
 1964 *Gibbula (Colliculus) sosensis* Cossmann & Peyrot, 1916 – Brébion, p. 106, pl. 2, figs 34, 35.

Material and dimensions – Maximum height 7.3 mm, width 8.7 mm. **St-Clément-de-la-Place:** NHMW 2016/

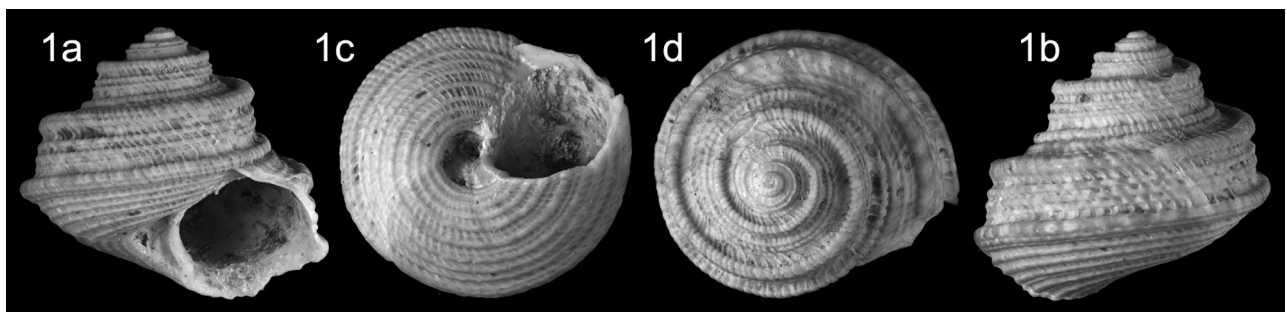


Plate 28. *Colliculus insignis* (Millet, 1854); 1. NHMW 2016/0103/0039, height 5.5 mm, width 5.9 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

0103/0039 (1), NHMW 2016/0103/0040 (50+), RGM.1309600 (4), RGM.1309618 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0041 (50+), RGM.1309510 (37), RGM.1309511 (50+), RGM.1309516 (39), RGM.1309518 (50+), RGM.1309726 (5), RGM.1347852 (45), RGM.1347916 (12), RGM.1347996 (47), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0116 (50+), LC (50+), FVD (50+). **Beugnon**: NHMW 2016/0103/0042 (3), RGM.1309527 (1), RGM.1309537 (34), RGM.1309738 (13), RGM.1309539 (2), RGM.1309629 (6).

Discussion – This species is easily recognised by its sculpture composed of strongly developed shoulder and peribasal cords, which make the whorl profile sharply bi-angular, with two weaker cords running between these major cords. The axial sculpture of close-set lamellar growth lines, which cross the ribs elevated, give the surface a somewhat scabrous appearance. However, the name *Gibbula (Colliculus) sosensis* Cossmann & Peyrot, 1917 must give way to the older name *Trochus insignis* Millet, 1854. The original description highlights the strong spiral sculpture: ‘*Insignis, Millet. – Sceaux, Thorigné. – Cette espèce a quelques rapports avec le genre Dauphinula [incorrect spelling of Delphinula Gray, 1847], par sa bouche, dont les bords sont comme réunis, à raison de la décurrence des bords columellaires (1854, p. 156).*’ This description was later enlarged: ‘*Trochus insignis, Millet. Coq. petite, courte, composée de 5 tours de spire, chacun d’eux creusé en gouttière spirale est entouré de quatre liserets arrondis, dont deux plus minces, placés au centre. Dessous bombé, couvert de fines stries. Ombilic lisse, assez profond. Hauteur et diamètre, 6 à 7 millimètres. Sceaux, Thorigné, Renauleau (Millet, 1865, p. 582).*’ The description leaves little doubt that it refers to this species. We cannot satisfy the requirements of Article 23.9.1.2 (ICZN 1999a) to consider Millet’s name a *nomen oblitum*. Therefore *Colliculus insignis* (Millet, 1854) must take priority over *Colliculus sosensis* (Cossmann & Peyrot, 1917).

The most similar species is *Colliculus neraudeaui* Ceulemans, Van Dingenen & Landau, 2016, from the lower Pliocene Assemblage III locality of Le Pigeon Blanc, Loire-Atlantique, NW France, but *C. insignis* differs in being smaller-shelled, in having two cords between the stronger shoulder and basal cords instead of one in *C. neraudeaui*, in having more numerous but finer cords on the base and a narrower, shallower umbilicus. The lamellar axial growth lines seen in *C. insignis* seem to be absent in *C. neraudeaui*, although the surface of the latter, which is known from a single complete specimen plus several fragments, is somewhat abraded.

Millet (1854, 1865) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Renauleau and Thorigné, to which Brébion (1964, p. 107) added St-Clément-de-la-Place.

Distribution – Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1916). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964).

Genus *Gibbula* Risso, 1826

1826 *Gibbula* Risso, p. 134. Type species (by subsequent designation, Herrmannsen, 1847, p. 473): *Trochus magus* Linnaeus, 1758, present-day, Mediterranean.

***Gibbula brebioni* nov. sp.**

Plate 29, figs 1-2

Type material – Holotype MNHN.F.A57689, height 8.7 mm, width 7.5 mm; paratype 1 NHMW 2016/0103/0108, height 9.7 mm, width 8.0 mm; paratype 2 NHMW 2016/0103/0109, height 8.2 mm, width 8.0 mm; paratype 3 NHMW 2016/0103/0110, height 9.5 mm, width 8.1 mm; paratype 4 RGM.1309753, height 7.4 mm, width 6.4 mm; paratype 5 RGM.1309772, height 7.4 mm, width 6.7 mm.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/0111 (10 + 50 juveniles), RGM.1309754 (10), RGM.1309773 (9), LC (11), FVD (14). **Sceaux-d'Anjou**: NHMW 2016/0103/0216 (8), RGM.1309657 (4), FVD (2). **Renauleau**: NHMW 2016/0103/1431 (1), LC (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Gibbula* species of small size, with regularly conical spire, shallow suture, sculpture of fine, close-set spiral cords, much narrower than their interpaces, axial sculpture restricted to prosocline growth lines, and weak columellar fold.

Description – Shell small, trochiform, with regularly conical spire. Protoconch paucispiral, composed of 1.5 smooth whorls. Teleoconch of 5.5 whorls, profile of early whorls convex, weaker so abapically, periphery at abapical suture. Suture weakly impressed, linear. Sculpture of fine, close-set spiral cords, about one quarter width of their interspaces, irregularly interrupted by strongly prosocline growth lines. Last whorl angled at base. Base not sharply delimited, bearing narrow, shallow umbilicus and about 14 concentric cords. Aperture subtrigonal, outer lip simple, bevelled edge, roundly angled at periphery. Peristome incomplete. Columella bearing weak fold placed just below mid-height. Parietal callus poorly developed, restricted to a thin callus wash. Colour pattern of vertical flammules is preserved.

Discussion – At first glance *Gibbula brebioni* nov. sp. can be confused with *Gibbula striatellata* (Millet, 1865); both are about the same size and both have a regularly

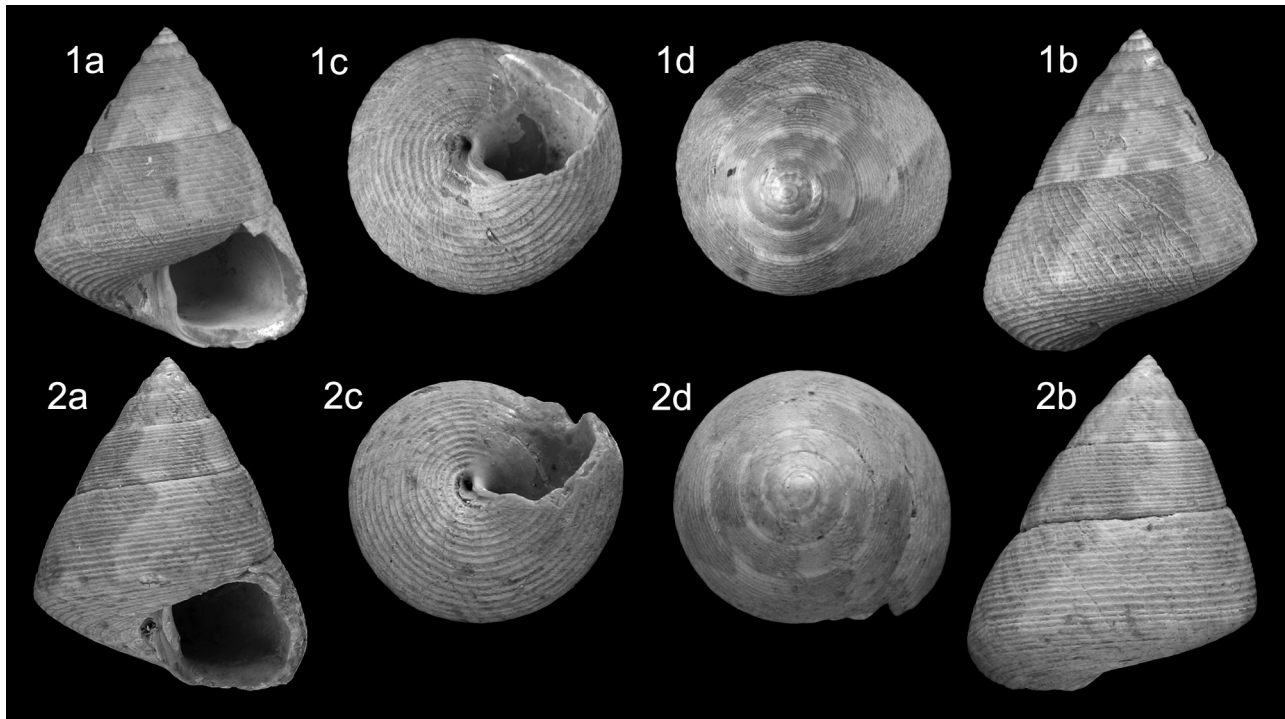


Plate 29. *Gibbula brebioni* nov. sp.; 1. **Holotype** MNHN.F.A57689, height 8.7 mm, width 7.5 mm; 2. **Paratype 1** NHMW 2016/0103/0108, height 9.7 mm, width 8.0 mm. Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

conical shell shape, however, *G. brebioni* has finer spiral sculpture and lacks the swollen suprasutural cord present in *G. striatellata*, moreover, the suture is deeper in *G. striatellata*. The character of the base is similar in both species; a shallow, narrow umbilicus and dense spiral cords.

In the present-day faunas the Mediterranean *G. spratti* (Philippi, 1844) also has dense spiral sculpture and a narrow, shallow umbilicus, but differs in having a less regularly conical profile, the whorls are more convex, especially the last whorl, which is regularly rounded and not angled at the base. *Gibbula adriatica* (Philippi, 1844) has a similar shell profile, but coarser spiral sculpture. In the fossil assemblages none of the *Gibbula* species figured by Cossmann & Peyrot (1917) from the lower and middle Miocene Aquitaine Basin of France have such fine spiral sculpture.

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

***Gibbula clanculiforma* nov. sp.**

Plate 30, fig. 1

Type material – Holotype NHMW 2016/0103/0249, height 5.5 mm, width 5.8 mm.

Other material – Known only from holotype.

Etymology – Named reflecting the superficial resem-

blance to shells of the genus *Clanculus*. *Gibbula* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Gibbula* species of small size, with low conical spire, sculpture composed of numerous beaded spiral cords on both dorsum and base, adapical cord slightly more strongly developed, last whorl with rounded periphery in which base is not strongly delimited from dorsum, narrow, but deep umbilicus, and single weak columellar tubercle.

Description – Shell small, solid, trochiform, with low conical spire. Protoconch not preserved. Teleoconch of four weakly convex whorls, with periphery at abapical suture. Suture impressed, shallowly canaliculate. Sculpture on first teleoconch whorl of three cords, with a fourth appearing on second half of first whorl below adapical suture, crossed by close-set, prosocline axial ribs forming fine reticulated pattern, with small tubercles developed at intersections. Abapically, axial sculpture weakens, visible only in interspaces between cords, cords increase in number, irregular in strength and become strongly beaded, the adapical cord more strongly developed. Last whorl depressed, slightly concave below suture, strongly rounded at periphery, bearing eight beaded cords above periphery. Base poorly delimited,

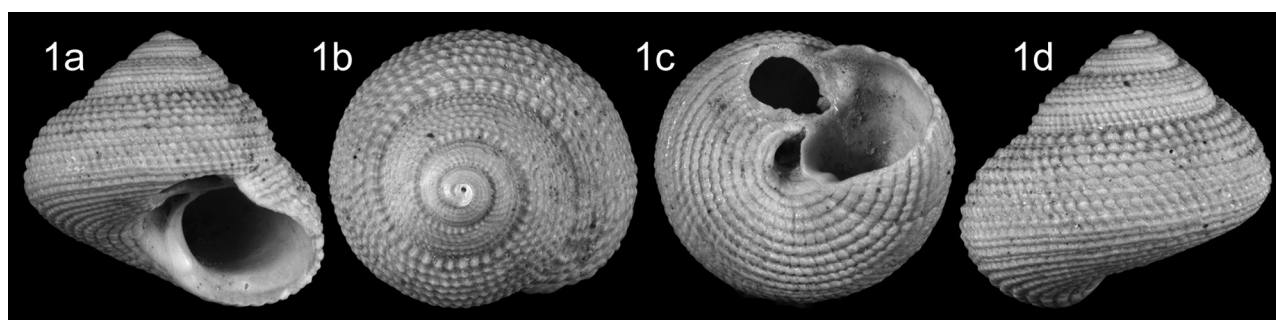


Plate 30. *Gibbula clanculiforma* nov. sp.; 1. **Holotype** NHMW 2016/0103/0249, height 5.5 mm, width 5.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

bearing 13 beaded cords, narrowly but deeply imbilicate. Peristome incomplete. Outer lip simple, slightly concave adapically, rounded and somewhat flared abapically, smooth within. Columella excavated, bearing weak tubercle placed just below mid-height. Columella callus erect, forming medial border of umbilicus. Parietal callus poorly developed.

Discussion – Although represented by a single specimen, *Gibbula clanculiforma* nov. sp. is so unlike any of its congeners that it merits description. At first glance the sculpture is similar to that of shells of the genus *Clanculus* de Montfort, 1810, especially the strongly beaded species like *Clanculus (Clanculopsis) baccatus* (Defrance, 1824) (see above), but *Clanculus* species have a very characteristic columellar and umbilical structure (see Pl. 15, figs 1-4), absent in *G. clanculiforma*. Based on shell shape and sculpture, placement in the Calliostomatidae Thiele, 1924 could also be a possibility, but these species have a smooth columella. The small very solid nature of the shell and the small but well developed columellar tubercle lead us to include this small shell within the Cantharidinae Gray, 1857, genus *Gibbula* Risso, 1826. There are no Neogene to present-day eastern Atlantic or Mediterranean species with which this species can be compared. Some of the *Gibbula* species from the Pliocene North Sea Basin such as *G. octosulcata* (Nyst, 1835) and *G. beetsi* van Regteren Altena, 1954 are similar in shape and have beaded spiral cords, but are clearly not conspecific.

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

***Gibbula conicomagus* nov. sp.**

Plate 31, figs 1-2

Type material – Holotype NHMW 2016/0103/1654, height 14.1 mm, width 11.7 mm; paratype 1 NHMW 2016/0103/1655, height 14.8 mm, width 11.4 mm (incomplete).

Other material – Maximum height 13.7 mm, width 13.3 mm (incomplete). **Renauleau**: FVD (2).

Etymology – Name reflecting the sculpture, similar to that of the *G. magus* species group and the conical shell shape. *Gibbula* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Gibbula* species of medium size, with regularly conical shell shape, rugose sculpture of low axial folds crossed by six spiral cords, abapical cord reinforced forming periphery, fine scabrous axial sculpture in interspaces between cords, last whorl angled at peribasal cord, base flattened bearing about six cords and narrow umbilicus.

Description – Shell medium-sized, solid, trochiform, with regularly conical spire. Protoconch not preserved. Teleoconch of 5.5 almost flat-sided whorls, with periphery at abapical suture. Suture deeply impressed, linear. Sculpture of weakly developed, low, opisthocline axial rugae and six spiral cords; abapical cord strengthened forming periphery. Numerous fine axial lamellae visible in interspaces between cords, so that sculpture grossly rugose, finely scabrous. Last whorl angled at base. Base flattened, sharply delimited by rounded peribasal cord, bearing narrow, shallow umbilicus and about six concentric cords. Aperture subtrigonal, outer lip simple, beveled edge, angled at periphery. Peristome incomplete. Columella bearing weak fold placed just below mid-height. Parietal callus not developed.

Discussion – The sculpture of *Gibbula conicomagus* nov. sp. composed of opisthocline axial rugae, crossed by spiral cords with fine axial lamellae present in the interspaces between the cords suggests that it belongs to the *G. magus* species group, although it differs from *G. magus* (Linnaeus, 1758), *G. sagus* (Defrance, 1828) and *G. fanulum* (Gmelin, 1791) in having a regularly conical spire with almost flat sided whorls. Moreover, unlike its congeners mentioned above, the axial rugae are hardly raised. In these characters it is similar to the species from the middle Miocene Karaman Basin of Turkey recorded as *G. cf. sagus* by Landau *et al.* (2013), which also has a regular conical spire and weak axial rugae, but the

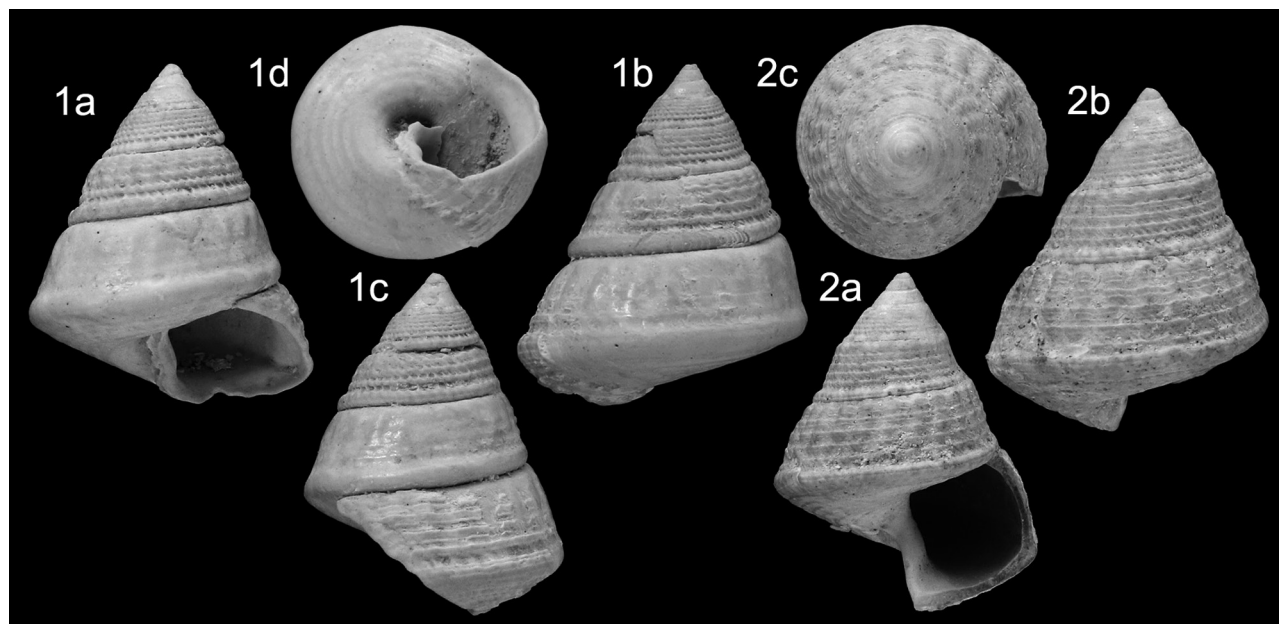


Plate 31. *Gibbula conicomagus* nov. sp.; 1. **Holotype** NHMW 2016/0103/1654, height 14.1 mm, width 11.7 mm; 2. **Paratype 1** NHMW 2016/0103/1655, height 14.8 mm, width 11.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Turkish species has a broader apical angle and finer and more irregular spiral sculpture.

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

***Gibbula fanulum* (Gmelin, 1791)**

Plate 32, fig. 1

- *1791 *Trochus fanulum* Gmelin, p. 3573.
- 1964 *Gibbula (Forskalea) fanulum* Gmelin in Linné, 1790 [sic] – Brébion, p. 113, pl. 3, fig. 7.
- 2003 *Gibbula (Forskalea) fanulum* (Gmelin, 1791) – Landau *et al.*, p. 49, pl. 11, fig. 1 (cum syn.).
- 2004 *Gibbula (Forskalea) fanulum* (Gmelin in L., 1790) [sic] – Chirli, p. 70, pl. 28, figs 11, 12, pl. 29, figs 1-5.

Material and dimensions – Maximum height 10.6 mm,

width 11.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0099 (1), NHMW 2016/0103/0100 (50+), RGM.1309506 (50+), RGM.1309507 (30), RGM.1309522 (50+ juveniles), RGM.1309559 (2), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0103 (13), LC (24), FVD (19). **Renauleau**: NHMW 2016/0103/1414 (32), LC (22), FVD (25).

Discussion – *Gibbula fanulum* (Gmelin, 1791) is a very characteristic species, with its strongly nodular sculpture at the shoulder and deep groove between the shoulder and strong, rounded basal cord. This characteristic sculpture makes it difficult to confuse *G. fanulum* with any of its congeners. Pracchia (1998) considered the presence or absence of the strong axial nodules on the periphery in Italian Pliocene populations of *G. fanulum* an ecophenotypic character, the nodular form inhabiting rocky environment and the smoother form living on sandy substrate, without intermediate forms. The specimens from the Assemblage I locality of St-Clément-de-la Place are

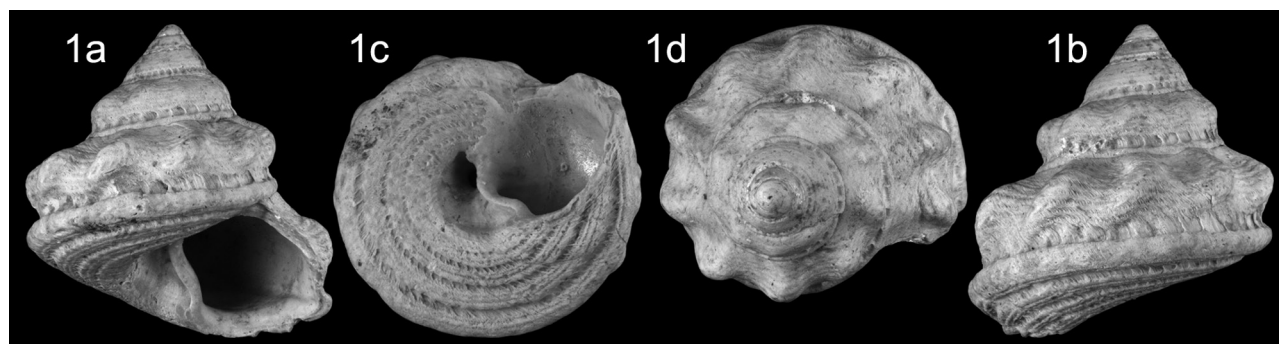


Plate 32. *Gibbula fanulum* (Gmelin, 1791); 1. NHMW 2016/0103/0099, height 9.4 mm, width 9.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

strongly nodular, suggesting a rocky environment nearby. As repeatedly encountered in this monograph, the Assemblage I specimens are considerably smaller than the Mediterranean Pliocene and present-day shells, which attain up to 21 and 19 mm in height respectively (Landau *et al.*, 2003; Poppe & Goto, 1991).

Brébion (1964, p. 113) recorded this species from only Assemblage I localities (Sceaux-d'Anjou, Renauleau, Thorigné, St-Clément-de-la-Place, St-Michel). These are the stratigraphically oldest records for the species.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: central Mediterranean, Italy (Chirli, 2004), Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2003); central Mediterranean, Italy (Sacco, 1896a; Malatesta, 1974; Spadini, 1986; Pracchia, 1988). Pleistocene: western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1916; Malatesta, 1960; Brambilla *et al.*, 1988; Dell'Angelo & Forli, 1995). Present-day: southern Portugal and Mediterranean, shallow waters, where it prefers *Posidonia* fields (Poppe & Goto, 1991).

***Gibbula marianae* nov. sp.**

Plate 33, fig. 1

Type material – Holotype NHMW 2016/0103/0677, height 6.1 mm, width 6.4 mm; paratype 1 NHMW 2016/0103/0677, height 6.0 mm, width 5.7 mm; paratype 2 MNHN.F. A57941, height 6.2 mm, width 5.8 mm, **Sceaux-d'Anjou**. Paratype 3 RGM.1309601, height 4.2 mm, width 4.5 mm, **St. Clément-de-la-Place**.

Other material – **Sceaux-d'Anjou**: RGM.1348010 (4), FVD (2).

Etymology – Named after Mariana Mihai, lawyer and wife of the second author, in recognition of her support and patience. *Gibbula* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Gibbula* species of small size, with low conical shell shape, strong spiral sculpture composed of elevated cords, strongly beaded by close-set axial lamellae; on last whorl two stronger cords above periphery, with two weaker cords between, periphery marked by thickened peribasal cord, flattened imperforate base bearing six cords, and thickened columella bearing poorly delimited tooth.

Description – Shell small, low trochiform. Protoconch paucispiral, surface smooth. Teleoconch of four depressed whorls separated by shallow suture. Sculpture on first teleoconch whorl composed of three narrow, elevated cords. Abapically, ad- and abapical cords strengthen; abapical cord strongly dominant. On penultimate whorl fourth cord appears above suture. Close-set, strongly prosocline axial lamellae cross cords forming beads, most strongly developed on ad- and abapical cords. Last whorl acutely angled at base, bearing strongly beaded cords 1 and 3, cord 2 weaker, with a further weak cord intercalated between cords 1 and 2. Peribasal cord delimiting base strongly developed, weakly beaded. Base flattened, bearing six narrow equal cords; umbilicus absent. Aperture subquadrate. Outer lip with bevelled edge, angled at periphery. Columella thickened, sloping abaxially, bearing poorly-delimited tooth abapically. Parietal callus not developed.

Discussion – *Gibbula marianae* nov sp. is easily separated from its congeners by its strongly beaded spiral sculpture. This sculpture is reminiscent of the *Colliculus* species discussed previously [*i.e.* *C. insignis* (Millet, 1854)], but the shell lacks the deep umbilicus that we associate with that genus. We cannot find any European fossil or extant species with which to usefully compare this species, which has so far only been found at Sceaux-d'Anjou and St. Clément-de-la-Place.

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

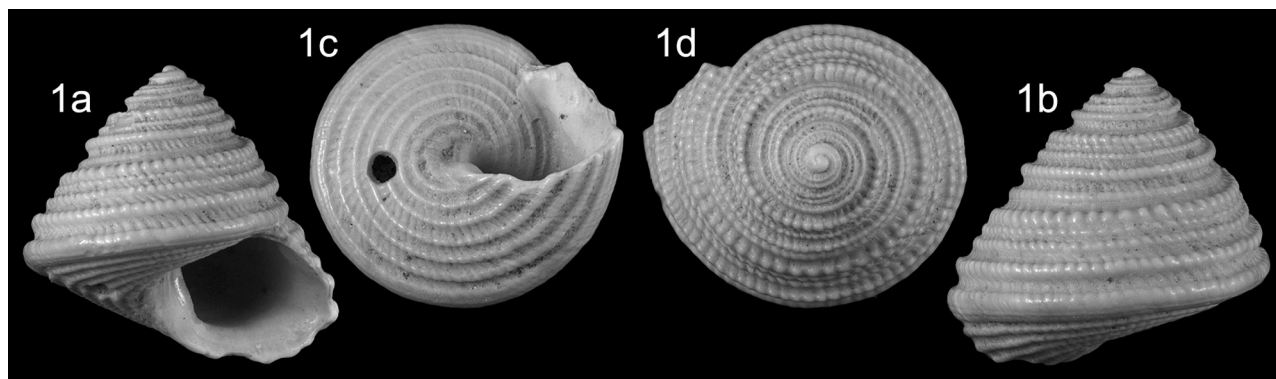


Plate 33. *Gibbula marianae* nov sp.; 1. **Holotype** NHMW 2016/0103/0677, height 6.1 mm, width 6.4 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Gibbula provosti* Ceulemans, Van Dingenen & Landau, 2016**

Plate 34, figs 1-2

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

*2016a *Gibbula provosti* Ceulemans, Van Dingenen & Landau, p. 62, pl. 4, fig. 6; pl. 5, fig. 1.

Material and dimensions – Maximum height 7.5 mm, width 8.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0112-0113 (2), NHMW 2016/0103/0114 (9 + 30 juveniles), RGM.1309756 (45 juveniles), RGM.1309771 (50+ juveniles), LC (3), FVD (20). **Sceaux-d’Anjou**: NHMW 2016/0103/0218 (21), RGM.1309691 (2), RGM.1309703 (1), RGM.1309731 (2), RGM.1309762 (13), RGM.1309765 (10), RGM.1347917 (1), LC (10), FVD (12). **Renaleau**: LC (1).

Discussion – The species described and illustrated by Brébion (1964, p. 109, pl. 3, fig. 3) as *Gibbula (Colliculus) varia* var. *termieri* Dollfus mss. (emend) (*nomen nudum*) was formally described as *Gibbula provosti* Ceulemans, Van Dingenen & Landau, 2016, based on material from the lower Pliocene Assemblage III locality of Le Pigeon Blanc. However, the species is commoner and better preserved at the upper Miocene Assemblage I locality of St-Clément-de-la-Place. *Gibbula provosti* is characterised by its strongly depressed spire, its surface covered by fine, narrow spiral cords, its strongly oblique columella bearing a relatively welldeveloped tooth, its base bearing prominent cords and growth lines, and its narrow smooth umbilicus. The plentiful material at St-Clément-

de-la-Place allows us to make several further observations not included in the original description. There is an important change in shape with ontogeny. Juvenile shells are even more strongly depressed and lack the concave adapical half to the last whorl seen in adult specimens (Pl. 34, fig. 2). This can be seen just developing at the aperture in the juvenile shell illustrated (Pl. 34, fig. 1). Secondly, a colour pattern is preserved, especially in the juvenile shells consisting of spiral rows of dots or circles similar to that seen in several present-day European *Gibbula* species [*i.e.* *G. umbilicaris* (Linnaeus, 1758)]. This colour pattern was not commented on in the original description, but can be seen in paratype 3 from Le Pigeon Blanc (NHMW 2015/0133/0068; Ceulemans *et al.*, 2016a, pl. 5, fig. 1).

Gibbula provosti is similar to *G. varia* (Linnaeus, 1758) from the Pliocene to present-day Mediterranean, but differs in 1) being smaller in size, 2) having a more depressed shell, especially the last whorl, 3) having finely beaded spiral cords, 4) having more prominent sculpture on the base, 5) having a more oblique columella, 6) having a more strongly developed columellar tooth, and 7) having a narrower umbilicus.

A similar species was figured by Brébion (1964, pl. 3, figs 1, 2) under the name *G. varia* var. *monodontoïdes* (Millet, 1854) (*nomen nudum*; made available by Millet, 1865) from localities in Assemblages I and II. This species has a less depressed shell than *Gibbula provosti* and a biangular whorl profile, the last whorl angled at the shoulder and base. It is similar to *G. varia*, but was said to differ in the complete absence, or almost so, of the umbilicus, which is covered by a columellar callus. Unfortunately, no basal view was offered by Brébion and we have found no further specimens of this species.

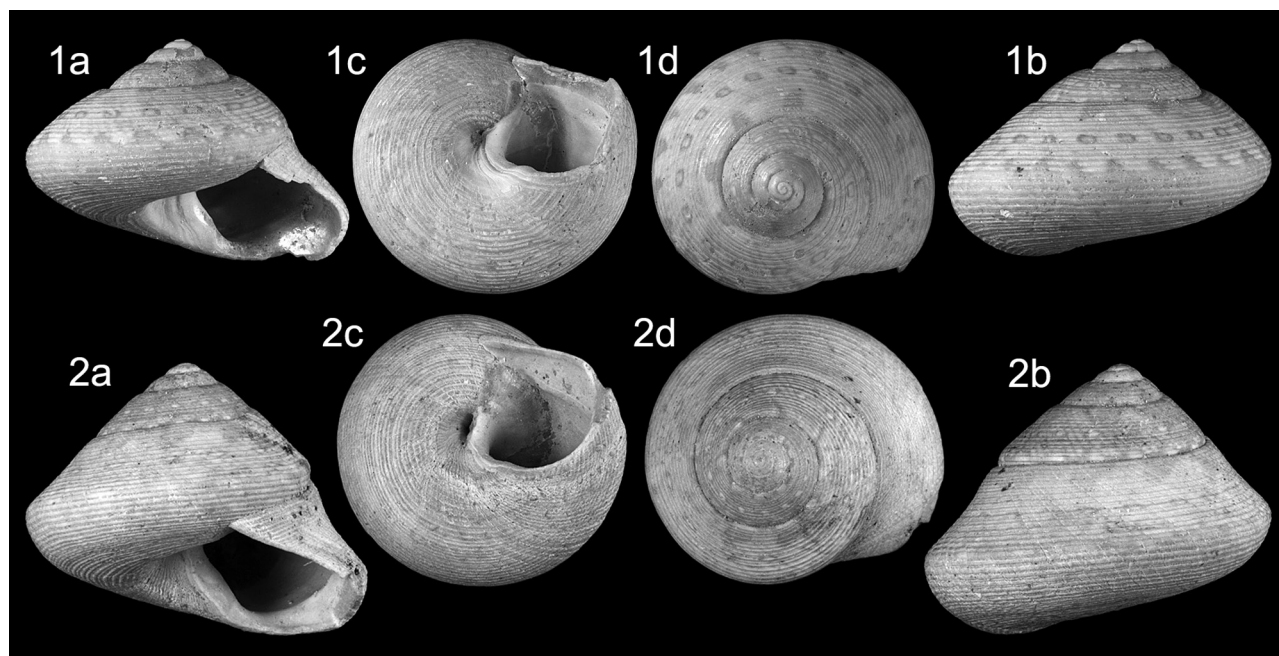


Plate 34. *Gibbula provosti* Ceulemans, Van Dingenen & Landau, 2016; 1. NHMW 2016/0103/0112, height 4.6 mm, width 6.7 mm; 2. NHMW 2016/0103/0113, height 6.7 mm, width 8.2 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Brébion (1964, p. 110) recorded *G. provosti* from the Assemblage III localities of Le Pigeon Blanc and Le Giron-dor, to which we add the Assemblage I locality of St-Clément-de-la-Place.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016a).

***Gibbula sagus* (Defrance, 1828)**

Plate 35, figs 1-3

- *1828 *Trochus sagus* Defrance, p. 478.
- 1854 *Trochus Sagus* Millet, p. 156.
- 1903 *Gibbula saga* Defrance – Dollfus *et al.*, p. 7, pl. 32, figs 3, 4.
- 1917 *Gibbula pseudomagus* d’Orbigny – Cossmann & Peyrot, p. 110, pl. 3, figs 63-65.
- 1938 *Gibbula saga* Defrance – Peyrot, p. 26, pl. 1, figs 22-23.
- 1949 *Gibbula sagus* Defrance, 1828 – Glibert, p. 50, pl. 3, fig. 4.
- 1964 *Gibbula sagus* Defrance, 1826 [*sic*] – Brébion, p. 102.

Material and dimensions – Maximum height 12.0 mm, width 12.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0102 (1), NHMW 2016/0103/1653 (1), NHMW 2016/0103/0100 (6), RGM.1309517 (31 juveniles), LC (50+), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0104 (8), RGM.1309512 (50+ juveniles), RGM.1309513 (13 juveniles), RGM.1309514 (8 juveniles), RGM.1309519 (3), RGM.1309520 (5), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1652 (1), NHMW 2016/0103/0115 (50+), LC (40), FVD (23). **Beugnon:** NHMW 2016/0103/0667 (4), RGM.1309508 (50+), RGM.1309538 (5), RGM.1309741 (50+, mainly juveniles), LC (6).

Discussion – *Gibbula sagus* (Defrance, 1828) from the northwestern French Atlantic middle Miocene is similar to *G. magus* (Linnaeus, 1758), but differs in having a less depressed shell, with a less angular last whorl periphery and a less depressed base. The basal cords are more strongly developed and elevated in comparison to *G. magus*, in which the basal sculpture is reduced to low concentric ridges. These differences are evident when middle Miocene populations from the Loire Basin are compared with present day *G. magus*. The upper Miocene specimen at hand from the Asemblage I localities

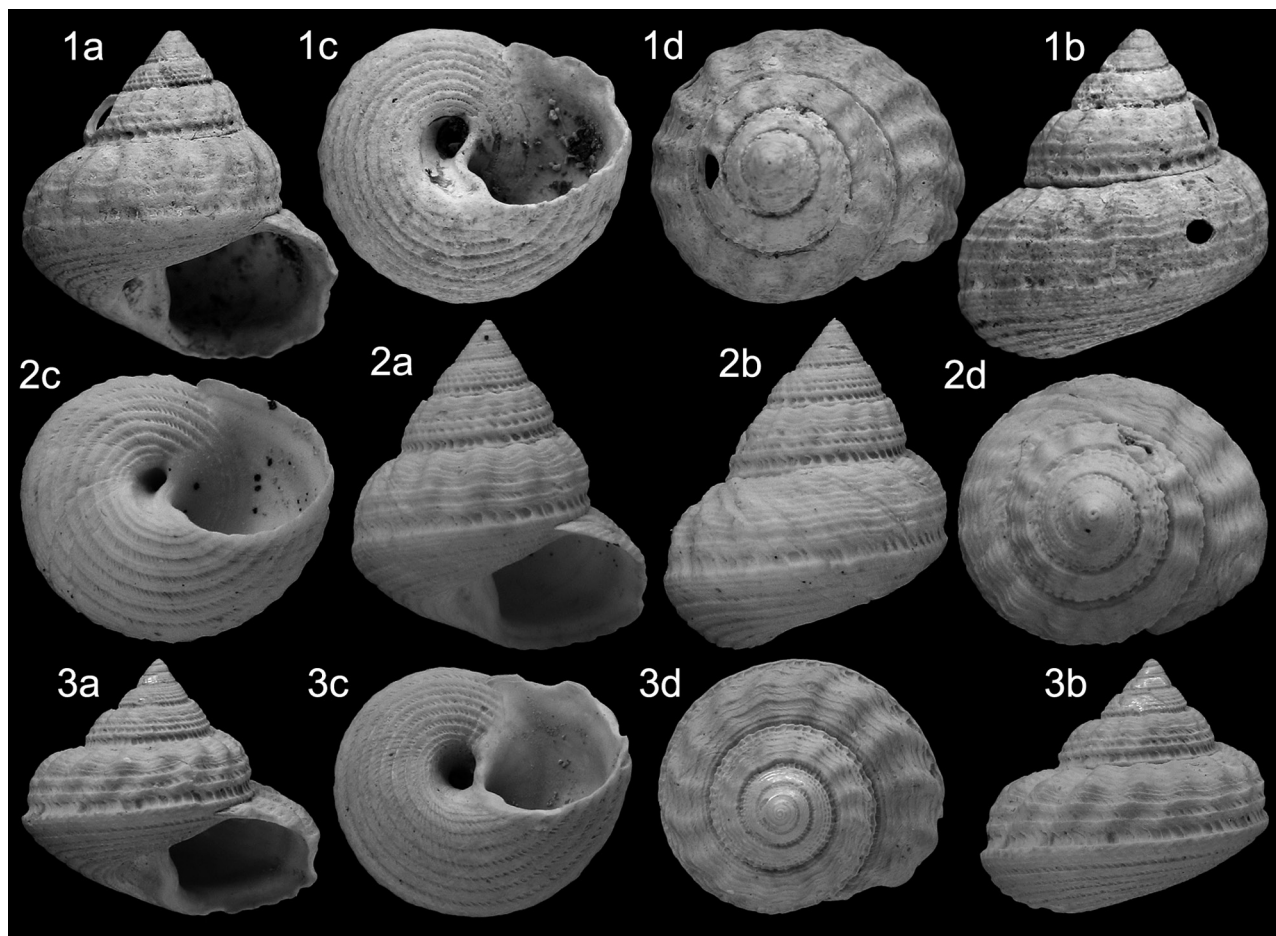


Plate 35. *Gibbula sagus* (Defrance, 1828); 1. NHMW 2016/0103/0101, height 10.7 mm, width 10.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place; 2. NHMW 2016/0103/1652, height 9.9 mm, width 8.9 mm. Renauleau. 3. NHMW 2016/0103/1653, height 9.9 mm, width 11.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

are here assigned to *G. sagus*; although smaller than specimens from the Loire Basin, the spire is relatively tall, the base not strongly depressed and the basal cords are strongly developed, as typical for *G. sagus* (Pl. 35, figs 1-2). Occasional specimens are more depressed with a more strongly developed peripheral cord (Pl. 35, fig. 3), as seen in *G. magus*. However, we consider these to be *G. sagus*, as the axial folds on the last whorl are developed until the peripheral cord, whereas in *G. magus* the folds tend to be restricted to the shoulder, and the basal sculpture is strong. Nevertheless, the two species are undoubtedly closely similar and may represent an evolutionary series.

This species was recorded from the lower and middle Miocene Aquitaine Basin of France as *G. pseudomagus* (d'Orbigny, 1852), which Cossmann & Peyrot (1917, p. 110) said differed from *G. magus* in being higher spired, the last whorl less angular at the periphery and the umbilicus narrower, less clearly delimited than in the extant species. These are the same differences as those between *G. sagus* and *G. magus* and we agree with Glibert (1949, p. 51) in considering *G. pseudomagus* (d'Orbigny, 1852) and junior subjective synonym of *G. sagus*.

Brébion (1964, p. 103) recorded this species from Assemblage I localities (Sceaux-d'Anjou, Renauleau, Thorigné, St-Clément-de-la-Place, Beaulieu). He also noted that Dollfus (1905) had listed it from the Assemblage IV locality of Gourbesville, however, we provisionally exclude this record from the distribution until it is verified.

Distribution – Lower Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1917). Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1917), Loire Basin, France (Peyrot, 1938; Glibert, 1949). Upper Mi-

ocene: Atlantic (Tortonian), NW France (Millet, 1854; Brébion, 1964), Cacela Basin, Portugal (Dollfus *et al.*, 1903).

Gibbula striatellata (Millet, 1865)

Plate 36, figs 1-2

1854 *Trochus Striatellatus* Millet, p. 156 (*nomen nudum*).

*1865 *Trochus striatellatus* Millet, p. 582.

1964 *Gibbula striatellata* Millet, 1854 [*sic*] – Brébion, p. 104, pl. 2, figs 32, 33.

Type material – Syntypes: Sceaux-d'Anjou, Musée d'Angers, France (*vide* Brébion, 1964, p. 104).

Material and dimensions – Maximum height 12.5 mm, width 11.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0105 (1), NHMW 2016/0103/0106 (29 + 20 juveniles), RGM.1309597 (8), RGM.1309752 (13), RGM.1309755 (23), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0107 (22), RGM.1309632 (4), RGM.1309656 (4), RGM.1309727 (3), RGM.1309763 (5), RGM.1309766 (7), LC (8), FVD (10). **Renauleau**: NHMW 2016/0103/1501 (1), NHMW 2016/0103/1432 (4), LC (8), FVD (7).

Discussion – The original description reflects well the character of this species: ‘*Trochus striatellatus*, Millet. Coq. en cône court, composée de 5 tours de spire légèrement striés, séparés par une suture légèrement renflée en cordon net sur ses bords. Dessous ombiliqué et couvert de fines stries. Ouverture angulaire, garnie d'un léger bourrelet intérieur. Hauteur et diamètre: 7 millimètres.

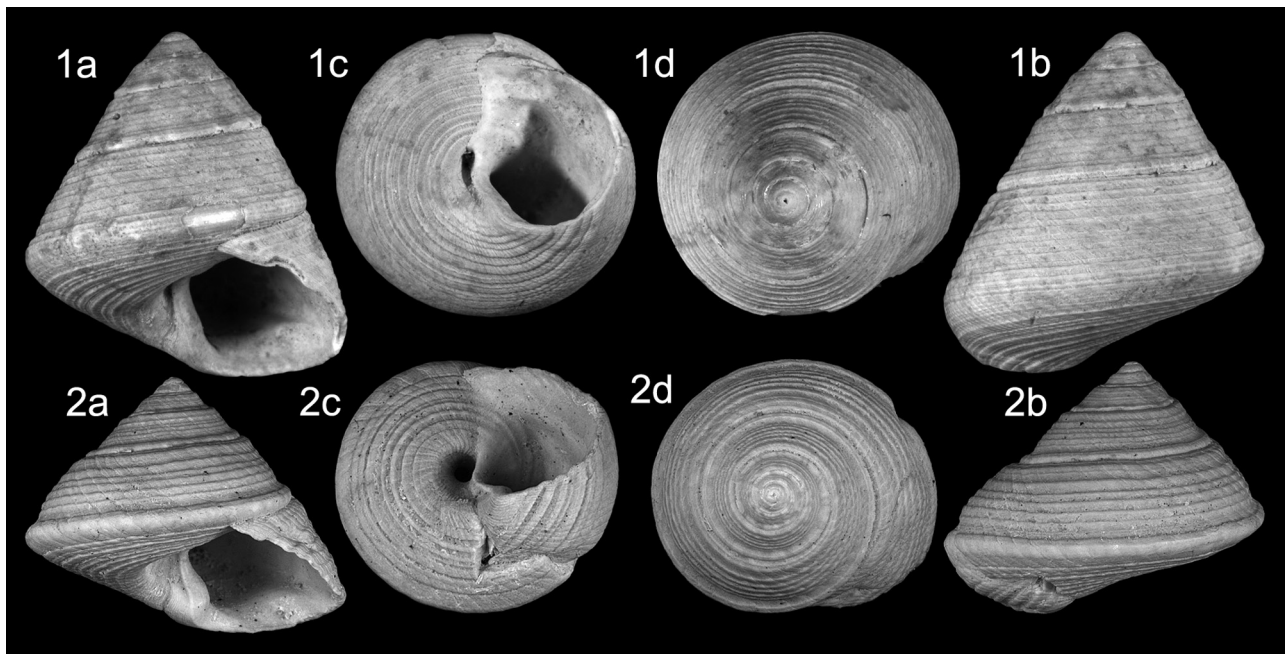


Plate 36. *Gibbula striatellata* (Millet, 1865); 1. NHMW 2016/0103/0105, height 10.8 mm, width 9.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/1501, height 11.2 mm, width 13.2 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Sceaux (Millet, 1865, p. 582). The height of the shell is somewhat variable, as seen in the series illustrated, which reflects the two extremes (Pl. 36, figs 1-2). On the spire whorls lie about six flattened, subequal cords above the broader, elevated suprasutural cord, which is also covered with secondary cords. The suture is deeply impressed. The suprasutural cord continues along the periphery of the last whorl, delimiting the base. The basal angulation is variable, roundly angled in some specimens (Pl. 36, fig. 1), sharply in others (Pl. 36, fig. 2). The base bears a narrow, shallow umbilicus and is covered in irregular cords. The columella bears a weak fold just below mid-columella. This species is most like the Pliocene to present-day eastern Atlantic and Mediterranean *G. cineraria* (Linnaeus, 1758), but that species differs in not having a swollen suprasutural cord and in having a deeper umbilical perforation.

The spiral sculpture is not unlike that of *G. provosti* Ceulemans, Van Dingenen & Landau, 2016 from the lower Pliocene Assemblage III locality of Le Pigeon Blanc, but that species is more depressed and lacks the swollen suprasutural cord.

Millet (1854, 1865) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and Thorigné, to which Brébion (1964, p. 105) added Renauleau and St-Michel and we add St-Clément-de-la-Place. We note that the specimens from Renauleau are somewhat flatter with the peripheral cord more strongly swollen than seen in the St-Clément-de-la-Place specimens, however, we consider them conspecific.

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

Genus *Paroxyste* Schultz, 1969

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

1969 *Paroxyste* Schultz, p 217.

***Paroxyste trochiformis* (Millet, 1865)**

Plate 37, fig. 1

1854 *Pitonellus trochiformis* Millet, p. 157 (*nomen nudum*).

*1865 *Pitonellus trochiformis* Millet, p. 584.

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

2016a *Paroxyste turoniensis* (Glibert, 1949) – Ceulemans *et al.*, p. 66, pl. 6, fig. 2.

Material and dimensions – Maximum height 11.1 mm, width 17.6 mm. **Renauleau:** NHMW 2016/0103/1425 (1), LC (4), FVD (3). **Beugnon:** RGM.1309515 (7 juveniles), RGM.1309525 (1), RGM.1309526 (1 juvenile), RGM.1309540 (2 juveniles).

Discussion – The specimens from Renauleau are typical for *Paroxyste turoniensis* (Glibert, 1949), which is characterised by its relatively low-spire, subcarinate base, and having the whorls ornamented by six to eight spiral cords, without secondary sculpture, subsutural folds are absent, and the umbilical callus is broad and closely adherent, filling the umbilicus. Ceulemans *et al.* (2016a) recorded this species from the younger lower Pliocene Assemblage III locality of Le Pigeon Blanc and noted that this was the stratigraphically youngest record for the species and for the typical ‘Miocene’ *Paroxyste* species-group, which differ from those in the Pliocene in having a completely closed umbilicus and only few Miocene species have subsutural folds, which are usually present in the Pliocene *Paroxyste patulum* (Brocchi, 1814).

However, in Ceulemans *et al.* (2016a) we failed to notice that Glibert’s name is a junior synonym of *Pitonellus trochiformis* Millet, 1865. Millet’s original description ‘*Pitonellus trochiformis*, Millet. *Coq. comme discoïdale ou en cône racourci, composée de 6-7 tours de spire arrondis en dessus, bien séparés les uns des autres, garnis chacun de 6 filets arrondis, dont le plus gros, au sommet, touche la suture. Le dessous, légèrement concave et légèrement strié, porte un ombilic complètement recouvert par une callosité lisse, qui ne dépasse pas la hauteur de ses bords. Diamètre: 28 millimètres; longueur: 20-22 millimètres* (1865, p. 584)’ leaves little doubt that he was referring to this species. Although Glibert’s name is better known, we cannot satisfy the requirements of Article 23.9.1.2 (ICZN 1999a) and therefore *Paroxyste trochiformis* (Millet, 1865) must take priority.



Plate 37. *Paroxyste trochiformis* (Millet, 1865); 1. NHMW 2016/0103/1425, height 11.1 mm, width 17.6 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

The stratigraphically older Aquitanian and Burdigalian Atlantic species *P. burdigalensis* (Cossmann & Peyrot, 1917) differs in being lower spired and having secondary spiral sculpture between the primary spiral cords. *Paroxystele orientale* (Cossmann & Peyrot, 1917) from the middle Miocene eastern Mediterranean and Paratethys differs in having more numerous spiral cords, the base is more rounded and the umbilical callus is narrower, not completely filling the umbilicus.

Millet (1865) recorded this species from the Assemblage I localities of Renauleau, Doué, Sceaux-d'Anjou, Thorigné, to which Brébion (1964, p. 117) added St-Michel, Les Pierres Blanches and Beaulieu.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Ceulemans *et al.*, 2016a).

Genus *Phorcus* Risso, 1826

Type species (by subsequent designation, Bucquoy *et al.*, 1885) – *Phorcus margaritaceus* Risso, 1826, present-day, France (Mediterranean).

- 1826 *Phorcus* Risso, p. 133.
- 1847 *Osilinus* Philippi, p. 20. Type species (by subsequent designation, Opinion 1930, 1999b): *Trochus turbinatus* Born, 1778, present-day, Mediterranean.
- 1852 *Neptheusa* Leach in Gray, p. 146, 174. Type species (by monotypy): *Trochus crassus* Pulteney, 1799, present-day, British Isles.
- 1852 *Trochocochlea* Mörch, p. 142. Type species (by subsequent designation, Bucquoy *et al.*, 1885):

Trochus turbinatus Born, 1778, present-day, Mediterranean.

- 1884b *Caragolus* Monterosato, p. 43. Type species (by subsequent designation, Crosse, 1885): *Trochus turbinatus* Born, 1778, present-day, Mediterranean.

***Phorcus gallicophorcus* nov. sp.**

Plate 38, figs 1-2

Type material – Holotype MNHN.F.A57690, height 5.5 mm, width 5.3 mm; paratype 1 MNHN.F.A57691, height 5.1 mm, width 4.0 mm; paratype 2 NHMW 2016/0103/0119, height 4.7 mm, width 4.1 mm; paratype 3 NHMW 2016/0103/0120, height 4.9 mm, width 4.2 mm; paratype 4 RGM.1309747, height 3.2 mm, width 3.2 mm; paratype 5 RGM.1309748, height 3.7 mm, width 3.1 mm.

Other material – **St-Clément-de-la-Place**: Maximum height 5.1 mm, width 4.6 mm. NHMW 2016/0103/0121 (34), LC (20), FVD (25). **Sceaux-d'Anjou**: NHMW 2016/0103/0217 (8).

Etymology – Compound name reflecting the Latin name for the Province of Gaul, 'Gallia', which now includes France, and the genus *Phorcus*. *Phorcus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Phorcus* species of small size, with solid shell, relatively tall spire, convex spire whorls, sculptured

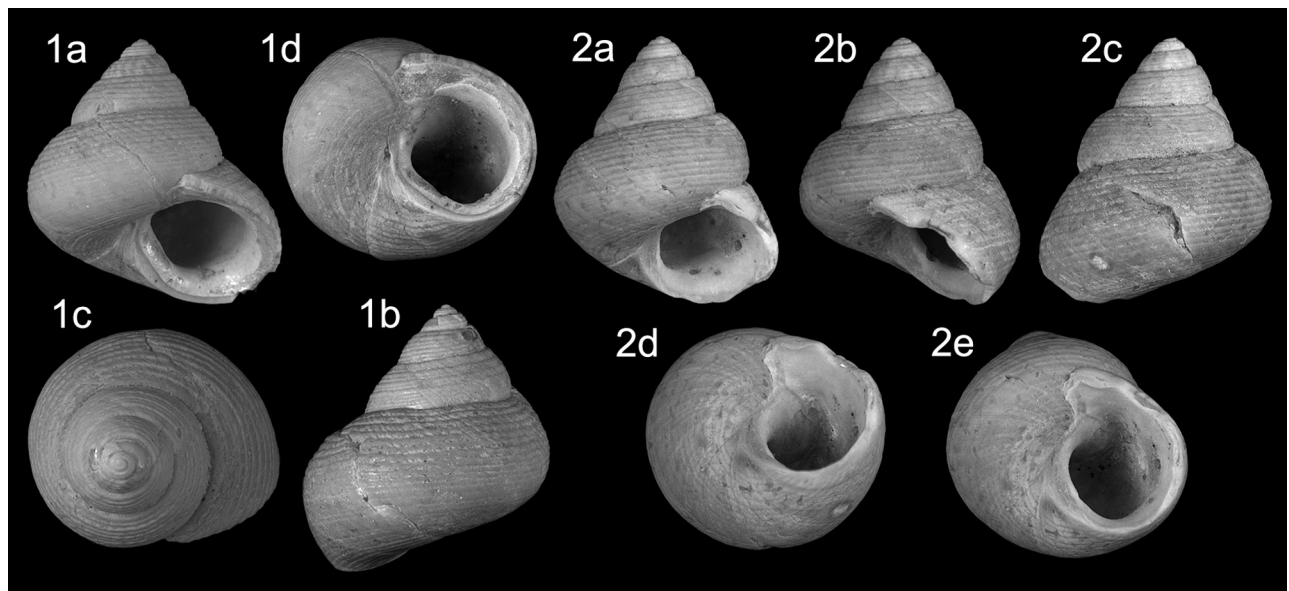


Plate 38. *Phorcus gallicophorcus* nov. sp.; 1. **Holotype** MNHN.F.A57690, height 5.5 mm, width 5.3 mm; 2. **Paratype 1** MNHN.F.A57691, height 5.1 mm, width 4.0 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

by rounded cords, beaded in adapical portion, imperforate base covered by rounded cords, and subobsolete columellar thickening.

Description – Shell small, solid, trochiform. Protoconch paucispiral, composed of 1.5 smooth whorls. Teleoconch of five relatively tall convex whorls, periphery at abapical suture. Suture impressed, linear. Sculpture of close-set spiral cords, slightly wider than their interspaces, beaded by strongly prosocline growth lines to a variable degree in adapical portion, especially last whorl. Last whorl inflated, evenly rounded to roundly angled at base. Base not sharply delimited, imperforate, bearing about eight rounded concentric cords. Aperture subtrigonal, outer lip simple, bevelled edge, rounded and slightly flared abapically. Peristome incomplete. Columella sloping strongly abaxially, bearing subobsolete thickening just below mid-height. Columella callus narrow, sharply delimited; parietal callus poorly developed.

Discussion – Although much smaller shelled than its present-day European congeners, the very thick shell, rounded whorls and apertural characters, with a strongly thickened outer lip, shallowly abaxially sloping columella with a subobsolete thickening lead us to place this species in the genus *Phorcus* Risso, 1826 rather than *Gibbula*. These shells are not juveniles, as the outer lip is strongly thickened and numerous specimens available to us are all similar.

It resembles a minute *P. turbinatus* (Born, 1778), but is slightly taller spired and has narrower spiral cords.

Phorcus gallicophorcus nov. sp. is superficially similar to a group of Pliocene North Sea Basin *Gibbula* species, characterised by *G. obconica* (S.V. Wood, 1848), which also has a small, solid shell (Marquet, 1998, fig. 20), but that species has narrower spiral cords and finer and more conspicuous beading and more numerous cords on the base. *Gibbula beetsi* van Regteren Altena, 1954 from the Pliocene of Belgium and The Netherlands differs similarly in having finer and stronger beading, but also differs in having a more depressed, broader shell, with a canalculated suture and a small umbilicus (Pouwer

& Wesselingh, 2012, fig 12), almost completely closed in some specimens (Marquet, 1998, fig. 18b). *Gibbula nehalenniae* van Regteren Altena, 1954, also from the Pliocene of Belgium and The Netherlands, was considered a *forma* or subspecies of *G. obconica* by Marquet (1995, 1998, respectively), but we agree with Pouwer & Wesselingh (2012, p. 156) in considering that species closer to *G. beetsi*. Most importantly, all these North Sea Basin *Gibbula* species differ in having an almost vertical columella, whereas in *Phorcus* it is strongly abaxially sloping.

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

Superfamily Turbinoidea Rafinesque, 1815

Family Turbinidae Rafinesque, 1815

Genus *Bolma* Risso, 1826

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

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

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

***Bolma granosa* (Borson, 1821)**

Plate 39, figs 1-2

*1821 *Trochus granosus* Borson, p. 67, pl. 2, fig. 6.

1827 *Turbo calcar* DeFrance, p. 520 (*non* Linnaeus, 1758).

1854 *Turbo Calcar* Defr. – Millet, p. 158.

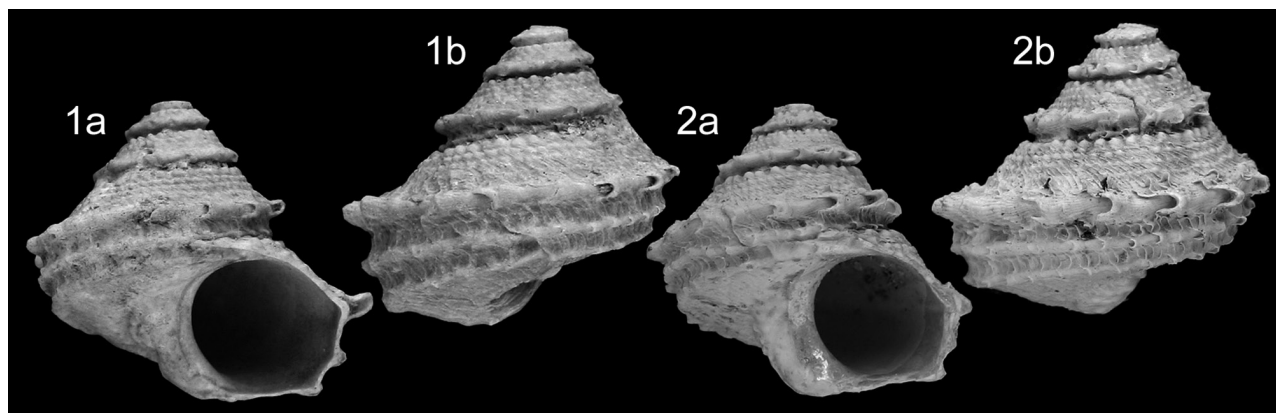


Plate 39. *Bolma granosa* (Borson, 1821); 1. NHMW 2016/0103/0230, height 11.5 mm, width 12.6 mm; 2. NHMW 2016/0103/0231, height 11.3 mm, width 11.9 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

- 1938 *Bolma miocalcar* Peyrot, p. 36, pl. 1, figs 29-30.
 1964 *Astraea (Bolma) granosa* Borson, 1821 – Brébion, p. 135.
 2003 *Bolma (Bolma) granosa* (Borson, 1821) – Landau *et al.*, p. 30, pl. 7, fig. 2 (*cum syn.*).

Material and dimensions – Maximum height about 33.0 mm (incomplete). **St-Clément-de-la-Place:** NHMW 2016/0103/0230-0231 (2), NHMW 2016/0103/0232 (4 + 50 juveniles), RGM.1309595 (20 adults and subadults), RGM.1348013 (9), LC (20), FVD (27). **Sceaux-d’Anjou:** NHMW 2016/0103/0233 (12 + 15 juveniles), RGM.1309576 (12 subadult + juveniles and opercula), RGM.1309578 (50+ subadults and juveniles), RGM.1309577 (50+ adults and subadults), RGM.1309579 (5 juveniles), RGM.1309587 (10+ subadults and juveniles), LC (50+), FVD (50+). **Renauleau:** NHMW 2016/0103/1433 (4 incomplete), LC (40), FVD (23).

Discussion – *Bolma granosa* (Borson, 1821) is characterised by its finely beaded spiral sculpture on the subsutural ramp and three strong cords mid-whorl on the last whorl, the adapical cord forming short open spines. *Bolma granosa* is a small shelled species for the genus, and most of the specimens from the Assemblage I localities are even smaller than those from the middle Miocene Loire Basin of France reported by Glibert (1949, p. 76) (maximum most specimens Assemblage I height 11.5 mm vs. Loire Basin 18.0 mm). The exception is one fragmentary specimen from Renauleau that is considerably larger than the rest and suggests a maximum height of about 33 mm. Landau *et al.* (2003) reported the last occurrence for the species from the lower upper Pliocene of the Estepona Basin, southern Spain, although these Pliocene specimens are not identical to those from Assemblage I; they are larger shelled (maximum 23.9 mm) and have a few

weak beaded spiral cords on the base as opposed to close-set wavy axial ribs in the Assemblage I specimens. However, one of Glibert’s (1949, pl. 4, fig. 7b) specimens from the Loire Basin also has beaded cords on the base.

Brébion (1964, p. 136) recorded *B. granosa* widely from the Assemblage I localities (Sceaux-d’Anjou, Thorigné, St-Clément-de-la-Place, Les Pierres Blanches, Beaulieu, Chalonnès, Contigné, St-Jacques).

Distribution – Middle Miocene: Atlantic, Loire Basin (Peyrot, 1938; Glibert, 1949); Proto-Mediterranean, Italy (Sacco, 1896a; Pavia, 1976). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1896a). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (Landau *et al.*, 2003).

Bolma cf. meynardi (Michelotti, 1847)

Plate 40, figs 1-3

- cf. *1847 *Turbo Meynardi* Michelotti, p. 177, pl. 7, fig. 4.
 1854 *Turbo Trochleatus* Millet, p. 158 (*non* zu Münster, 1841).
 cf. 2013 *Bolma meynardi* (Michelotti, 1847) – Landau *et al.*, p. 30, text-fig. 15/1, pl. 1, figs 9-12 (*cum syn.*).
 1964 *Astraea (Bolma) trochleata* Millet, 1854 – Brébion (*partim*), p. 131, pl. 3, figs 18, 19 (Assemblage I records only).

Material and dimensions – Maximum height 29.7 mm (incomplete), width 37.6 mm. **St-Clément-de-la-Place:** RGM.1309690 (1). **Sceaux-d’Anjou:** FVD (9). **Renauleau:** NHMW 2016/0103/1434-1436 (3), NHMW 2016/0103/1437 (36 adult fragments and juveniles), LC (50+), FVD (50+).

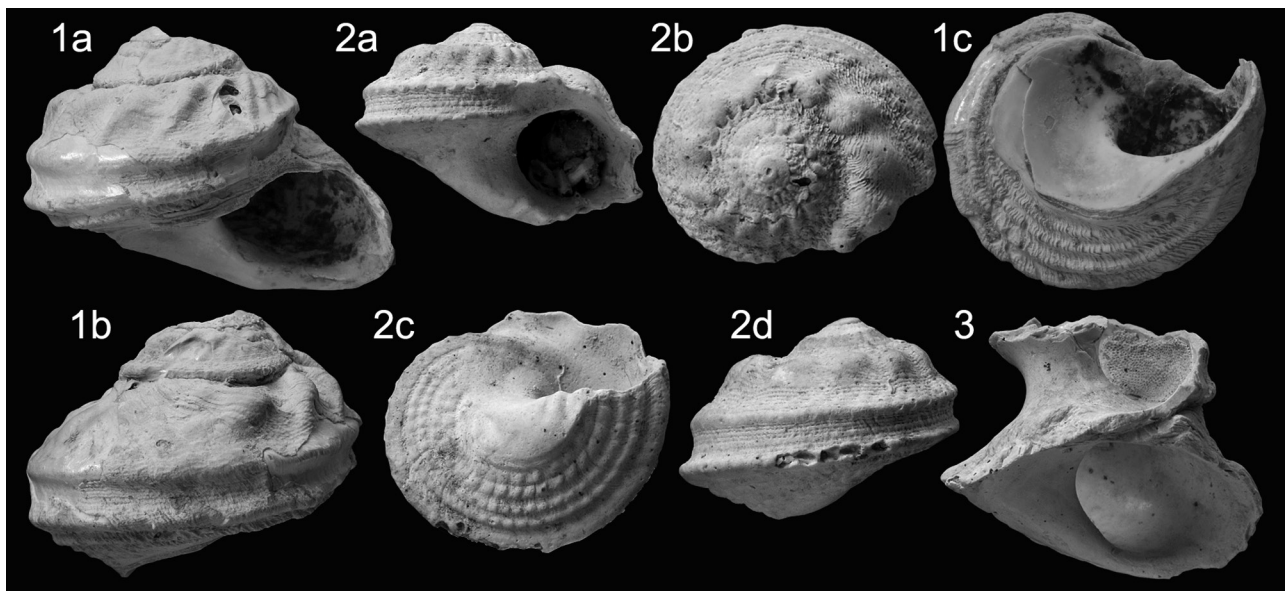


Plate 40. *Bolma cf. meynardi* (Michelotti, 1847); 1. NHMW 2016/0103/1434, height 29.7 mm, width 37.6 mm; 2. NHMW 2016/0103/1436, height 14.3 mm, width 20.3 mm; 3. NHMW 2016/0103/1439, height 31.8 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – The specimens illustrated here belong to the *Bolma rugosa* species-group. Landau *et al.* (2013, p. 30) considered the Miocene populations of ‘*Bolma rugosa*’ to represent *Bolma meynardi* (Michelotti, 1847) and restricted *B. rugosa* (Linné, 1767) to the Pliocene to present-day populations. *Bolma meynardi* differs from *B. rugosa* in having less stepped early teleoconch whorls resulting in a lower spire, in having less nodular rugae, the rugae extending to the sutures, and in *B. rugosa* the basal callus is less extensive than in *B. meynardi*, but more excavated by a central depression, which ends as a double denticle at the columellar abapical extremity, not present in *B. meynardi*. Furthermore, the suture on the second half of the last whorl in *B. meynardi*, when viewed aperturally, is placed between the base and mid-whorl height, whereas in *B. rugosa* the suture is at or below the base. The Pliocene and Recent forms, although somewhat different, cannot be separated consistently (see Landau *et al.*, 2013).

This species group is represented in the Assemblage I deposits by adults from Renauleau and one specimen from St-Clément-de-la-Place, where all specimens found are either incomplete or worn, suggesting transport prior to deposition. Juveniles are found at other sites, such as Sceaux-d’Anjou. Nevertheless, this upper Miocene Renauleau population is interesting, as the shells show intermediate features between the two species compared above. Like the typical Miocene *B. meynardi*, the shell is low-spired (Pl. 40, figs 1a, 2a), the rugae are not nodular and extend to the suture (Pl. 40, figs 1b, 2b), and the basal callus does not end as a double denticle at the columellar abapical extremity (Pl. 40, figs 1a, 2a, 3). Conversely, with *B. rugosa* these Renauleau specimens share a relatively narrow basal callus, which is strongly excavated centrally in fully grown specimens (Pl. 40, figs 1c) and in adult specimens the suture on the second half of the last whorl is placed at the base (Pl. 40, figs 1a, 3). One further difference is the strikingly bicarinate periphery, the whorl profile concave between the two (Pl. 40, fig. 1a), which persists onto the last whorl in adult specimens (Pl. 40, fig. 2a). Although both *B. meynardi* and *B. rugosa* can have the periphery marked by stronger cords, they are neither as strongly developed, nor is the whorl profile between the cords as concave.

It is not possible to attribute the Renauleau specimens to *B. meynardi* or *B. rugosa*. Millet (1854) erected the name *Turbo trochleatus* for juvenile shells from Sceaux-d’Anjou, but this is a junior homonym of *T. trochleatus* zu Münster, 1841. The specimen illustrated by Brébion (1964, pl. 3, figs 18-19) show a shell almost identical to the juvenile illustrated here (Pl. 40, fig. 2). Based on the material at hand, we consider it undesirable to erect a new species/subspecies. We prefer to leave the Renauleau population in open nomenclature as *B. cf. meynardi* as they are Miocene and the shell shape and sculpture are closer to the Miocene form.

Landau *et al.* (2013, p. 31, text-fig. 15/1, 32) illustrated a large specimen from the upper Miocene Tortonian Atlantic of Cacula (southern Portugal) that was typical for *B. meynardi* and attributed all upper Miocene records

to this species. These intermediate forms from the more northern Tortonian of northwestern France suggest the modern species may have arisen at these more northern latitudes.

Brébion (1964, p. 45) recorded this species [as *A. (B.) trochleata*] from Assemblage I localities of Sceaux-d’Anjou, Thorigné, Les Pierres Blanches and Beaulieu. Here we add St-Clément-e-la-Place and Renauleau. We have not included his Assemblage III records which were shown by Ceulemans *et al.* (2016a, p. 66) to be *B. rugosa*. Brébion (1964, p. 134) recorded and illustrated specimens ascribed to *A. (B.) italica* (Sacco, 1896) from Assemblages I and II. *Astraea (B.) italica* was described as a subspecies of *Trochus muricatus* Dujardin, 1837, which is a junior synonym of *Turbo baccatus* Defrance, 1827 (Glibert, 1949, p. 73) from the middle Miocene Loire Basin of France. The specimens illustrated by Brébion lack the tubercles characteristic of the species and we therefore doubt this record. We have not seen any northwestern French upper Miocene material we would ascribe to *B. baccata*. It is more likely that the specimens illustrated by Brébion are unusual juvenile specimens of *Bolma cf. meynardi*, which is highly variable.

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

Family Calliostomatidae Thiele, 1924

Subfamily Calliostomatinae Thiele, 1924

Genus *Calliostoma* Swainson, 1840

Subgenus *Calliostoma s. str.*

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

1840 *Calliostoma* Swainson, p. 218.

For generic synonymy see Ceulemans *et al.* (2016a, p. 68).

Note – The abundance and diversity of calliostomids in the upper Miocene Assemblage I localities of northwestern France is one of the most striking aspects of this fauna. The species are almost all small shelled for the genus, but outstandingly variable in shape, from depressed lentiform to tall conical with a coeloconoid spire, the whorls regularly convex to strongly angular or biangular and the surface almost unsculptured to strongly sculptured and spiny. There is a far greater variation in shape than in any other European Neogene fossil assemblage, and the species shapes are certainly more varied than the more or less regularly conical shell shape with spiral or beaded sculpture living in European waters today. Indeed, the only character all these forms share is the honeycomb microsculpture on the protoconch, typical for the genus *Calliostoma* (Hickman & McLean, 1990, p. 109). This strikingly diverse shell form seen in the radiation of *Calliostoma* species from Assemblage I suggests that gener-

ic/subgeneric characters in calliostomids, based on shell form, may not be an indication of monophyletic groups and we therefore refrain from using them. We are also not aware of any molecular studies supporting the division of European calliostomids into genera/subgenera.

Although the genus was relatively well represented in the lower Pliocene northwestern French Assemblage III localities discussed by Ceulemans *et al.* (2016a), these species are similar in shape and size to Pliocene to present-day congeners from Europe and share little in common with the earlier Assemblage I calliostomids. Therefore, the discussion and comparison following most of the new species is relatively short due to the absence of similar species with which to compare.

Calliostoma alternatum (Millet, 1865)

Plate 41, figs 1-2

- 1854 *Trochus Alternatus* Millet, p. 157 (*nomen nudum*).
 *1865 *Trochus alternatus* Millet, p. 583.
 1964 *Calliostoma alternatum* Millet, 1854 [*sic*] – Brébion, p. 78, pl. 1, figs 22-24.

Type material – Syntypes: Sceaux-d’Anjou, lost (*vide* Brébion, 1964, p. 78).

Material and dimensions – Maximum height 6.4 mm; width 4.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0058 (1), NHMW 2016/0103/0059 (1), NHMW 2016/0103/0060 (50+), LC (50+), FVD (50+). **Sceaux-d’Anjou**: NHMW 2016/0103/0062 (48), RGM.1309652 (1), RGM.1309682 (20), RGM.1309694 (4), RGM.1347998 (12), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0061 (21), LC (40), FVD (23).

Discussion – *Calliostoma alternatum* (Millet, 1865) is characterised by its small size, relatively tall narrow conical spire and its sculpture composed of beaded cords, three subequal cords below suture, the 4th cord stronger, with some of the beads strengthened to form tubercles followed by a 5th cord of equal strength to the three sub-sutural cords. The base is imperforate and bears nine subequal cords, slightly wider than their interspaces.

Axial growth lines are most strongly developed on the base, weakly beading the basal cords in some specimens. Although the most striking feature of this species is the tuberculate 4th cord, its development is quite variable, with some specimens hardly developing tubercles. Millet (1854, 1865) recorded the species only from the Assemblage I locality of Sceaux-d’Anjou, to which Brébion (1964, p. 79) added St-Clément-de-la-Place and Les Pierres Blanches. Renauleau is added herein.

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

Calliostoma baccatum (Millet, 1865)

Plate 42, figs 1-2

- 1854 *Trochus Baccatus* Millet, p. 157 (*nomen nudum*).
 *1865 *Trochus baccatus* Millet, p. 582.
 2016a *Calliostoma baccatum* (Millet, 1865) – Ceulemans *et al.*, p. 70, pl. 9, figs 1, 2 (*cum syn.*).

Material and dimensions – Maximum height 15.0 mm; width 12.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0156-0157 (2), NHMW 2016/0103/0159 (20), RGM.1309761 (5), LC (10), FVD (27). **Sceaux-d’Anjou**: 2016/0103/0158 (17), RGM.1309649 (18), RGM.1309700 (4), RGM.1309775 (12), LC (15), FVD (17).

Original description – ‘*Trochus baccatus*, Millet. Coq. en cône assez allongé, composée, de 8-9 tours de spire, quelquefois un peu bombés et couverts de 5 rangs de perles fines. Hauteur: 11-12 millimètres; diamètre à la base: 8 millimètres. Elle présente une variété plus allongée, dont les tours de spire sont bombés. Th., Sc, Ren. (Millet, 1865, p. 582)’.

Revised description – Shell of medium size and thickness; spire moderately elevated, conical. Protoconch paucispiral, covered in honeycomb surface sculpture. Teleoconch consisting of about 7-8 straight-sided whorls, with periphery just above abapical suture. Suture linear, superficial. Sculpture of five beaded cords of irregular strength, the two abapical cords become fused on later

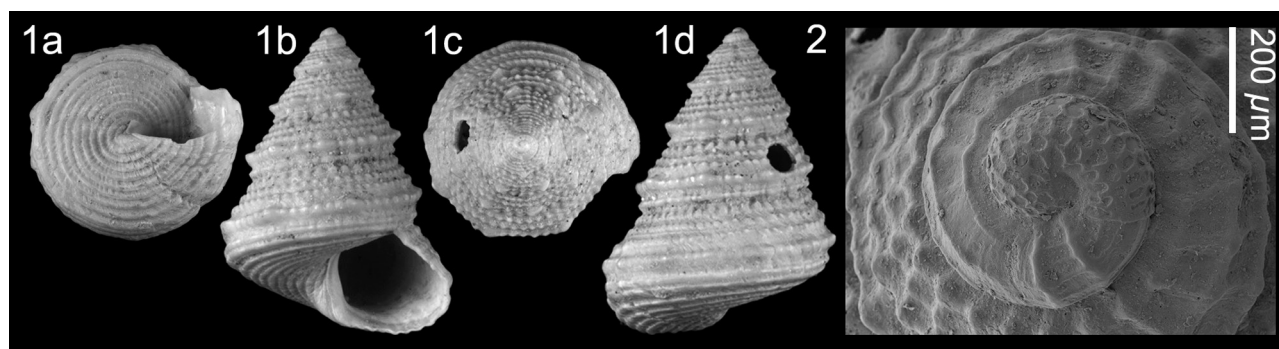


Plate 41. *Calliostoma alternatum* (Millet, 1865); 1. NHMW 2016/0103/0058, height 6.4 mm, width 4.8 mm; 2. NHMW 2016/0103/0058, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

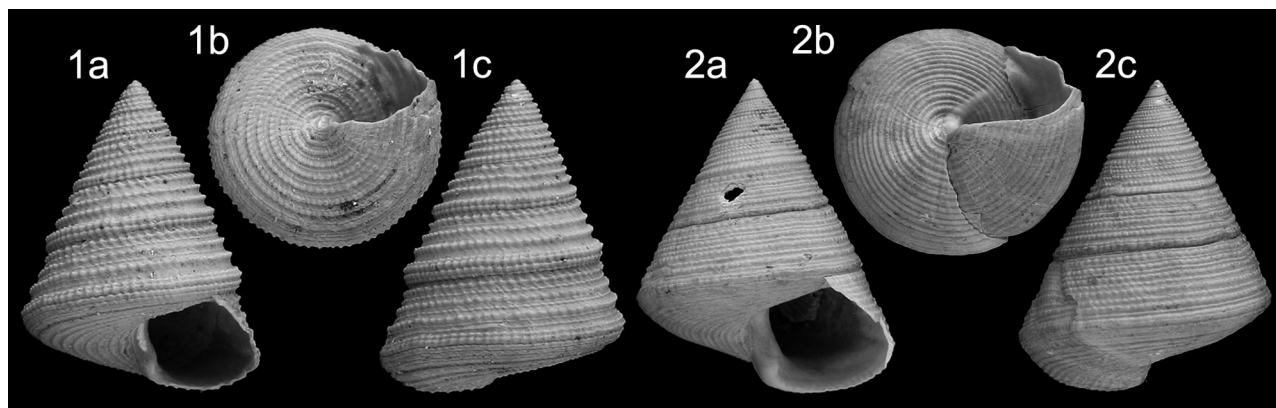


Plate 42. *Calliostoma baccatum* (Millet, 1865); 1. NHMW 2016/0103/0156, height 12.0 mm, width 9.0 mm; 2. NHMW 2016/0103/0157, height 14.6 mm, width 11.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

whorls, forming a raised bifid peripheral band. Secondary cords intercalated in some to all interspaces on last whorl. Last whorl roundly angled at periphery. Base not sharply delimited, bearing about 8 narrow beaded cords. Aperture tangential; peristome discontinuous, outer lip not thickened, rounded at periphery. Columella sloping weakly abaxially, bearing a weak columellar thickening abapically.

The two specimens figured illustrate extremes in development of the spiral sculpture, which can be finely, but distinctly beaded to smooth, or almost so. Most specimens show a beaded or sub-obsolete beaded sculpture intermediate between the two figured.

Discussion – Ceulemans *et al.* (2016a, p. 70) pointed out that the established name for this species, *Calliostoma taumomiliare* Sacco, 1896 was a junior subjective synonym of *Calliostoma baccatum* (Millet, 1865). The Assemblage III material at hand to Ceulemans *et al.* did not have the protoconch preserved, however, the specimen from St-Clément-de-la-Place figured here (NHMW 2016/0103/0156; Pl. 42, fig. 1) has a perfectly preserved protoconch showing a paucispiral nucleus covered in a honeycomb pattern, confirming its placement in the genus *Calliostoma*.

Brébion (1964, p. 75) recorded this species from localities belonging to Assemblage I-III and commented on the great variability seen. In his description he noted that the base could be convex or flattened and the basal cords beaded or not. Ceulemans *et al.* (2016a) considered the Le Pigeon Blanc population not to be so variable. This is not true of the Assemblage I populations which vary greatly in apical angle, width and flattening of the base, just as described by Glibert (1949) and Brébion (1964). *Calliostoma baccatum* is the only *Calliostoma* species found both in Assemblage I and Assemblage III deposits. *Calliostoma baccatum* (Millet, 1865) is superficially similar to *Jujubinus proximus* (Millet, 1865). Both species are of similar size and have five rows of beaded primary cords. In perfectly preserved specimens the protoconch separates the two, as *Jujubinus* species have smooth pro-

toconchs. However, in most specimens the protoconch surface sculpture is abraded. The teleoconch shell of *C. baccatum* differs from *J. proximus* in usually having a wider apical angle, the shell is less solid, especially the outer lip, which is thinner in *C. baccatum*. On later whorls the abapical two cords fuse and form a peripheral raised band in *C. baccatum*, which is not the case in *J. proximus*, and there is more secondary sculpture, which starts earlier. In *J. proximus* there is at most 1-2 spiral threads between the uppermost cords on the last whorl. Finally, *C. baccatum* lacks the interal ridge within the aperture bordering the siphonal canal and although it does have a slight columella swelling abapically, it is weaker than in *J. proximus*. For further discussion see Ceulemans *et al.* (2016a, p. 70).

Distribution – Lower Miocene: Burdigalian, Italy (Sacco, 1896a); Paratethys, Austria (Harzhauser *et al.*, 2015). Middle Miocene: Loire Basin, France (Glibert, 1949). Upper Miocene: Atlantic, Tortonian, Messinian, NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016a).

Calliostoma biangulatum nov. nom.

Plate 43, figs 1-2

- 1854 *Trochus Heliciformis* Millet, p. 156 (*nomen nudum*).
- 1865 *Trochus heliciformis* Millet, p. 582 (*non* von Zieten, 1832).
- 1964 *Jujubinus (Strigosella) heliciformis* Millet, 1854 [*sic*] – Brébion, p. 120, pl. 3, fig. 13 (*non T. heliciformis* von Zieten, 1832).

Type material – Syntypes: Thorigné, Sceaux-d'Anjou and Renauleau, Musée d'Angers, France (*vide* Brébion, 1964, p. 120).

Material and dimensions – Maximum height 11.3 mm,

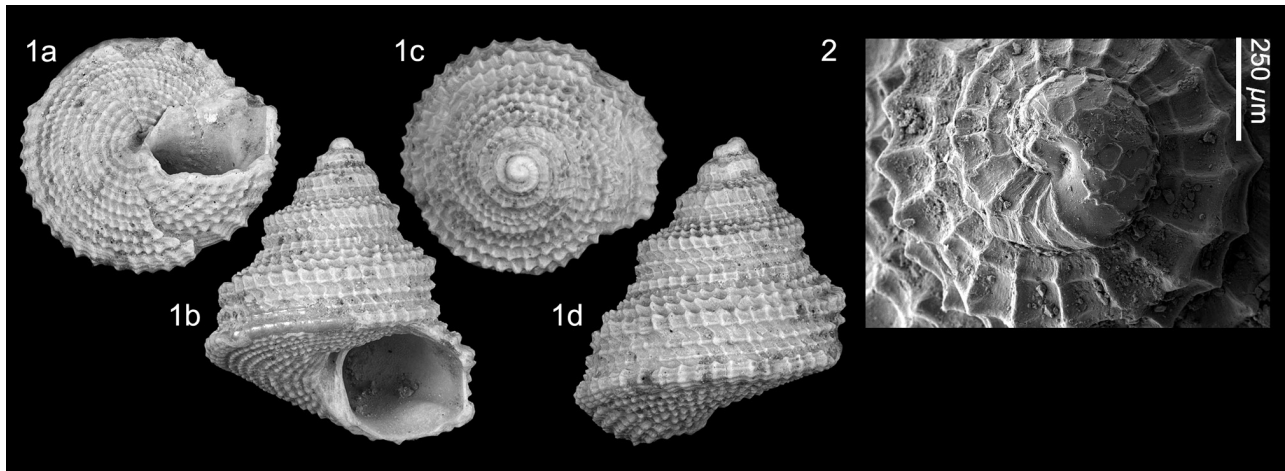


Plate 43. *Calliostoma biangulatum* nov. nom.: 1. NHMW 2016/0103/0131, height 5.8 mm, width 5.5 mm; 2. NHMW 2016/0103/0134, detail of protoconch (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

width 9.2 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0131-0134 (4), NHMW 2016/0103/0135 (4), RGM.1309598 (3), LC (1), FVD (5). **Sceaux-d'Anjou:** NHMW 2016/0103/0183 (18), RGM.1309596 (5), RGM.1309603 (14), RGM.1309701 (1), RGM.1309734 (1), RGM.1347918 (1), RGM.1347999 (7), LC (5), FVD (8).

Etymology – Name reflecting the biangular shape of the last whorl. *Calliostoma* gender neuter.

Locus typicus – Given as Sceaux-d'Anjou, Renauleau and St-Clément-de-la-Place.

Stratum typicum – Tortonian, upper Miocene.

Original description – ‘*Trochus heliciformis*, Millet. *Coq. conique, composée de 7-8 tours de spire disposés en vis et couverts de rangs de perles qui se touchent réciproquement. Dessous légèrement concave, marqué d'une fente ombilicale et revêtu de rangs de perles alternant de grosseur. Longueur: 13 millimètres; diamètre à la base, 10 millimètres. Sc, Th., Ren.* (Millet, 1865, p. 582)’.

Revised description – Shell small, trochiform. Protoconch paucispiral, of 1.2 whorls bearing honeycomb surface sculpture, the holes in the sculpture relatively large ($dp = 435 \mu\text{m}$, $dn = 170 \mu\text{m}$). Junction with teleoconch sharply delimited by elevated scar. Teleoconch of four whorls. Spire whorls with flat subsutural ramp, sharply angled at shoulder, straight-sided to abapical suture. Sculpture of fine spiral cords; two on subsutural ramp, paired, closer-set cords at shoulder and above suture, one further cord between cord-pairs at shoulder and suture. Crowded prosocline lamellae cross cords, forming short pointed tubercles at intersections, giving sculpture spiny appearance. Last whorl biangular at shoulder and base, profile slightly concave between angulations, sculpture of two cords on subsutural platform, paired cords forming shoulder and peribasal carina; two further

cords between carinae. Base sharply angled, strongly depressed, bearing eight primary concentric cords, with secondary threads in some interspaces. Umbilicus shallow, narrow. Aperture ovate, outer lip simple, not flared, columella smooth. Columellar callus hardly developed, parietal callus thin.

Discussion – With this species we offer a revised description to supplement the short original one given by Millet (1865, p. 582). Unfortunately, *Trochus heliciformis* Millet, 1865 is a junior homonym of *T. heliciformis* von Zieten, 1832 and therefore invalid. We erect the replacement name *Calliostoma biangulatum* nov. nom.

This species is very characteristic with its highly sculptured surface and biangular last whorl. There are no European fossil or present-day congeners with which it can be usefully compared. Brébion (1964) placed it in the genus/subgenus *Jujubinus* (*Strigosella*), but the honeycomb patterned protoconch shows it to be a calliostomiid (Pl. 43, fig. 2).

Millet recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Renauleau, Thorigné, to which Brébion (1964, p. 121) added St-Clément-de-la-Place. We note that Brébion did not refind the species at Renauleau and despite intensive collecting neither did we.

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

***Calliostoma contractum* (Millet, 1865)**

Plate 44, figs 1-7

1854 *Trochus Depressus* Millet, p. 156 (*non* Gmelin, 1791).

1854 *Trochus Contractus* Millet, p. 157 (*nomen nudum*).

1865 *Trochus depressus* Millet, p. 582 (*non* Gmelin, 1791).

*1865 *Trochus contractus* Millet, p. 583.

- 1964 *Calliostoma contractum* Millet, 1854 [sic] – Brébion, p. 97, pl. 2, fig. 22.
 1964 *Gibbula (Steromphala) depressa* Millet, 1854 [sic] – Brébion, p. 111, pl. 3, fig. 6 (non *Trochus depressus* Gmelin, 1791).

Type material – Syntypes: Thorigné and Sceaux-d’Anjou, lost (*fide* Brébion, 1964, p. 98).

Material and dimensions – Maximum height 15.2 mm; width 14.6 mm. **St-Clément-de-la-Place**: NHMW 2016/

- 0103/0167-0169 (3), NHMW 2016/0103/0256-0259 (4), NHMW 2016/0103/0170 (50+), LC (1), FVD (22). **Sceaux-d’Anjou**: NHMW 2016/0103/0171 (45), RGM.1309630 (1), RGM.1309665 (3), RGM.1309678 (7), RGM.1309689 (10), RGM.1309692 (2), RGM.1309704 (6), RGM.1309730 (7), RGM.1309768 (10), RGM.1348000 (19), LC (10), FVD (27). **Renaleau**: NHMW 2016/0103/0172 (12), LC (5), FVD (3).

Discussion – Millet (1865) validated his earlier (1854) name *Trochus contractus* with the following description:

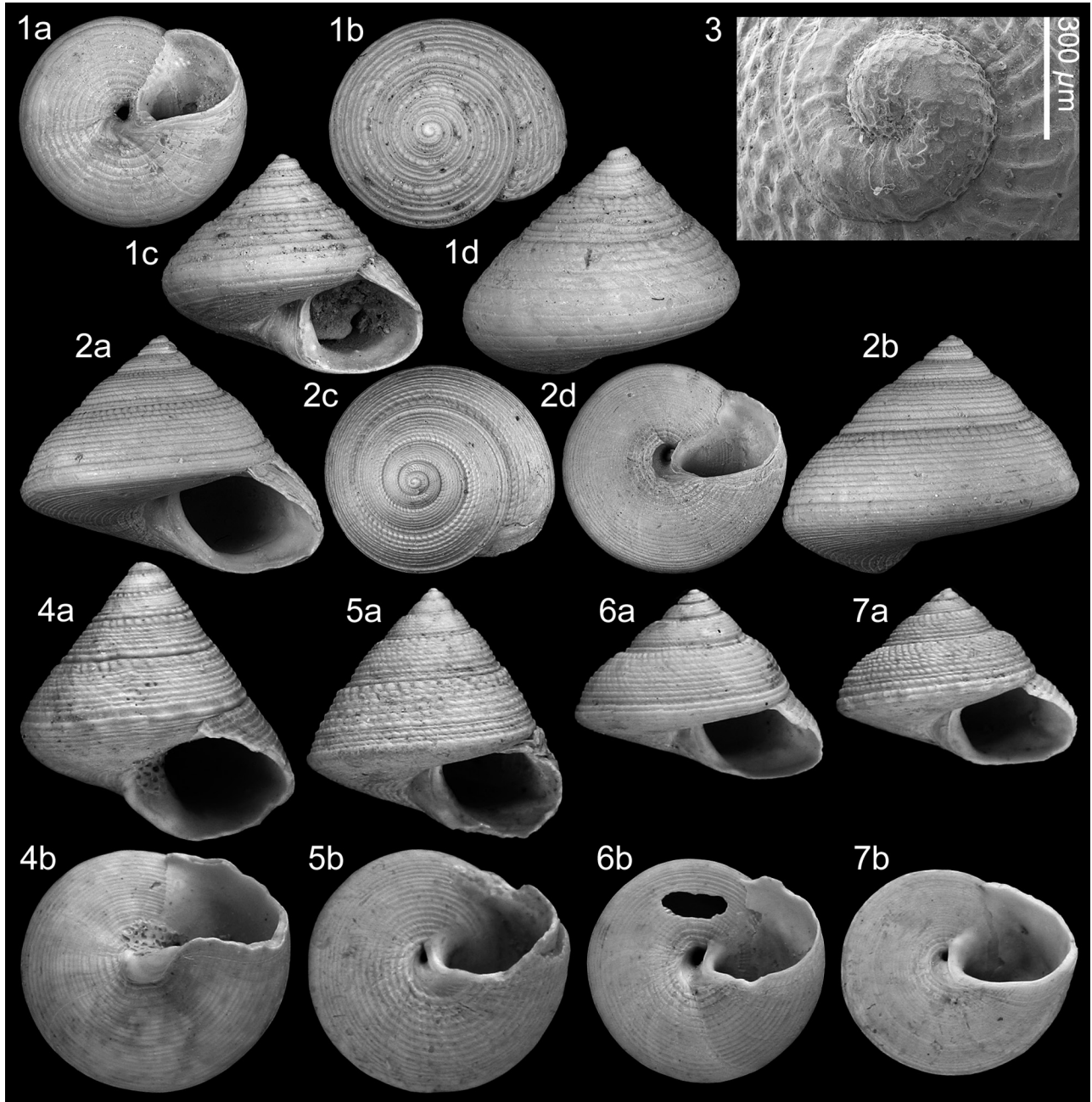


Plate 44. *Calliostoma contractum* (Millet, 1865); 1. NHMW 2016/0103/0167, height 5.0 mm, width 5.6 mm; 2. NHMW 2016/0103/0168, height 7.4 mm, width 8.8 mm; 3. NHMW 2016/0103/0169, detail of protoconch (SEM image); 4. NHMW 2016/0103/0256, height 8.8 mm, width 8.5 mm; 5. NHMW 2016/0103/0257, height 8.1 mm, width 8.2 mm; 6. NHMW 2016/0103/0258, height 6.7 mm, width 7.9 mm; 7. NHMW 2016/0103/0259, height 6.2 mm, width 7.7 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

‘*Trochus contractus*. Millet. *Coq. en cône racourci, aiguë au sommet, composée de 6 tours de spire disjoints par une suture assez profonde, couronnant un rang de petites perles. Chaque tour en outre présente 5 petits cordonnets. Dessous légèrement concave, couvert de stries fines. Hauteur et diamètre: 8 à 9 millimètres. Sc. Th.* (1865, p. 583)’. Although this is a fair description of the predominant form, this is probably the most variable of the Assemblage I calliostomiids. The shell can be strongly depressed (Pl. 45, figs 6-7) to regularly conical elevated (Pl. 45, figs 4-5), although as described by Millet, in all forms the apex is pointed. Only the most adapical cord is strongly beaded, with the second cord weakly beaded in most specimens (Pl. 45, fig. 1), although more abapical cords are beaded in some specimens (Pl. 45, figs 2, 6) and occasionally all cords are beaded (Pl. 45, figs 5, 7). The basal angulation can be roundly (Pl. 45, figs 1, 4) to acutely angled (Pl. 45, figs 2, 6, 7). The basal sculpture of close-set, non-beaded concentric cords is well developed in most specimens, although the thickness of the cords is variable, and in some specimens the cords are obsolete mid-base (Pl. 45, fig. 7). Millet erected another taxon *Trochus depressus* Millet, 1854 (*nomen nudum*) described later in Millet (1865) (junior homonym of *Trochus depressus* Gmelin, 1791) as: ‘*Trochus depressus*, Millet. *Coq. orbiculaire, légèrement conique, composée de 5 tours de spire, le dernier plus grand que tous les autres ensemble, caréné inférieurement, portant 6 stries, dont la plus élevée, plus grosse que les autres, est couverte de petites perles. La partie inférieure munie d’un trou ombilical, est couverte de très-petites stries. Hauteur: 6 à 7 millimètres; diamètre: 8-9 millimètres. Sceaux. Rare* (1865, p. 582). The main difference between Millet’s two species is that *T. contractus* has an imperforate base and *T. depressus* has a small umbilicus. In our opinion *T. depressus* applies to the extremely flattened form of this species, but numerous intermediates occur, with a small deep umbilicus (Pl. 45, figs 1, 2, 6), shallow (Pl. 45, figs 7) to imperforate (Pl. 45, fig. 4). There is little with which to compare this species. Brébion (1964, p. 98) compared it to *C. conuloides* (Lamarck, 1822), which is now considered a junior subjective synonym of *C. zizyphinum* (Linnaeus, 1758), but this is a much larger species, with a less depressed shell and a more regularly conical spire, and the adapical cords are not usually beaded, and if so less strongly. Millet (1854, 1865) recorded his two species *T. depressus* and *T. contractus*, herein synonymised from the Assemblage I localities of Sceaux-d’Anjou and Thorigné, to which Brébion added Renauleau, St-Clément-de-la-Place and Les Pierres Blanches.

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

***Calliostoma gibbuliforme* nov. sp.**

Plate 45, figs 1-3

1964 *Calliostoma multistriatum* var. *andegavensis* Brébion, p. 79, pl. 1, fig. 25 (*nomen nudum*).

Type material – Holotype MNHN.F.A57692, height 3.5 mm, width 4.4 mm; paratype 1 MNHN.F.A57693, height 3.7 mm, width 5.0 mm; paratype 2 NHMW 2016/0103/0123, height 4.4 mm, width 5.1 mm; paratype 3 NHMW 2016/0103/0124, height 4.0 mm, width 5.1 mm; paratype 4 NHMW 2016/0103/0125, height 2.3 mm, width 3.2 mm; paratype 5 RGM.1309749, height 3.1 mm, width 3.6 mm; paratype 6 RGM.1309750, height 3.2 mm, width 3.6 mm.

Other material – Maximum height 3.2 mm, width 4.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0126 (28), RGM.1309751 (12), RGM.1309757 (6), LC (10), FVD (14). **Sceaux-d’Anjou**: NHMW 2016/0103/0219 (14), RGM.1348001 (3), LC (5), FVD (8). **Renauleau**: LC (1).

Etymology – Name reflecting the shell shape resembling a *Gibbula* species. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, low trochiform shell shape, with spiral sculpture of which only first and sometimes second cords are beaded, spiral sculpture weakening abapically, strongly convex last whorl, rounded or slightly angular at peripheral cord, flattened base with weak concentric sculpture restricted to periumbilical area, and deep, narrow umbilicus.

Description – Shell small, depressed, low trochiform. Protoconch paucispiral, of 1.2 whorls bearing honeycomb surface sculpture with small pits ($dp = 435 \mu\text{m}$, $dn = 215 \mu\text{m}$). Junction with teleoconch sharply delimited by abrupt end to protoconch sculpture. Teleoconch of 3.5 low convex whorls, with periphery at abapical suture, separated by impressed suture. Sculpture on first teleoconch whorl of three rounded spiral cords, increasing in number to four on second teleoconch whorl, five on penultimate whorl. Cords strongly developed and rounded on some specimens, flattened in other, subobsolete on the last teleoconch whorl in most specimens. The adapical cord is conspicuously beaded by prosocline axial growth lines; in some specimens the second cord is also weakly beaded, abapical cords smooth, one or two most abapical cords more strongly developed. Last whorl depressed, rounded or slightly angular at peripheral cord, base flattened, smooth, except for 3-4 weak cords adjacent to, and strengthening towards umbilicus. Umbilicus narrow, deep. Aperture ovate, outer lip simple, rounded to somewhat angled at periphery, slightly flared abapically. Columella short, smooth. Columellar callus thickened, sharply delimited. Colour pattern is preserved in some specimens consisting of tiny white dots over the cords (Pl. 46, fig. 3).

Discussion – This new species, together with *Calliostoma quaggoides* nov. sp. (see below), form a small group

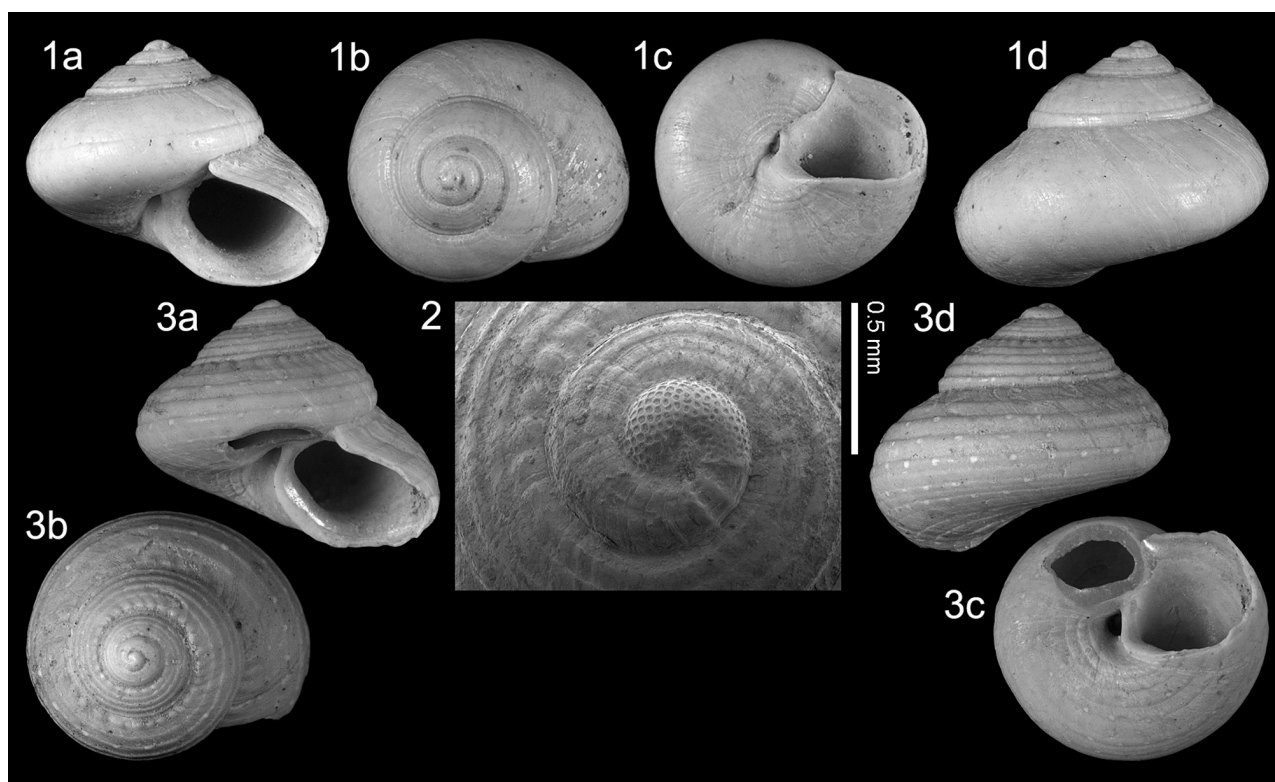


Plate 45. *Calliostoma gibbuliforme* nov. sp.; 1. **Holotype** MNHN.F.A57692, height 3.5 mm, width 4.4 mm; 2. **Paratype 4** NHMW 2016/0103/0125, detail of protoconch (SEM image); 3. **Paratype 2** NHMW 2016/0103/0123, height 4.4 mm, width 5.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

of *Calliostoma* Swainson, 1840 species that at first sight would be placed in the Cantharidinae Gray, 1857, genus *Gibbula* Risso, 1826, but they lack a columellar fold and, more importantly, they have the honeycomb protoconch microsculpture so typical of the genus *Calliostoma*.

Calliostoma gibbuliforme nov. sp. is variable in shape; the last whorl periphery is rounded in some specimens, a bit angular in others. The number of spiral cords is constant, but their strength is strongly variable. One, or less frequently the two most adapical cords, are beaded and one, or less frequently two of the most abapical cords, are more strongly developed forming one or two peripheral carinae. The character of the base and aperture are relatively constant.

The only species with which *C. gibbuliforme* could be confused is *C. quaggoides*, which differs in having an even more depressed shell, with a single subsutural cord, which is not beaded and having colour pattern preserved in almost all specimens consisting of axial stripes rather than spots as seen in *C. gibbuliformis*.

Brébion (1964, p. 79) described this species based on two specimens from Renauleau as var. *andegavensis* of *Calliostoma multistriatum* (Wood in Kendall & Bell, 1886) from the Gelasian Pleistocene of St Erth, England, however, that species is even more depressed with a lower spire and weaker spiral sculpture.

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

Calliostoma echinatum (Millet, 1865)

Plate 46, fig.1

- 1854 *Trochus Echinatus* Millet, p. 157 (*nomen nudum*).
- *1865 *Trochus echinatus* Millet, p. 583.
- 1911 *Eucyclus echinatus* Millet – Cossmann, p. 328.
- 1964 *Eucyclus* (?) *echinatus* Millet, 1854 [*sic*] – Brébion, p. 70, pl. 1, fig. 17.

Type material – Syntypes: Sceaux-d’Anjou and Thorigné, lost (*vide* Brébion, 1964, p. 71).

Material and dimensions – Maximum height 7.4 mm; width 6.2 mm. **Sceaux-d’Anjou**: NHMW 2016/0103/0144 (1), NHMW 2016/0103/0145 (9), RGM.1309590 (2), RGM.1348019 (2 fragments), LC (2), FVD (3). **Renauleau**: NHMW 2016/0103/0146 (1), LC (2).

Discussion – Millet (1865) validated his earlier (1854) *nomen nudum* with this description: ‘*Trochus echinatus*, Millet. *Coq. petite, conique, aiguë, composée de 7 tours de spire couverts d’expansions lamellaires, placées par rangées et disposées en tubes plus ou moins ouverts en dessous et tronqués au sommet. Ces expansions ou tubes qui s’emboîtent les uns dans les autres en se relevant au sommet, présentent un rang plus saillant qui occupe le centre de chaque tour. Hauteur: 7 millimètres; diamètre: 5-6 millimètres. Sc., Ren. Très-remarquable et très rare espèce* (1865, p. 583).’ This description highlights the

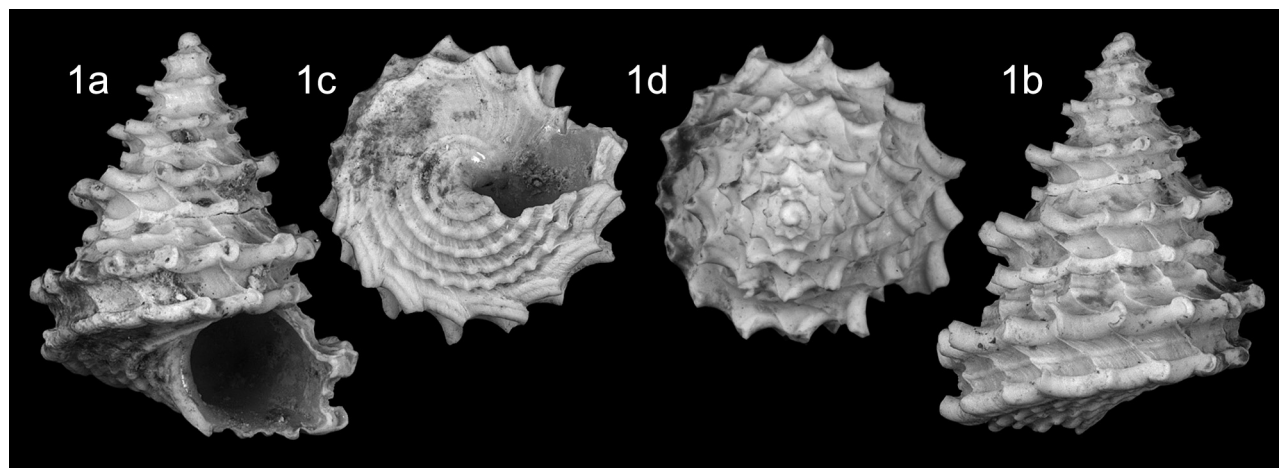


Plate 46. *Calliostoma echinatum* (Millet, 1865); 1. NHMW 2016/0103/0144, height 5.8 mm, width 4.4 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

most outstanding character of this species, which is the long open lamellar spines that develop at the intersections where the axial lamellae cross the primary cords.

Cossmann (1918, p 328) placed this shell in the genus *Eucyclus* Eudes-Deslongchamps, 1860, member of the Eucyclidae Koken, 1896. However, in our opinion the resemblance to shells of this genus is superficial. Although not figured as all of the specimens have an abraded protoconch, remnants of the typical calliostomiid honeycomb pattern are preserved in some shells. The only species with a similar shell is *Calliostoma lamellatum* nov. sp. (see below), which has the same tall conical trochiform shell shape and type of sculpture, but differs in having more numerous spiral cords and axial lamellae that are scabrous at the sculptural intersections, but not spinous as they are in *C. echinatum*. Although, as discussed above, the protoconch surface is abraded in the specimens of *C. echinatum* at hand, it is well-preserved in one of our specimens of *C. lamellatum* and shows the calliostomiid honeycomb surface pattern (Pl. 48, fig. 2). Therefore we place both of these species in the genus *Calliostoma* Swainson, 1840.

Both Millet (1854, 1865) and Brébion (1964, p. 71) recorded this species from Assemblage I localities of Sceaux-d'Anjou and Renauleau.

We note that the placement of Millet's species in the genus *Calliostoma* renders the present-day Caribbean *C. echinatum* Dall, 1881 a secondary homonym. We therefore propose the name *C. caribbechinatum* nom. nov. for Dall's species.

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

***Calliostoma gratiosum* (Millet, 1865)**

Pl. 47, figs 1-4

1854 *Trochus Gratiosus* Millet, p. 156 (*nomen nudum*).

*1865 *Trochus gratiosus* Millet, p. 582.

1964 *Calliostoma (Ampullotrochus) laureatus* Mayer, 1874 – Brébion, p. 98, pl. 2, figs 23-26 (*non* Mayer, 1874).

Material and dimensions – Maximum height 23.9 mm, width 21.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0161 (1), NHMW 2016/0103/0150 (1), NHMW 2016/0103/0162 (16), RGM.1309672 (7), RGM.1309707 (4), LC (3), FVD (19). **Sceaux-d'Anjou:** NHMW 2016/0103/0163 (1), NHMW 2016/0103/0164 (50+), RGM.1309651 (9), RGM.1309670 (6), RGM.1309696 (7), RGM.1309706 (2), RGM.1309718 (19), RGM.1309777 (8), LC (10), FVD (15). **Renauleau:** NHMW 2016/0103/174 (15), LC (10), FVD (8).

Discussion – Millet (1865) validated his earlier (1854) name *Trochus gratiosus* with the following description: 'Trochus gratiosus. Millet. Coq. en cône très-large à sa base, compose de 7-8 tours de spire aplatis, couverts de fines stries perlées, séparées les unes des autres par un filet saillant placé au-dessus de la suture: filet également perlé, et portant en outre un certain nombre de perles plus grosses, éloignées les unes des autres d'environ 3 millimètres. Hauteur: 14-15 millimètres; diamètre à la base: 13-14 millimètres. Th., Sc, Ren. (1865, p. 582)'

This description characterises the shell relatively well; we would add that both the adapical and abapical cords bordering the suture are more strongly developed, accentuating the suture and making it deeply impressed and that the fine beaded cords are of alternate strength on both the dorsum and the base. As noted by Millet, on the abapical cord every 3 mm or so three beads strengthen, the central one most, giving the periphery a slightly crenulated appearance. The periphery of the last whorl is delimited by two strengthened cords of roughly equal weight. The protoconch is paucispiral and typical for calliostomids, covered in a honeycomb pattern (Pl. 47, fig. 3). One specimen from Renauleau (Pl. 47, fig. 4) is twice the size of specimens from other Assemblage I localities sampled, has finer sculpture and the peripheral cords on

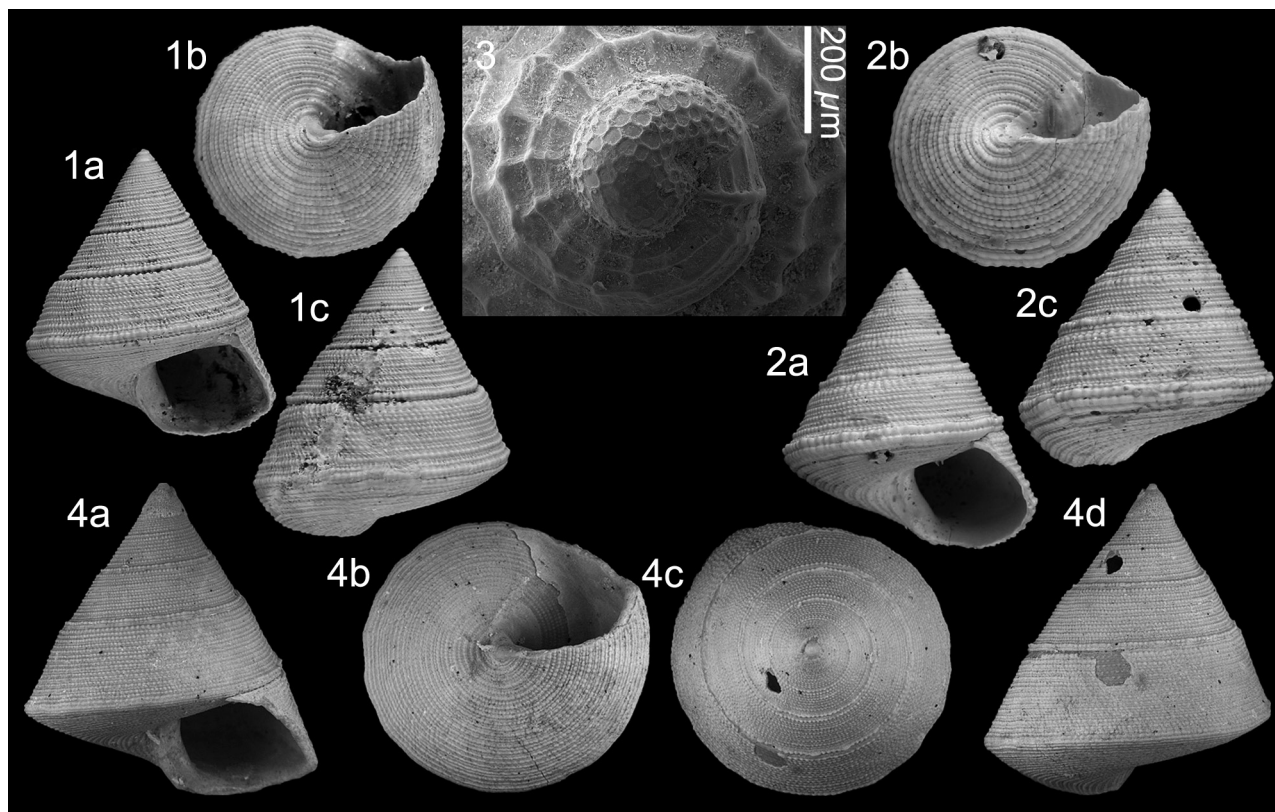


Plate 47. *Calliostoma gratiosum* (Millet, 1865); 1. NHMW 2016/0103/0161, height 14.9 mm, width 12.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place; 2. NHMW 2016/0103/0163, height 12.6 mm, width 11.6 mm. La Presselière, Sceaux-d'Anjou; 3. NHMW 2016/0103/0150, detail of protoconch (SEM image); 4. NHMW 2016/0103/1497, height 21.5 mm, width 20.1 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the last whorl are weaker. However, we consider it to fit within the intraspecific variability for *Calliostoma gratiosum* (Millet, 1865).

Brébion (1964, p. 98) considered Millet's species conspecific with *Trochus laureatus* Mayer, 1874 described from the upper Pliocene of Italy, giving priority to the junior name. We have not seen Mayer's type, but from the description and his own discussion he likens it to *C. granulatum* (von Born, 1778), saying it differs in being smaller, more pointed, with finer spiral sculpture and a crenulated base. The description and comparison also place it close to two other Mediterranean Pliocene species illustrated by Landau *et al.* (2003) belonging to the same species group: *C. opisthetonus* (Fontannes, 1880) and *C. scutiiformis* (Sacco, 1896). All these species differ from *C. gratiosum* in being larger shelled, in having more coelocoid spires and therefore a more pointed apex, coarser, less strongly beaded spiral sculpture and a more flattened base. As mentioned above, we have not seen Mayer's species, but the shell illustrated does not seem conspecific with *C. gratiosum*. The shells illustrated by Glibert (1952, pl. 1, fig. 4) as *C. laureatum* from the North Sea Basin Belgian Miocene differ from *C. gratiosum* in the same characters discussed above. The shell illustrated by Janssen (1984, pl. 44, fig. 3) as *C. laureatum* from the Dutch Miocene differs slightly from other illustrations of that species in having a rounded periphery on the last

whorl not delimited by strengthened basal cords.

Millet (1854, 1865) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d'Anjou and Renauleau, to which Brébion (1964, p. 99) added St-Clément-de-la-Place and Contigné.

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

***Calliostoma lamellatum* nov. sp.**

Plate 48, figs 1-2

Type material – Holotype NHMW 2016/0103/0139, height 4.5 mm, width 3.4 mm; paratype 1 NHMW 2016/0103/0140, height 4.2 mm, width 3.3 mm; paratype 2 NHMW 2016/0103/0141, height 4.4 mm, width 2.5 mm (juvenile); paratype 3 NHMW 2016/0103/0142, height 3.4 mm, width 2.9 mm (juvenile); **St-Clément-de-la-Place**. Paratype 4 RGM.1309625, height 5.1 mm, width 3.4 mm; paratype 5 RGM.1309626, height 4.0 mm, width 2.9 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 6.9 mm, width 4.5 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/0143 (9), RGM.1309627 (1 juvenile), RGM.1348002 (2). **Renauleau**: NHMW 2016/0103/0160 (5).

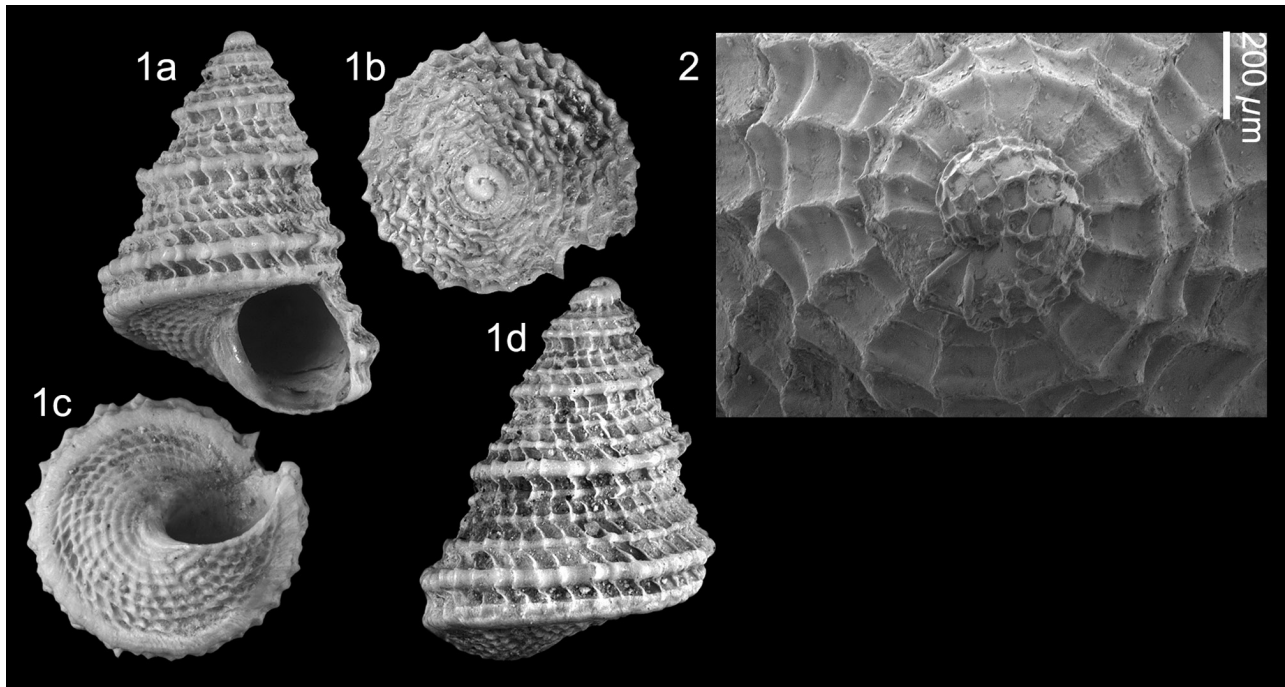


Plate 48. *Calliostoma lamellatum* nov. sp.; 1. **Holotype** NHMW 2016/0103/0139, height 4.5 mm, width 3.4 mm. 2. **Paratype 3** NHMW 2016/0103/0142, detail of protoconch (SEM image). Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Etymology – Name reflecting the characteristic raised axial lamellae seen in this species. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, with tall turbiniform shell shape, spiral sculpture of narrow cords with stronger peripheral and peribasal cords on last whorl, entire surface covered in prosocline axial lamellae, giving surface roughly scabrous appearance, and flattened, imperforate base.

Description – Shell small, tall trochiform, with conical spire. Protoconch paucispiral, of 1.3 whorls, bearing honeycomb surface sculpture. Junction with teleoconch sharply delimited by protoconch lip. Teleoconch of four whorls. Suture linear, superficial. First teleoconch whorl bearing two elevated spiral cords of roughly equal strength and raised, prosocline axial lamellae forming an evenly reticulate sculpture. On second whorl, a third weaker cord develops below adapical suture; abapical cord placed just above abapical suture strengthens forming periphery. On third whorl a fourth weaker cord develops again just below adapical suture. Last whorl with two narrow cords above stronger peripheral cord, below which lies an even stronger peribasal cord, delimiting base. Base flattened, imperforate, bearing eight narrow spiral cords, strengthening slightly towards centre. Entire basal surface cov-

ered with raised axial lamellae, which cross spiral sculpture, giving surface a roughly squamous appearance. Aperture rounded, outer lip simple, rounded at periphery, columella smooth. Columellar callus hardly developed, parietal callus not developed.

Discussion – As mentioned above, *Calliostoma lamellatum* nov. sp. is similar to *Calliostoma echinatum* (Millet, 1865), but differs in having more numerous spiral cords above the peripheral cord, in having the prominent peripheral and basal cords less strongly developed than in *C. echinatum*, and in having more numerous axial lamellae which are scabrous at the sculptural intersections, but do not form spines.

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

***Calliostoma michaeli* nov. sp.**

Plate 49, figs 1-2

Type material – Holotype NHMW 2016/0103/1498, height 15.0 mm, width 12.5 mm; paratype 1 NHMW 2016/0103/1499, height 15.6 mm, width 12.4 mm; paratype 2 MNHN.F.A57939, height 14.7 mm, width 12.3 mm.

Other material – Maximum height 16.0 mm, width 13.3 mm. NHMW 2016/0103/1500 (4), LC (5), FVD (6).

Etymology – Named after Michael Van Dingenen, son of the second author. *Calliostoma* gender neuter.

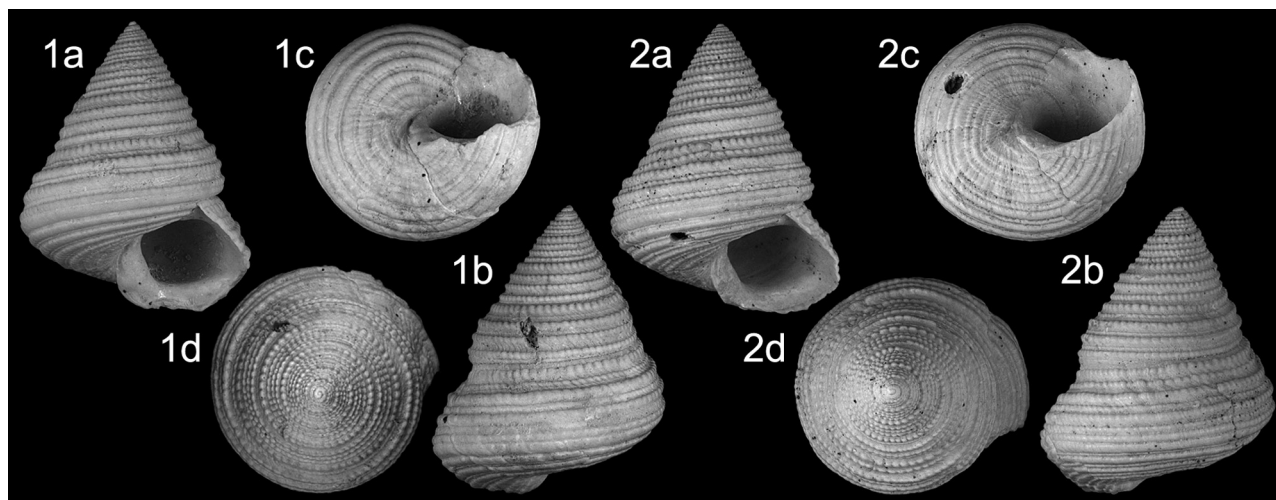


Plate 49. *Calliostoma michaeli* nov. sp.; 1. **Holotype** NHMW 2016/0103/1498, height 15.0 mm, width 12.5 mm; 2. **Paratype 1** NHMW 2016/0103/1499, height 15.6 mm, width 12.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species, of medium-size, with relatively tall spire, whorls becoming progressively more convex, rounded last whorl, sculpture four beaded primary cords with secondary beaded cord in interspaces on last whorl, and rounded imperforate base bearing broad concentric cords.

Description – Shell of medium size and thickness, trochiform, with relatively tall, somewhat scalate spire. Protoconch paucispiral, of 1.3 whorls; surface abraded in all specimens. Teleoconch of five whorls, with periphery at suture. Suture linear, superficial. First half teleoconch whorl bearing two spiral cords and prosocline axial ribs, slightly weaker than cords, forming reticulate sculpture. Second half of first whorl, a third cord develops below adapical suture, rapidly gaining in strength, becoming predominant; axial ribs disappear, cords become beaded. Second whorl, fourth beaded cord appears above suture. Third whorl bearing four beaded cords; stronger subsutural cord and three weaker subequal cords below. Penultimate and last whorls becoming progressively more convex, with secondary beaded cords intercalated in the interspaces. Last whorl convex, bearing beaded cords of alternate strength, rounded at periphery. Peribasal cord bifid, base rounded, imperforate, bearing 6-7 prominent irregular, subobsoletely beaded cords. Aperture subquadrate, outer lip simple, rounded at periphery, columella smooth. Columellar callus thickened and everted, parietal callus thin.

Discussion – *Calliostoma michaeli* nov. sp. is one of the larger *Calliostoma* species in the Assemblage I fauna. Its sculpture of four primary beaded cords on the later whorls is somewhat similar to that of *C. spinosum* nov. sp., but the secondary cords are far more developed; in *C. spinosum*

secondary sculpture is absent or restricted to a single thread between cords 1 and 2 on the last whorl. Moreover, *C. michaeli* is larger shelled, the later whorls are more convex and the basal cords are not as clearly beaded as they are in *C. spinosum*. *Calliostoma baccatum* (Millet, 1865), also from the Assemblage I fauna, has a more regularly and broadly conical spire, less convex later spire whorls, and an angled base with finer basal sculpture.

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

***Calliostoma microgemmatum* nov. sp.**

Plate 50, fig. 1

Type material – Holotype NHMW 2016/0103/0136, height 5.0 mm, width 4.4 mm; paratype 1 NHMW 2016/0103/0137, height 4.1 mm, width 4.3 mm (juvenile); paratype 2 NHMW 2016/0103/0138, height 3.1 mm, width 3.4 mm (juvenile); **St-Clément-de-la-Place**. Paratype 3 RGM.1309680, height 3.8 mm, width 3.9 mm; paratype 4 RGM.1309733, height 4.9 mm, width 5.4 mm; **Sceaux-d'Anjou**. Paratype 5 MNHN.F.A57942, height 4.7 mm, width 4.1 mm; paratype 6 MNHN.F.A57943, height 4.4 mm, width 4.1 mm; **Renauleau**.

Other material – Maximum height 6.5 mm, width 5.3 mm **St-Clément-de-la-Place**: LC (1). **Sceaux-d'Anjou**: RGM.1348003 (6), LC (1). **Renauleau**: NHMW 2016/0103/0198 (18), LC (5), FVD (7).

Etymology – Compound name from Latin ‘micro-’ prefix meaning tiny, and ‘gemmatum’, adjective meaning jewelled, describing the sculpture of finely beaded cords. *Calliostoma* gender neuter.

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

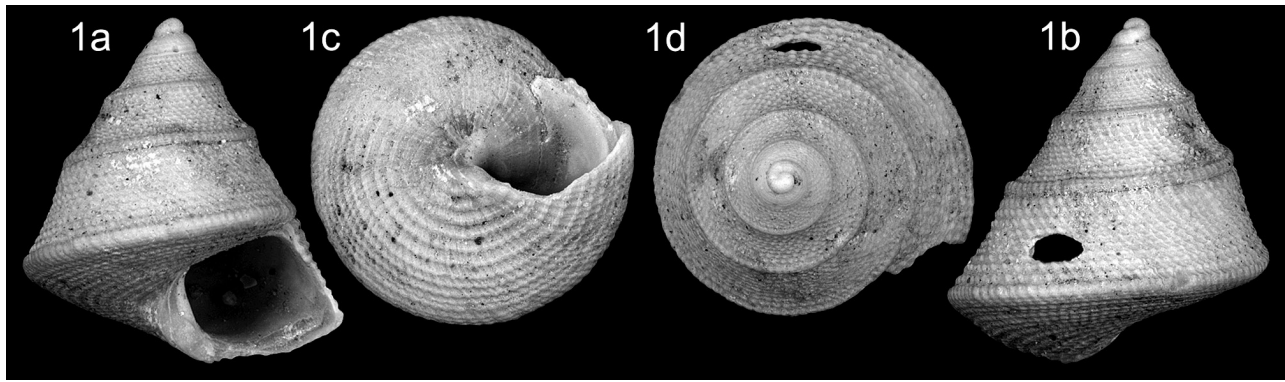


Plate 50. *Calliostoma microgemmatum* nov. sp.; 1. **Holotype** NHMW 2016/0103/0136, height 5.0 mm, width 4.4 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, with concave whorl profile from second teleoconch whorl, sculptured by close-set, finely beaded spiral cords, with prominent suprasutural cord delimiting base on last whorl, and flattened, imperforate base bearing similarly finely beaded cords.

Description – Shell small, trochiform. Protoconch paucispiral, of 1.3 whorls bearing honeycomb surface sculpture. Junction with teleoconch sharply delimited by end of protoconch sculpture. Teleoconch of four whorls. Suture linear, impressed. First teleoconch whorl convex, bearing eight narrow spiral cords, close-set in adapical half of whorl, strengthening slightly and wider spaced towards lower suture. From second whorl, profile concave. Spiral cords increase in number, ten on penultimate and last whorl, irregular in strength. A suprasutural cord becomes swollen, rounded and elevated, forming periphery. Axial growth lines increase in strength from second whorl, finely beading spiral sculpture. Last whorl regularly concave to prominent peribasal cord. Base imperforate, strongly depressed, bearing about 13 finely beaded cords, strengthening and wider-set towards centre. Aperture subquadrate, outer lip simple, angled at periphery, columella smooth. Columellar callus hardly developed, parietal callus reduced to thin callus wash.

Discussion – *Calliostoma microgemmatum* nov. sp. is uncommon in the Assemblage I localities. It is a characteristic species with its concave teleoconch whorls and finely beaded spiral sculpture. The protoconch was too worn to image in all specimens, but remnants of the typical calliostomiid honeycomb surface sculpture are present. It is difficult to find similar congeners with which to compare this species; small specimens of *Calliostoma gratiosum* (Millet, 1865), also from the Assemblage I fauna are similar in having very finely gemmate sculpture, but the whorls profile is less concave, and a spiral on either side of the suture becomes reinforced, whereas in *C. microgemmatum* only the suprasutural cord becomes swollen.

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

***Calliostoma milletigranum* nov. nom.**

Plate 51, figs 1-3

- 1854 *Trochus Millegranus* Millet, p. 157 (*nomen nudum*).
 1865 *Trochus millegranus* Millet, p. 584 (*non* Philippi, 1836).
 1964 *Calliostoma milleti* Brébion, p. 91, pl. 2, figs 12-13. (*nom. nov. pro T. millegranus* Millet, 1865, *non* Philippi, 1836) (*nomen nudum*).

Type material – Syntypes: Sceaux-d'Anjou, lost (*vide* Brébion, 1964, p. 91).

Material and dimensions – Maximum height 13.7 mm; width 13.1 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1491 (1), NHMW 2016/0103/0201-202 (2), NHMW 2016/0103/0203 (2), RGM.1309664 (2), RGM.1309684 (2), RGM.1309770 (2), LC (1). **Renauleau**: NHMW 2016/0103/1483 (2 adult + 6 juveniles), LC (2), FVD (1).

Etymology – Compound name reflecting Brébion's (1964) intention of naming the species after Millet and Millet's original epithet describing the beaded sculpture. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Original description – ‘*Trochus millegranus*, Millet. *Coq. en cône court, composée de 5 à 6 tours de spire; les premiers saillants, arrondis, les derniers, sur un plan oblique, présentent une surface plate; et tous sont couverts de petits grains plus ou moins arrondis, qu'on ne peut voir qu'au foyer d'une forte loupe. Le dessous légèrement bombé est couvert de stries fines, peu apparentes. Hauteur: 9-10 millimètres; diamètre: 8 millimètres. Sc. Très-rare.* (Millet, 1865, p. 584)’.

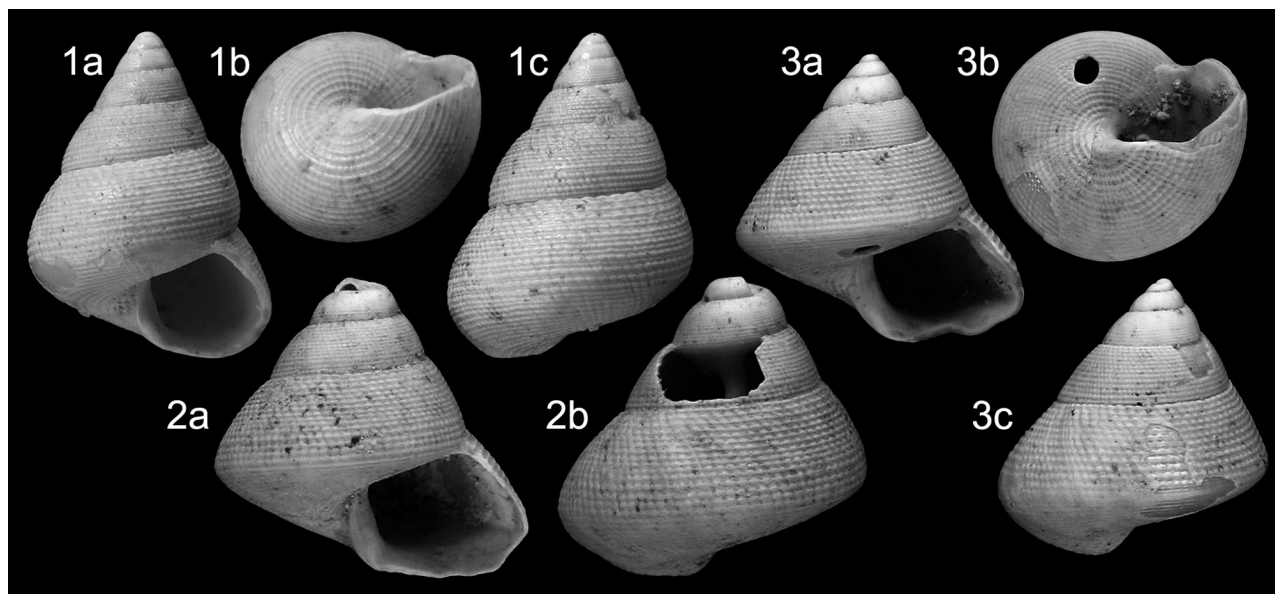


Plate 51. *Calliostoma milletigranum* nov. nom.: 1. NHMW 2016/0103/1491, height 10.8 mm, width 8.4 mm; 2. NHMW 2016/0103/0201, height 8.1 mm, width 7.8 mm; 3. NHMW 2016/0103/0202, height 7.7 mm, width 7.4 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – Millet's (1865, p. 583) description faithfully describes this species and validates his earlier *nomen nudum* (Millet, 1854, p. 157). Unfortunately it is a junior homonym of *T. millegranus* Philippi, 1836, which is itself a junior subjective synonym of the Pliocene present-day Mediterranean *Clelandella miliaris* (Brocchi, 1814). This is probably the most finely sculptured of the Assemblage I calliostomids, with the greatest number of spiral cords, about 14 on the penultimate whorl, which are very finely beaded by the prosocline growth lines. The height of the spire and the basal angulation are quite variable, as seen in the series illustrated (Pl. 51, figs 1-3). The base is poorly delimited and similarly sculptured by about 18 cords.

Millet (1854, 1865) recorded the species from the Assemblage I locality of Sceaux-d'Anjou, to which Brébion (1964, p. 92) added Renauleau.

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

***Calliostoma miotorulosum* nov. nom.**

Plate 52, figs 1-3

1865 *Trochus torulosus* Millet, p. 583 (*non* Philippi, 1845).

1964 *Calliostoma torulosum* Mayer, 1874 – Brébion, p. 92, pl. 2, fig. 14. (*non T. torulosus* Philippi, 1845).

Type material – Syntypes: Sceaux-d'Anjou, Musée d'Angers, France (*vide* Brébion, 1964, p. 93).

Material and dimensions – Maximum height 9.8 mm; width 7.1 mm. **St-Clément-de-la-Place**: NHMW 2016/

0103/0175 (1), NHMW 2016/0103/0180 (1), NHMW 2016/0103/0176 (15), RGM.1309745 (2), LC (1), FVD (16). **Sceaux-d'Anjou**: NHMW 2016/0103/0177 (1), NHMW 2016/0103/0178 (15), RGM.1309631 (7), RGM.1309663 (4), RGM.1309681 (11), RGM.1309697 (1), RGM.1309712 (4), RGM.1309717 (1), RGM.1309722 (3), RGM.1309728 (4), RGM.1309778 (1), RGM.1348004 (3), LC (5), FVD (8). **Renauleau**: NHMW 2016/0103/0179 (11), LC (5), FVD (10). **Beugnon**: RGM.1309677 (1).

Etymology – Honouring Millet's original trivial name '*torulosus*', adding the prefix '*mio-*' reflecting the Miocene period in which it lived. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Original description – '*Trochus torulosus*, Millet. *Coq. conique, aiguë, composée de 7-8 tours de spire couverts de stries fines, coupées ou ciselées obliquement par des stries plus fines encore. Chaque tour, en outre, est bordé inférieurement par un fort bourrelet arrondi, ciselé verticalement, et sur lequel on remarque çà et là quelques renflements en forme de perle. Dessous anguleux, couvert de stries simples. Hauteur: 10-11 millimètres; diamètre: 9-10 millimètres. Sceaux.* (Millet, 1865, p. 583).'

Discussion – Millet's (1865, p. 583) description faithfully describes this species. Unfortunately it is a junior homonym of *T. torulosus* Philippi, 1845, which is itself a junior subjective synonym of the present-day south

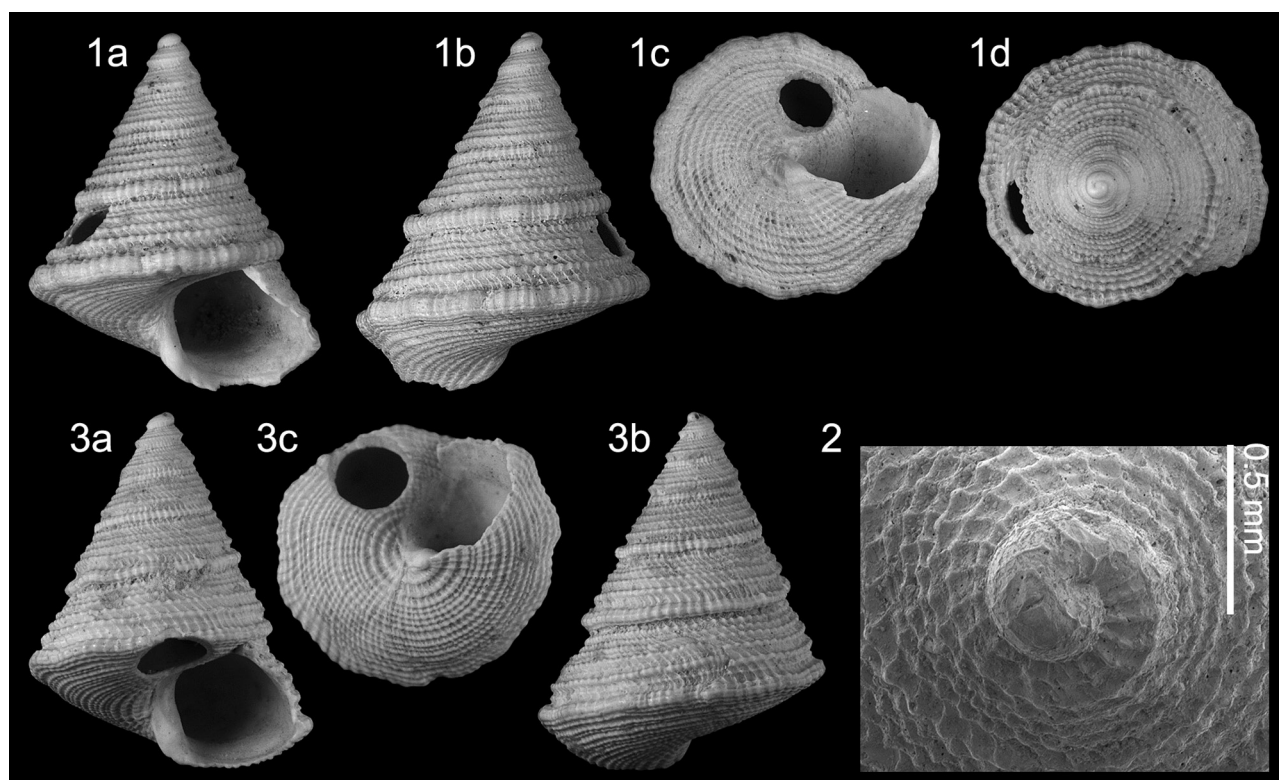


Plate 52. *Calliostoma mitorulosum* nov. nom.; 1. NHMW 2016/0103/0175, height 6.2 mm, width 5.1 mm; 2. NHMW 2016/0103/0180 detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place. 3. NHMW 2016/0103/0177, height 8.1 mm, width 6.1 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

eastern Pacific *Tegula quadricostata* (W. Wood, 1828). This small, but strongly sculptured calliostomiid, with its coeloconoid spire and strongly developed crenulated suprasutural cord, which on the last whorl forms the acutely angular periphery to the base is difficult to confuse with any of its congeners. The protoconch is typically calliostomiid with a honeycomb sculpture composed of rather narrow netting and wide holes in between ($dp = 465 \mu\text{m}$, $dn = 215 \mu\text{m}$).

Millet (1865, p. 583) recorded the species only from Sceaux-d'Anjou, but it is widely distributed in the Assemblage I localities (St-Clément-de-la-Place, Chalonnes, Renauleau; Brébion, 1964, p. 93).

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

***Calliostoma miotumidum* nov. nom.**

Plate 53, fig. 1

- 1854 *Trochus Tumidus* Millet, p. 157 (*nomen nudum*).
- 1865 *Trochus tumidus* Millet, p. 583 (*non T. tumidus* Montagu, 1803).
- 1964 *Calliostoma tumidum* Millet, 1854 [*sic*] – Brébion, p. 96, pl. 2, figs 19-20 (?21).

Type material – Syntypes: Thorigné and Sceaux-d'Anjou, Musée d'Angers, France (*vide* Brébion, 1964, p. 97).

Material and dimensions – Maximum height 14.5 mm, width 14.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1504 (1), NHMW 2016/0103/1505 (2), LC (2), FVD (1).

Etymology – Honouring Millet's original trivial name '*tumidus*', adding the prefix '*mio-*' reflecting the Miocene period in which it lived. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Original description – '*Trochus tumidus*, Millet. Coq. en cône raccourci, aiguë au sommet, composée de 7 tours de spire arrondis et comme gonflés, surtout les derniers tours; tous sont couverts de stries fines et rapprochées entre elles et présentent à la base un petit filet que détache la suture. Dessous bombé, lisse ou marqué seulement de quelques stries légères vers remplacement de l'ombilic. Hauteur et diamètre: 14 millimètres. Sc, Th.' (Millet, 1865, p. 583).

Revised description – Shell of medium size and thickness, low trochiform, with wide apical angle. Protoconch not preserved. Teleoconch of up to seven whorls; apex pointed, early whorls straight sided, last two whorls inflated. Suture superficial, linear. First two teleoconch whorls sculptured by five narrow cords, adapical cord

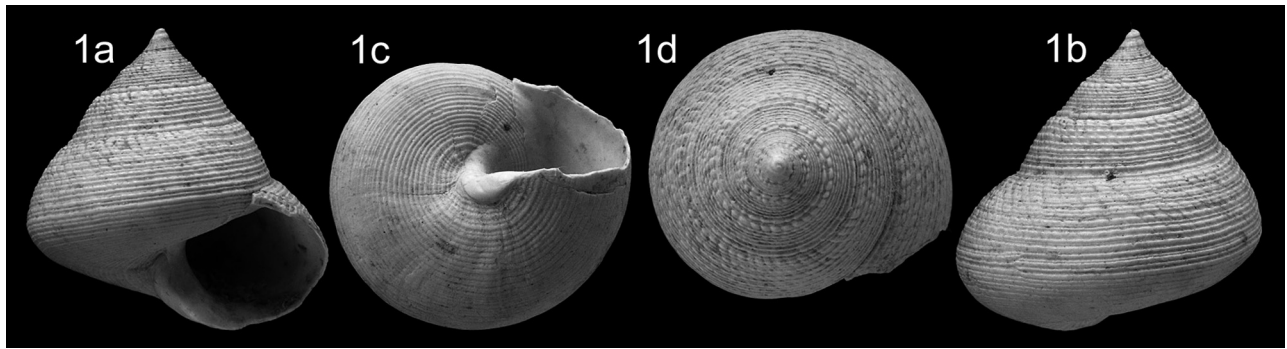


Plate 53. *Calliostoma miotumidum* nov. nom.; 1. NHMW 2016/0103/1504, height 14.5 mm, width 14.2 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

becoming beaded on second whorl. Third whorl ad- and abapical cords strengthen, beaded, with five finer cords in between. Fourth whorl adapical cord becomes bifid, six weaker finely beaded cords between ad- and abapical cords. Last whorl rounded at periphery, with secondary cords intercalated in all interspaces between primaries. Base not sharply delimited, imperforate, bearing numerous subequal smooth cords. Aperture rounded, outer lip simple, rounded at periphery. Columella callus strongly thickened and everted.

Discussion – Millet name *Trochus tumidus* is unfortunately a junior homonym of *T. tumidus* Montagu, 1803 [= *Gibbula tumida* (Montagu, 1803)], we propose the replacement name *Calliostoma miotumidum* nov. nom.

We have offered a revised description of this species, as Millet’s (1865, p. 583) text does not describe the spiral sculpture adequately. The superficial suture is bounded and accentuated above by a single beaded abapical cord of the preceding whorl and below by a bifid beaded adapical cord of the subsequent whorl. It is this character most importantly that separates it from *Calliostoma milletigranum* nov. nom., which is also sculptured by numerous finely beaded cords, but the ones closest to the suture are not strengthened. The base is also finely beaded in *C. milletigranum*, with less numerous cords than seen in this species, in which the crowded basal cords are smooth. As commented by Brébion (1964), this species is similar

to one illustrated by Harmer (1923, p. 714, pl. 58, figs 1-3) as *Trochus (Calliostoma) bullatus* (Philippi, 1844). We have not seen this species, but it seems to be larger and have fewer and slightly stronger beaded cords and in the Sicilian specimen illustrated by Philippi (1844, pl. 18, fig. 8) the cords bordering the suture are not strengthened. Millet (1854, 1865) recorded this species from the Assemblage I localities of Sceaux-d’Anjou and Thorigné, to which Brébion (1964, p. 97) added Renauleau and St-Clément-de-la-Place.

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

***Calliostoma planospirum* (Millet, 1865)**

Plate 54, fig. 1

- 1854 *Trochus Planospirus* Millet, p. 156 (*nomen nudum*).
- *1865 *Trochus planospirus* Millet, p. 582.
- 1964 *Calliostoma planospira* Millet, 1854 [*sic*] – Brébion, p. 80, pl. 1, figs 26-28.

Type material – Syntypes: St-Clément-de-la-Place, Thorigné and Sceaux-d’Anjou, Musée d’Angers, France (*vide* Brébion, 1964, p. 81).

Material and dimensions – Maximum height 26.2 mm;

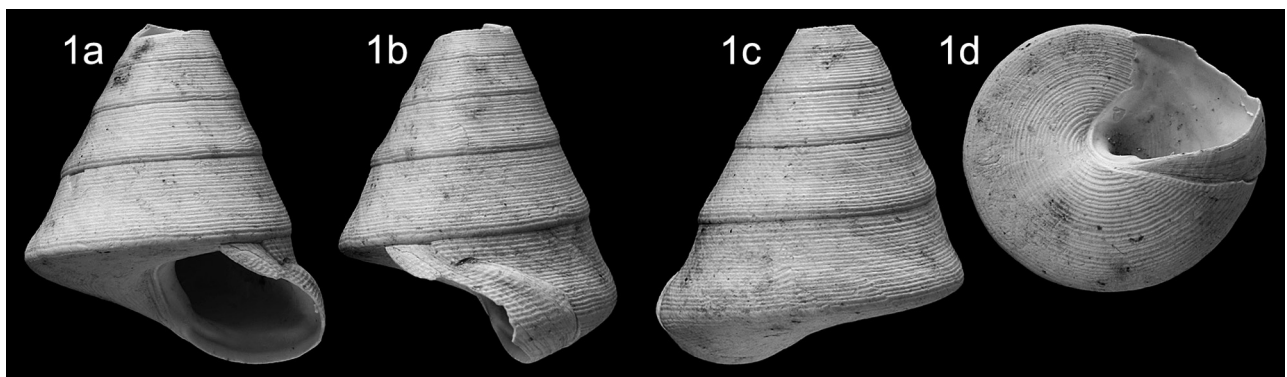


Plate 54. *Calliostoma planospirum* (Millet, 1865); 1. NHMW 2016/0103/1495, height 26.2 mm; width 23.3 mm. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

width 23.3 mm (incomplete). **Sceaux-d'Anjou**: NHMW 2016/0103/1495-1496 (2), RGM.1309666 (7 fragments), LC (3), FVD (1).

Original description – ‘Trochus planospirus, Millet. Coq. en cône régulier, aigu, de moyenne taille; composée de 11-12 tours de spire aplatis, et couverte de stries ou petits filets circulaires. Hauteur: 30 millimètres; diamètre: 24 millimètres. Saint-Clément, Sc, Th. (Millet, 1865, p. 582)’.

Discussion – *Calliostoma planospirum* (Millet, 1865) is the largest *Calliostoma* species in the Assemblage I fauna. There is little to add to Millet’s description, except to say that the whorls are narrowly swollen abapically, slightly overhanging the suture. This species is closely similar to the Pliocene to present-day *Calliostoma zizyphinum* (Linnaeus, 1758), but differs in having a taller spire and a more depressed base. The sculpture in *C. zizyphinum* is somewhat variable, but most specimens have broader cords than *C. planospirum* and a thickened abapical cord is usually present (see Giannuzzi-Savelli *et al.*, 1994, figs 158-168). In *C. planospirum* the cords are very fine and equal in width over the entire whorl.

Brébion (1964, p. 81) described a similar form, based on a couple of shells from Contigné, as var. *saccoi* (*nomen nudum*), differing from the type in having coarser beaded cords, in one specimen the cords of alternating strength. We have not come across this form, but doubt they are conspecific with *C. planospirum*.

Millet (1854, 1865) and Brébion (1964, p. 81) recorded this species from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Thorigné.

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

Calliostoma quaggaoides nov. sp.

Plate 55, figs 1-2

Type material – Holotype MNHN.F.A57682, height 3.3

mm, width 4.8 mm; paratype 1 MNHN.F.A57683, height 2.3 mm, width 4.0 mm; paratype 2 NHMW 2016/0103/0048, height 2.6 mm, width 5.3 mm; paratype 3 NHMW 2016/0103/0049, height 2.6 mm, width 4.5 mm; paratype 4 NHMW 2016/0103/0122, height 2.4 mm, width 4.2 mm; **St-Clément-de-la-Place**. Paratype 5 RGM.1309702, height 5.5 mm, width 6.7 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 4.6 mm, width 5.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0050 (49). **Sceaux-d'Anjou**: NHMW 2016/0103/0051 (10), RGM.1309633 (4), RGM.1309683 (3), RGM.1309710 (2), RGM.1309723 (1), RGM.1348020 (2), LC (2). **Renauleau**: NHMW 2016/0103/0118 (2), LC (1).

Etymology – Named after the extinct quagga zebra, referring to the zebra-like stripes. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, lenticular shell shape, with smooth whorls, except for single suprasutural cord, angular periphery, narrow umbilicus bordered by cord and colour pattern of white radial stripes.

Description – Shell small, depressed, lenticular. Protoconch paucispiral, of 1.2 whorls bearing honeycomb surface sculpture (dp = 360 μ m, dn = 160 μ m). Junction with teleoconch sharply delimited by abrupt end to protoconch sculpture. Teleoconch of three low convex whorls, with periphery at abapical suture, separated by impressed suture. Sculpture restricted to a single suprasutural cord. Last whorl depressed, angular at peripheral cord, base flattened, smooth, except for 3-4 weak cords adjacent to, and strengthening towards periumbilical cord. Umbilicus narrow, deep, smooth within. Aperture ovate, outer lip simple, angled at periphery. Columella weakly thickened,

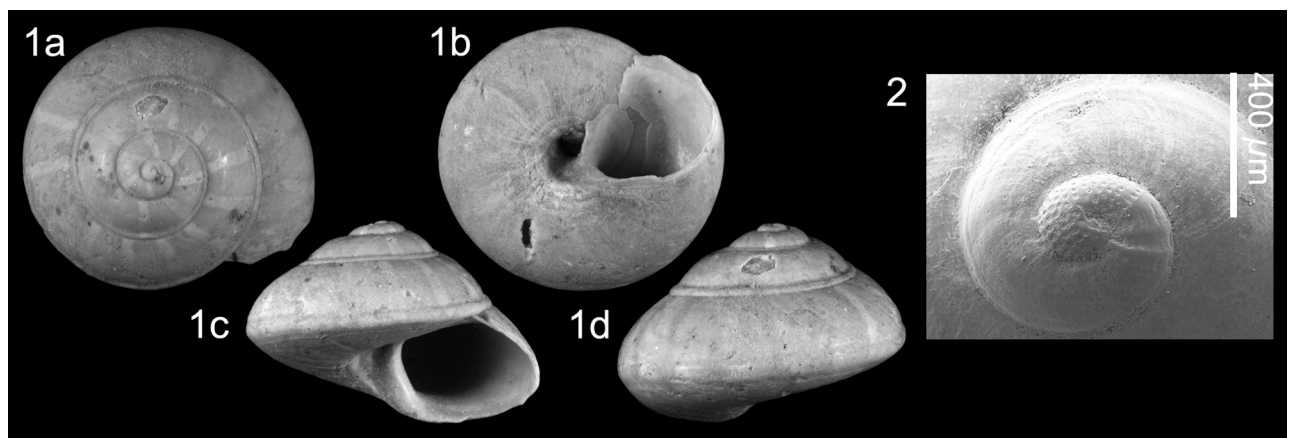


Plate 55. *Calliostoma quaggaoides* nov. sp.; 1. **Holotype** MNHN.F.A57682, height 3.3 mm, width 4.8 mm; 2. **Paratype 4** NHMW 2016/0103/0122, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

sloping abaxially. Colour pattern preserved in almost all specimens of fine, radial white stripes.

Discussion – At first sight this small lentiform species resembles a species of *Gibbula*, however, the paucispiral protoconch covered by honeycomb sculpture places it in *Calliostoma*. *Calliostoma gibbuliforme* nov. sp. also has a gibbuliform rather than trochiform shell shape, but is less depressed, has weak spiral cords, absent in *C. quaggoides*, and colour pattern of small white spots at the periphery rather than axial stripes. We cannot find any other eastern Atlantic fossil or present-day faunas even remotely similar to this shell to compare.

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

Calliostoma pagodulum (Millet, 1865)

Plate 56, figs 1-4

- 1854 *Trochus Pagodulus* Millet, p. 157 (*nomen nudum*).
 *1865 *Trochus pagodulus* Millet, p. 583.
 1964 *Calliostoma (Eucasta) pagodulum* Millet, 1854 [sic] – Brébion, p. 101, pl. 2, figs 29, 30.

Type material – Holotype: Thorigné or Sceaux-d'Anjou, Musée d'Angers, France (*fide* Brébion, 1964, p. 102).

Material and dimensions – Maximum height 13.5 mm,

width 10.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0043 (1), NHMW 2016/0103/0045 (1), NHMW 2016/0103/0044 (8), RGM.1309599 (2 fragments), LC (8), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0046 (19), RGM.1309536 (10), RGM.1309593 (1), RGM.1309671 (8), RGM.1347854 (5), RGM.1348005 (3), LC (8), FVD (12). **Renauleau**: NHMW 2016/0103/1502-1503 (2), NHMW 2016/0103/0047 (3), LC (15), FVD (9). **Beugnon**: RGM.1309534 (11), RGM.1309535 (4), RGM.1309739 (2), LC (2).

Discussion – *Calliostoma pagodulum* (Millet, 1865) is probably the most striking calliostomiid found in Assemblage I, characterised by having two strongly raised, weakly undulating cords on each whorl, with the interspaces deeply recessed. The cords are crossed by axial lamellae that interrupt the cords giving them a beaded/squamous appearance. Further weaker cords are present on the shoulder. The base bears a strong cord a short distance from the crenulated peribasal cord, with about eight further weaker beaded cords medially. The sculpture of *Calliostoma pagodulum* (Millet, 1865) is unlike that of any eastern Atlantic fossil or present-day *Calliostoma* species. Millet (1854, 1865) described this species from the Assemblage I localities of Sceaux-d'Anjou and Thorigné, to which Brébion (1964, p. 102) added St-Clément-de-la-Place.

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

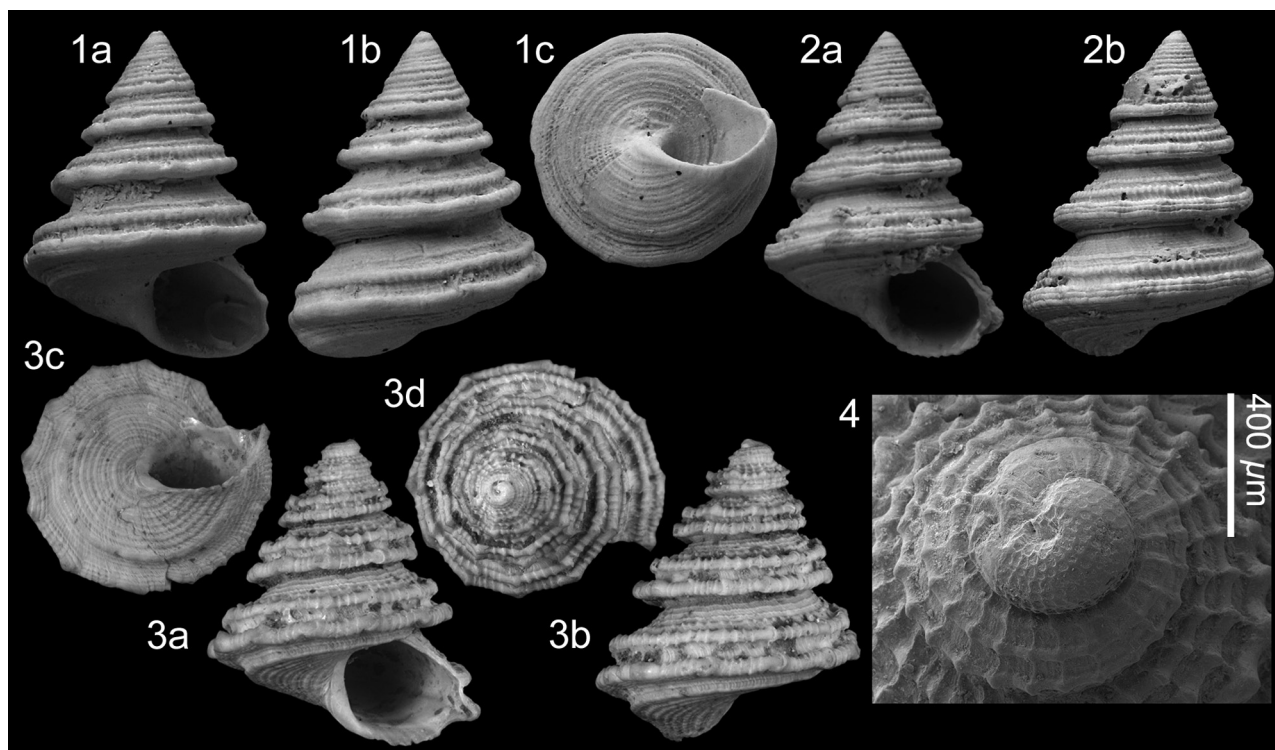


Plate 56. *Calliostoma pagodulum* (Millet, 1865); 1. NHMW 2016/0103/1502, height 11.3 mm, width 8.9 mm; 2. NHMW 2016/0103/1503, height 13.5 mm, width 10.0 mm; Renauleau; 3. NHMW 2016/0103/0043 (subadult), height 7.7 mm, width 6.3 mm; 4. NHMW 2016/0103/0045, detail of protoconch (SEM image), Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Calliostoma presselierense* nov. sp.**

Plate 57, figs 1-2

Type material – Holotype NHMW 2016/0103/0668, height 7.1 mm, width 3.9 mm; paratype 1 NHMW 2016/0103/1461, height 3.3 mm (juvenile); paratype 2 MNHN.F.A57940, height 4.7 mm, width 2.5 mm.

Other material – LC (1).

Etymology – Named after the farm in which the locality is situated, La Presselière, Sceaux-d'Anjou. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, with tall slender trochiform shell shape, spiral sculpture of two elevated narrow cords, with third weaker cord below suture, and about 25 prosocline axial lamellae forming pointed tubercles at intersections, flattened imperforate base delimited by smooth peribasal cord, bearing irregular cords without axial sculpture.

Description – Shell small, tall slender trochiform, with conical spire. Protoconch paucispiral, composed of 1.3 whorls, bearing honeycomb pattern. Teleoconch of six whorls. Suture linear, impressed. First teleoconch whorl bearing two narrow elevated spiral cords, abapical one slightly stronger forming periphery. Cords crossed by about 25 strongly prosocline axial lamellae forming pointed tubercles at intersections. On third whorl, third weaker cord develops below adapical suture. Last whorl with weak subsutural cord, two narrow subequal spinous cords mid-whorl, strong smooth peribasal cord delimiting base. Base flattened, imperforate, bearing five narrow spiral cords of irregular strength. Aperture rounded, outer lip simple, rounded at periphery, columella smooth. Columel-

lar callus narrow, thickened, parietal callus not developed.

Discussion – Although represented by a single adult specimen and two juveniles with the protoconch preserved, this species is so distinctive it warrants description. *Calliostoma presselierense* nov. sp., *C. lamellatum* nov. sp. and *C. echinatum* (Millet, 1865) form a species group with similar sculpture composed of narrow elevated cords and axial lamellae forming spines or pointed tubercles at the intersections. *Calliostoma presselierense* is the tallest and most slender of the group, the spines developed at the intersections are pointed tubercles rather than long open spines as in *C. echinatum* or short spines as in *C. lamellatum*. Moreover, the base in *C. presselierense* is devoid of axial sculpture, whereas there is some axial sculpture reticulating the basal cords in the other two species. *Calliostoma presselierense* has so far only been found at Sceaux-d'Anjou.

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

***Calliostoma spinosum* nov. sp.**

Plate 58, figs 1-6

1964 *Calliostoma deshayesi* Mayer, 1862 – Brébion, p. 76 (*non* Mayer, 1862).

Type material – Holotype MNHN.F.A57698, height 5.4 mm, width 4.5 mm; paratype 1 MNHN.F.A57699, height 5.4 mm, width 4.3 mm; paratype 2 NHMW 2016/0103/0209, height 6.0 mm, width 5.1 mm; paratype 3 NHMW 2016/0103/0210, height 6.8 mm, width 5.7 mm; paratype 4 NHMW 2016/0103/0211, height 6.3 mm, width 4.5 mm; paratype 5 NHMW 2016/0103/0214, height 5.8 mm, width 5.4 mm; paratype 6 NHMW 2016/0103/0212 (juvenile); paratype 7 RGM.1309602, height 3.7 mm, width 3.2 mm; **St-Clément-de-la-Place**. Paratype 8 RGM.1309660, height 7.2 mm, width 5.8 mm; paratype 9 RGM.1309661, height 6.9 mm, width 6.2 mm; **Sceaux-d'Anjou**.

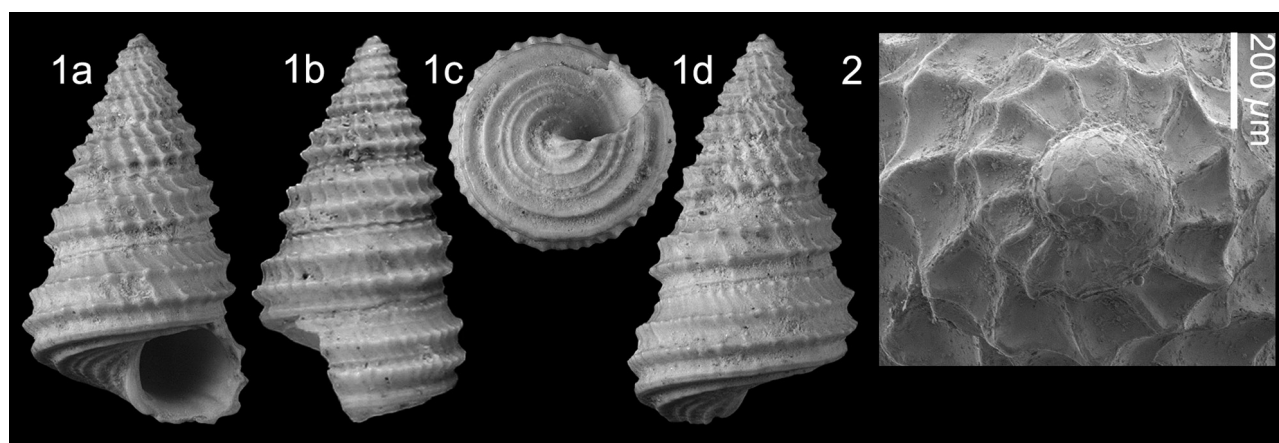


Plate 57. *Calliostoma presselierense* nov. sp.; 1. **Holotype** NHMW 2016/0103/0668, height 7.1 mm, width 3.9 mm; 2. **Paratype 1** NHMW 2016/0103/1461, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

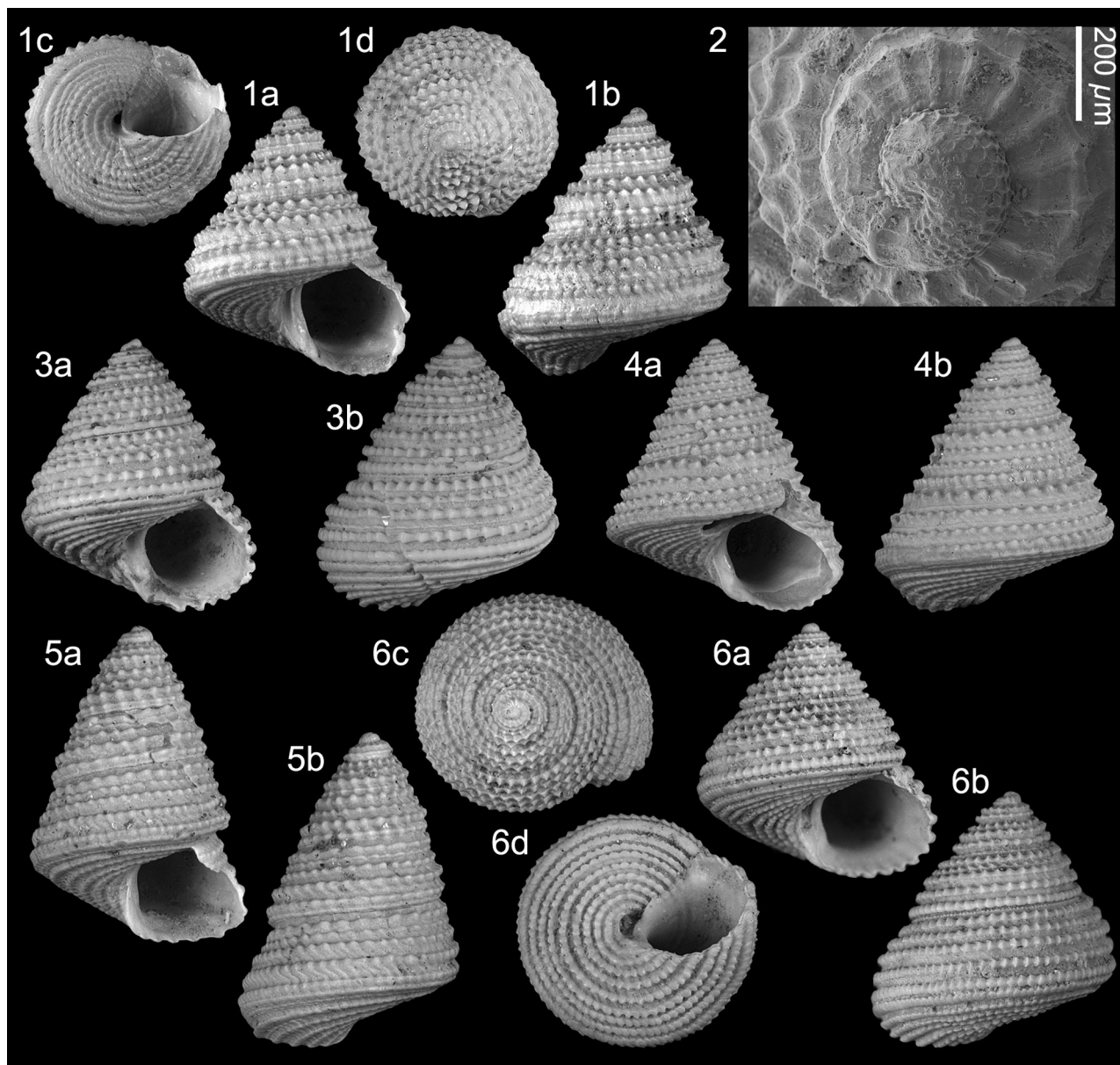


Plate 58. *Calliostoma spinosum* nov. sp.; 1. **Holotype** MNHN.F.A57698, height 5.4 mm, width 4.5 mm; 2. **Paratype 6** NHMW 2016/0103/0212, detail of protoconch (SEM image); 3. **Paratype 2** NHMW 2016/0103/0209, height 6.0 mm, width 5.1 mm; 4. **Paratype 3** NHMW 2016/0103/0210, height 6.8 mm, width 5.7 mm; 5. **Paratype 4** NHMW 2016/0103/0211, height 6.3 mm, width 4.5 mm; 6. **Paratype 5** NHMW 2016/0103/0214, height 5.8 mm, width 5.4 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Other material – Maximum height 5.8 mm, width 4.7 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0213 (50+), RGM.1309560 (1 juvenile), RGM.1309673 (14), RGM.1309746 (17), RGM.1309759 (18), LC (4), FVD (12). **Sceaux-d’Anjou:** NHMW 2016/0103/0220 (50+), RGM.1309662 (18), RGM.1309686 (17), RGM.1309693 (25), RGM.1309708 (1), RGM.1309711 (41), RGM.1309764 (11), RGM.1309776 (26), RGM.1348006 (41), LC (20), FVD (18). **Renauleau:** NHMW 2016/0103/0215 (50+), LC (50), FVD (34). **Beugnon:** RGM.1309675 (20), RGM.1309744 (1).

Etymology – Latin ‘*spinosus*, -a, -um’, adjective, meaning spiny; reflecting the sharp tubercles developed at the

sculptural intersections. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, with depressed, slightly scalate spire, sculptured by four primary spiral cords bearing sharp tubercles, angular depressed base bearing eight cords, and narrow umbilicus.

Description – Shell small, trochiform, with low, some-

what scalate spire. Protoconch paucispiral, of 1.1 whorls bearing honeycomb surface sculpture ($dp = 390 \mu\text{m}$, $dp = 160 \mu\text{m}$). Junction with teleoconch sharply delimited by end of protoconch sculpture. Teleoconch of four whorls. Suture linear, impressed. First teleoconch whorl bearing two elevated spiral cords of roughly equal strength and about 18 axial ribs, slightly weaker than cords, forming reticulate sculpture. On second whorl, a third cord develops above the abapical suture; on third whorl a fourth again just above abapical suture. On penultimate whorl adapical cord placed just below suture, second cord forms shoulder, third cord placed midway between shoulder and lower suture, fourth cord placed just above suture. Axial sculpture weakens abapically, but sharp pointed tubercles developed at intersections, most strongly developed on adapical cord. Last whorl bearing four primary spinous cords, secondary threads developed in interspaces between cords 1 and 2, and 2 and 3. Base sharply angled, flattened, delimited by bifid, non-spinous peribasal cord, bearing about eight irregular elevated cords beaded mid-base by prosocline growth line, narrowly umbilicate. Aperture rounded, outer lip simple, rounded at periphery, columella smooth. Columellar callus sharply delimited, parietal callus thin.

Discussion – As can be seen from the series illustrated, we have interpreted this species as being highly variable. The most distinctive character common to all these forms is the presence of four primary spiral cords on the dorsum of the penultimate and last whorls. Having said this, almost all the other characters are variable. The description offered above is based on what we consider the ‘typical’ form. Rather than include every variable factor in the description we will describe below some of the most important varieties.

Paratype 2 (Pl. 58, fig. 3) has the primary spiral cords strongly elevated, with denser, but less pointed tubercles, on the last whorl the secondary cord between primaries 1 and 2 is almost as strong as the primaries, the base is less flattened and the cords on the base are strongly raised and

strongly beaded towards the umbilicus.

Paratype 3 (Pl. 58, fig. 4) has a more regular conical spire, no secondary spiral sculpture is developed and the base is strongly flattened, the basal cords are less strongly developed, but all of them are beaded.

Paratype 4 (Pl. 58, fig. 5) has a more slender regular conical spire. On the last whorl the tubercles on the whorls are closer-set than usual and only five cords cover the base.

Paratype 5 (Pl. 58, fig. 6) is thickened and gerontic, the tubercles are close-set and lamellar and on the last whorl the secondary cord between primaries 1 and 2 is almost equal in strength to the primaries.

As well as these extreme morphs described above, in the occasional shell the basal cords are reduced to fine threads, and in some the tubercles seem less sharp, although they may be abraded. Between these morphs and the typical form lie numerous intermediate specimens. Despite this wide range of variability, *Calliostoma spinosum* nov. sp. is a distinctive species that can only be compared to *C. deshayesi* (Mayer, 1862) from the middle Miocene Loire Basin of France. They both have whorls bearing four primary spiral cords, but *C. deshayesi* is far higher spired, the beads on the cords are not spinous and the base bears fewer cords that are more finely or more weakly beaded.

Brébion (1964, p. 76) recorded this species from Assemblage I localities of Renaudeau and St-Michel, to which we add St-Clément-de-la-Place.

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

Calliostoma umbellum (Millet, 1865)

Plate 59, fig. 1

1854 *Trochus Umbella* Millet, p. 157 (*nomen nudum*).

*1865 *Trochus Umbella* Millet, p. 583.

1964 *Calliostoma umbella* Millet, 1854 [*sic*] – Brébion, p. 95, pl. 2, figs 17, 18.

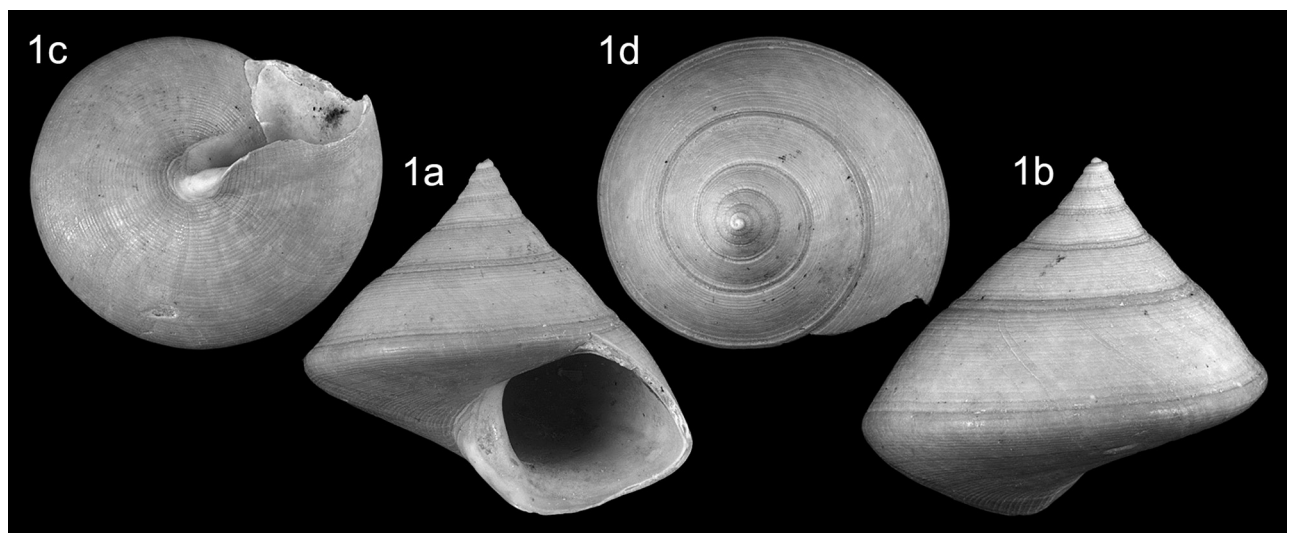


Plate 59. *Calliostoma umbellum* (Millet, 1865); 1. NHMW 2016/0103/0165, height 10.0 mm, width 11.0 mm. Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Type material – Syntypes: Thorigné, Sceaux-d’Anjou and Renauleau, Musée d’Angers, France (*vide* Brébion, 1964, p. 96).

Material and dimensions – Maximum height 10.5 mm, width 12.2 mm (incomplete). **St-Clément-de-la-Place**: NHMW 2016/0103/0165-0166 (2), LC (1). **Sceaux-d’Anjou**: NHMW 2016/0103/0173 (4), RGM.1309588 (4), RGM.1309659 (1), RGM.1309685 (3), RGM.1309705 (1), RGM.1309737 (1), LC (4). **Renauleau**: NHMW 2016/0103/1484 (11), LC (8), FVD (6).

Discussion – Millet (1865) validated his earlier (1854) name *Trochus umbella* with the following description: ‘*Trochus umbella*, Millet. *Coq. assez grande, en cône court, composée de 6-7 tours de spire portant des stries à peine marquées, mais présentant à la base de chaque tour un filet qui accompagne la suture et formant carène sur le dernier tour, ce dernier tour semble pouvoir s’engainer avec celui qui le touche et présente, d’ailleurs, selon la variété, une surface plane ou légèrement creusée vers le centre. Dessous bombé, lisse, étant marqué seulement de quelques stries courtes vers le bord collumellaire. Hauteur et diamètre: 15 millimètres. Th., Sc., Ren.* (1865, p. 583)’ There is little to add to this description except to draw attention to the change in spire profile with ontogeny from coeloconoid to cyrtconoid. It shows certain resemblance to the Pliocene to present-day European *C. zizyphinum* (Linnaeus, 1758), but this species is larger, with a taller regularly conical spire and stronger spiral sculpture. It is also somewhat similar to *C. planospirum* (Millet, 1865), but this species is higher spired with a flat base and has a different shell profile.

Brébion (1964, p. 96) recorded this species from Assemblage I localities (Sceaux d’Anjou, Thorigné and Renauleau), to which we add St-Clément-de-la-Place.

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

***Calliostoma verrucosum* nov. sp.**

Plate 60, figs 1-3

Type material – Holotype MNHN.F.A57694, height 4.4 mm, width 4.4 mm; paratype 1 NHMW 2016/0103/0184, height 6.2 mm, width 5.3 mm; paratype 2 NHMW 2016/0103/0185, height 5.4 mm, width 5.0 mm; paratype 3 NHMW 2016/0103/0186, height 5.1 mm, width 4.8 mm; paratype 4 NHMW 2016/0103/0187, height 3.4 mm, width 2.9 mm (incomplete juvenile); **St-Clément-de-la-Place**. Paratype 5 RGM.1309719, height 5.9 mm, width 5.7 mm; paratype 6 RGM.1309724, height 5.8 mm, width 5.4 mm; **Sceaux-d’Anjou**.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/0188 (3), LC (1), FVD (2). **Sceaux-d’Anjou**: RGM.1309699 (1), LC (1).

Etymology – Latin ‘*verrucosus*, -a, -um’ adjective, meaning warty, rough, reflecting the character of the sculpture. *Calliostoma* gender neuter.

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

Stratum typicum – Tortonian, upper Miocene.

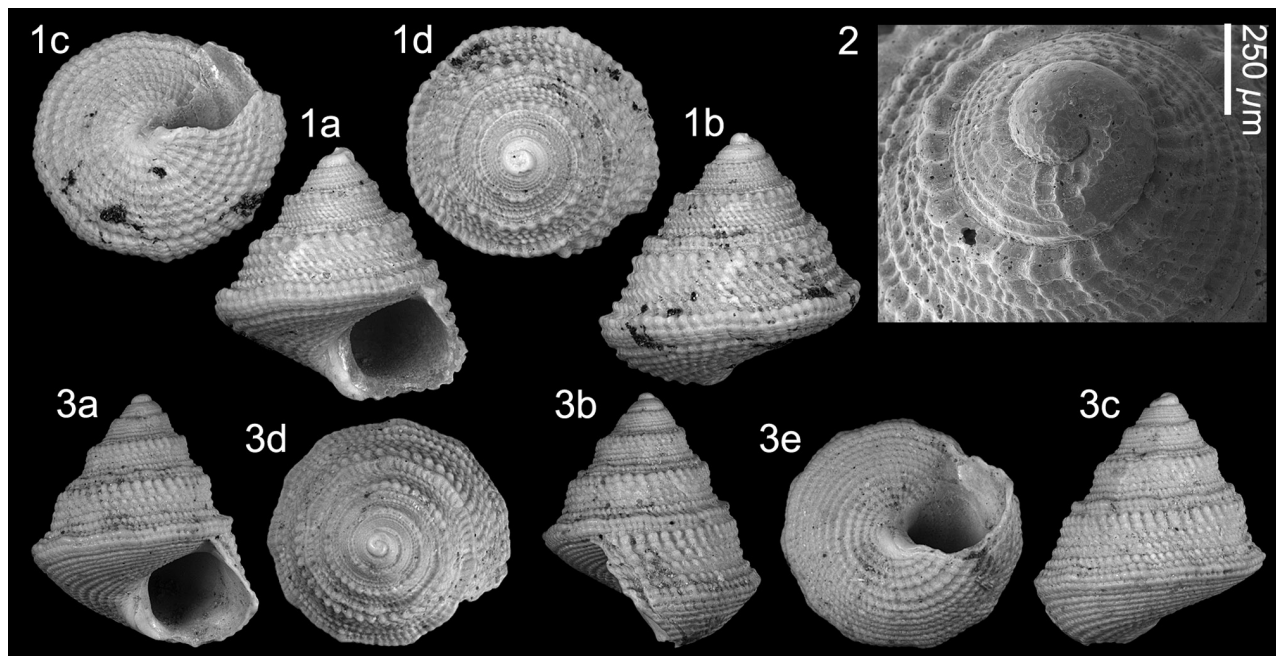


Plate 60. *Calliostoma verrucosum* nov. sp.; 1. **Holotype** MNHN.F.A57694, height 4.4 mm, width 4.4 mm; 2. **Paratype 4** NHMW 2016/0103/0187, detail of protoconch (SEM image); 3. **Paratype 1** NHMW 2016/0103/0184, height 6.2 mm, width 5.3 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Calliostoma* species of small size, with low turbiniiform shell shape, whorls strongly shouldered, concave in profile, with coarsely beaded shoulder cord, delimiting narrow subsutural platform and peribasal cord, finely beaded cords on rest of dorsum, and angular imperforate base covered in beaded cords.

Description – Shell small, depressed trochiform, with scalate spire. Protoconch paucispiral, of 1.3 whorls bearing honeycomb surface sculpture (dp = 560 μ m, dn = 255 μ m). Junction with teleoconch sharply delimited by end of protoconch sculpture. Teleoconch of four whorls. Suture linear, superficial. First teleoconch whorl bearing five spiral cords of roughly equal strength and prosocline close-set axial lamellae. On second half of first whorl adapical cord strengthens to form shoulder. Abapically, whorls shouldered, profile above and below shoulder concave, with shallow, narrow subsutural ramp bearing four finely beaded narrow cords, shoulder angled, abapical cord strengthens, three minor finely beaded cords between coarsely beaded shoulder and abapical cords. Close set axial lamellae raised between cords on shoulder. Last whorl with shoulder placed high, peribasal cord bifid, strongly beaded, delimiting base. Base depressed, imperforate, bearing eight beaded spiral cords. Aperture ovate, outer lip simple, roundly angled at periphery, columella smooth. Columellar callus hardly developed, parietal callus not developed.

Discussion – *Calliostoma verrucosum* nov. sp. is similar in size and in having a bicarinate last whorl to *C. biangulatum* nov. nom. (see above), but differs in having a more depressed spire, the sculpture is strongly tuberculate, whereas in *C. biangulatum* the sculpture is lamellate, the shoulder and peribasal cords in *C. verrucosum* are broader and more elevated and the basal cords are thicker. Finally, the holes in the honeycomb protoconch

surface sculpture are bigger in *C. biangulatum*.

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

***Calliostoma vibrayanum* (Dollfus & Dautzenberg, 1886)**
Plate 61, figs 1-2

- *1886 *Trochus (Ziziphinus) Vibrayanum* Dollfus & Dautzenberg, p. 141.
- 1949 *Calliostoma vibrayanum* (Tournouër mss.) Dollfus & Dautzenberg, 1886 – Glibert, p. 32, pl. 2, fig. 4.

Material and dimensions – Maximum height 5.2 mm, **St-Clément-de-la-Place**: LC (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0673-0674 (2), NHMW 2016/0103/0675 (5), RGM.1309658 (2), RGM.1309715 (6), RGM.1309767 (6), RGM.1348011 (1), LC (2), FVD (2).

Discussion – *Calliostoma vibrayanum* (Dollfus & Dautzenberg, 1886) is characterised by its broad conical spire with straight-sided to slightly coeloconoid profile composed of flat-sided whorls. The early teleoconch whorls bear weakly beaded cords. Abapically only the suprasutural cord strengthens; the cords above weaken, or in most specimens disappear completely. The base is imperforate, flattened, sharply delimited by a strong, rounded peribasal cord, and almost smooth, except for a few weak cords placed peripherally and medially. The aperture is ovate and the columella oblique and relatively strongly thickened abapically.

Other European fossil calliostomiids with a coeloconoid spire profile and beaded cords that weaken or become obsolete on the later teleoconch whorls are *C. audebardi* (de Basterot, 1825) from the lower Miocene Aquitaine Basin of

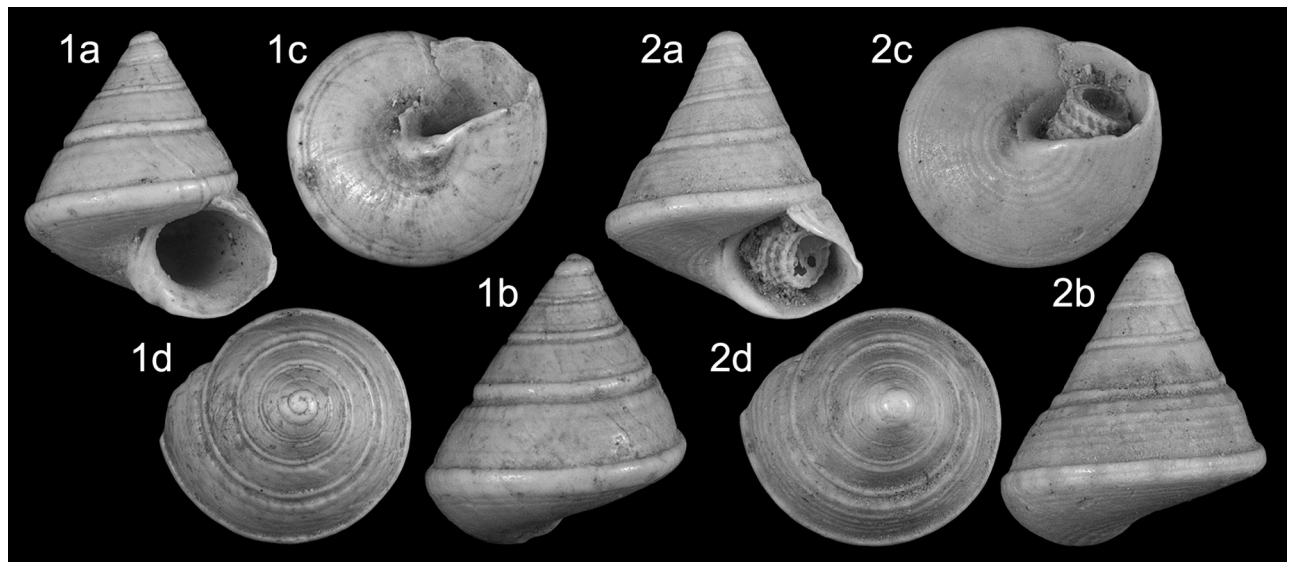


Plate 61. *Calliostoma vibrayanum* (Dollfus & Dautzenberg, 1886); 1. NHMW 2016/0103/0673, height 5.1 mm, width 4.4 mm; 2. NHMW 2016/0103/0674, height 5.1 mm, width 4.6 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

France, which differs in having more concave whorls, the cords weaken but persist subobsoletely beaded on the last whorl, and the cords both above and below the suture are more strongly developed, *C. benoisti* Cossmann & Peyrot, 1917 from the middle Miocene Aquitaine Basin which has a more pointed spire and a crenulated peribasal cord, and *C. xavieri* (Dollfus, Cotter & Gomes, 1903) from the upper Miocene Caceira Basin of southern Portugal, which differs in having the spiral sculpture persisting stronger on the last whorl and a more prominent peribasal cord. All three have stronger basal sculpture than *C. vibrayanum*.

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

***Calliostoma* cf. *zizyphinum* (Linnaeus, 1758)**

Plate 62, figs 1-2

- cf. *1758 *Trochus zizyphinus* Linnaeus, p. 759.
 cf. 2014 *Calliostoma zizyphinum* (Linné, 1758) – Pouwer & Wesselingh, p. 160, figs 31, 32.
 cf. 2016a *Calliostoma zizyphinum* (Linnaeus, 1758) – Ceulemans *et al.*, p. 71, pl. 9, figs 3, 4.

Material and dimensions – Maximum height 18.7 mm, width 15.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0180-0181 (5), NHMW 2016/0103/0182 (1), LC (1), FVD (3). **Sceaux-d’Anjou**: RGM.1309698 (4). **Renau-leau**: NHMW 2016/0103/1506 (4).

Discussion – The shells illustrated here as *Calliostoma* cf. *zizyphinum* (Linnaeus, 1758) from St-Clément-de-la-Place are relatively large and solid shelled compared to other calliostomiids in the Assemblage I deposits. They are very close in shape to the more strongly sculptured forms of *Calliostoma zizyphinum* (Linnaeus, 1758), especially specimen NHMW 2016/0103/0181 (Pl. 62, fig. 2), which also shows remnants of colour pattern on the

peripheral cord similar to that illustrated by Pouwer & Wesselingh (2014, fig. 32), which also has strong spiral sculpture. However, we are unsure if the specimens from St-Clément-de-la-Place are conspecific with the Pliocene to present-day *C. zizyphinum*, as the apical angle is narrower (especially specimen NHMW 2016/0103/0180, Pl. 62, fig. 1). Moreover, there seem to be fewer cords on the base. Ceulemans *et al.* (2016a) recorded the smoother form of *C. zizyphinum* from the lower Pliocene Assemblage III. *Calliostoma planospirum* (Millet, 1865), also from the Assemblage I fauna, is larger shelled, with finer spiral sculpture that does not form a thickened abapical cord and the base is flatter, again with weaker spiral sculpture. The Pliocene to present-day *C. conulus* (Linnaeus, 1758) is also similar, but has beaded early teleoconch whorls. *Calliostoma lauguieri* (Payraudeau, 1826) belongs to the same group of calliostomiid with regular conical spires. It has a narrower apical angle than *C. zizyphinum* and *C. conulus*, similar to the shells from St-Clément-de-la-Place, but differ in also having beaded early teleoconch whorls, although these disappear earlier than they do in *C. conulus*.

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

Subfamily Thysanodontinae Marshall, 1988
 Genus *Thysanodonta* Marshall, 1988

Type species (by original designation) – *Thysanodonta auklandiana* Marshall, 1988, present-day, New Zealand.

1988 *Thysanodonta* Marshall, p. 217.

***Thysanodonta chauvereauensis* nov. sp.**

Plate 63, figs 1-5

Type material – Holotype NHMW 2016/0103/0250,

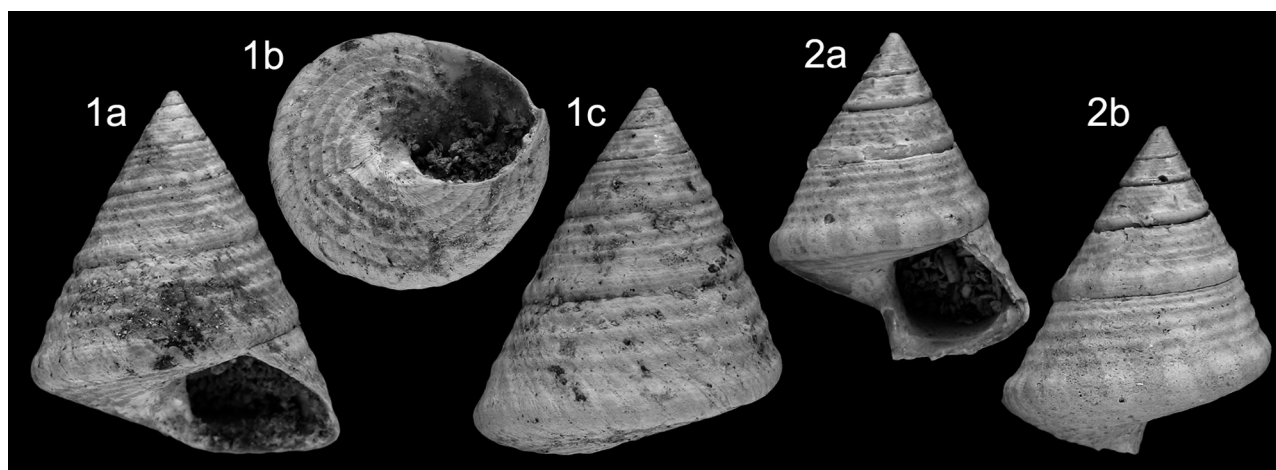


Plate 62. *Calliostoma* cf. *zizyphinum* (Linnaeus, 1758); 1. NHMW 2016/0103/0180, height 18.7 mm, width 15.5 mm; 2. NHMW 2016/0103/0181, height 15.8 mm, width 13.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

height 4.6 mm, width 3.7 mm; paratype 1 NHMW 2016/0103/0251, height 3.6 mm, width 3.2 mm; paratype 2 NHMW 2016/0103/0252, height 3.4 mm, width 2.8 mm; **St-Clément-de-la-Place**. Paratype 3 RGM.1309709, height 3.1 mm, width 2.6 mm; **Sceaux-d'Anjou**.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/0253 (7), LC (1), FVD (3). **Sceaux-d'Anjou**: NHMW 2016/0103/1492-1493 (2), RGM.1309592 (1), RGM.1348007 (2).

Etymology – Named after the farm on which the locality is situated, Le Grand Chauvèreau. *Thysanodonta* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Thysanodonta* species of small size, with tall

conical spire, in which first teleoconch whorl bears axial ribs, and single spinous shoulder cord that rapidly weakens abapically, spiral sculpture weakens abapically, last whorl with sharply beaded cords; 1-3 weaker abapically and two more prominent abapically, and imperforate, weakly sculptured, flattened base.

Description – Shell small, of medium thickness, with moderately high conical spire, flattened base. Protoconch paucispiral, composed of 1.5 whorls bearing honeycomb sculpture. Teleoconch consisting of four whorls. Suture linear, impressed. First teleoconch whorl sharply angular, bearing weak prosocline axial ribs, single spiral cord at shoulder forming spinous tubercles at intersections. Whorl profile straight to weakly concave above and below shoulder. On second teleoconch whorl a weaker beaded cord appears just below and just above sutures. Abapically, shoulder cord rapidly weakens, two abapical cords strengthen and further beaded cords appear above in some specimens. Last whorl straight-sided, sharply angled at base, bearing two strong abapical cords, the lower

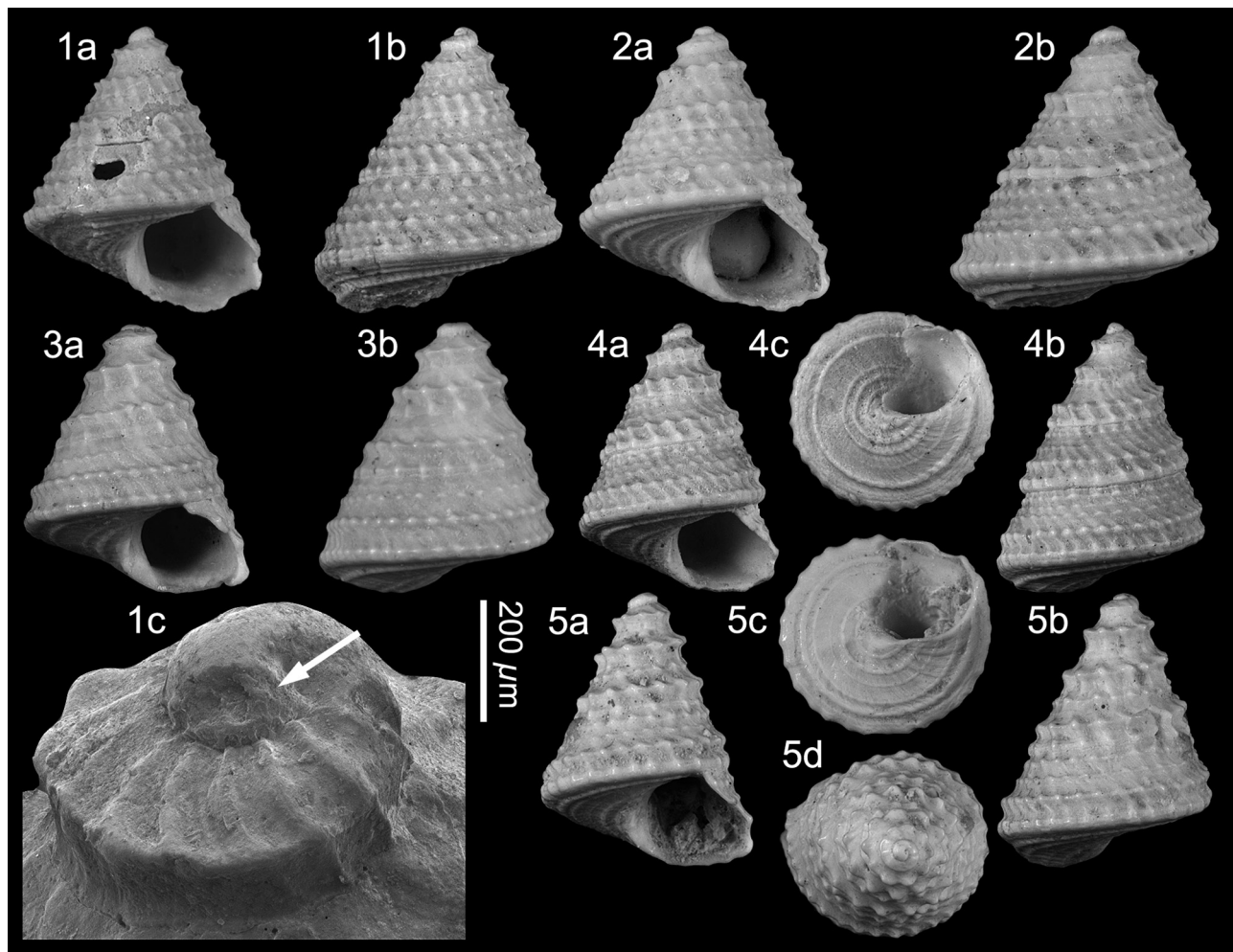


Plate 63. *Thysanodonta chauvèreauensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/0250, height 4.6 mm, width 3.7 mm, 1c, detail of protoconch (SEM image); 2. **Paratype 1** NHMW 2016/0103/0251, height 3.6 mm, width 3.2 mm; 3. **Paratype 2** NHMW 2016/0103/0252, height 3.4 mm, width 2.8 mm. Le Grand Chauvèreau, St-Clément-de-la-Place. 4. NHMW 2016/0103/1492, height 4.3 mm, width 3.5 mm; 5. NHMW 2016/0103/1493, height 4.1 mm, width 3.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

bordering the periphery and 1-3 weaker cords above. Base flattened, imperforate, bearing up to seven fine non-beaded cords of irregular strength, obsolete mid-base in some specimens. Aperture tangential; peristome discontinuous, outer lip not thickened, angled at periphery, smooth within. Columella straight, weakly thickened abapically.

Discussion – Marshall (1988) described a small group of calliostomids that differed mainly in their extremely distinctive jaw and radular characters; the slender teeth far longer than they are broad, indeed, the most slender of any known gastropod. The subfamily Thysanodontinae was erected for this group. Marshall (1988) suggested that they were suctorially feeding, possibly on cnidarians. Marshall (1988) also highlighted shell characters peculiar to the subfamily; although they have a paucispiral protoconch covered by honey-comb microsculpture like other calliostomids, the first 1.5-2.5 teleoconch whorls are unicarinate and the primary spiral cords all appear almost immediately at similar size. This is not seen in Calliostomatinae. Thysanodontinae were originally described from South Africa, Australia, New Zealand and New Caledonia, and Marshall commented on their vicariant distribution. The only two subsequent records including Thysanodontinae were from the same area (Marshall, 1995; Vilvens & Maestrati, 2006).

This is the first report of the subfamily in the European faunas. It is possible that further species occur, but remain unrecognised or misidentified as *Calliostoma* species. Three genera were described within the Thysanodontinae, of which the species from the upper Miocene of France is best included in the genus *Thysanodonta* Marshall, 1988. The spiral sculpture on the last whorl is a little different from that of the antipodean *Thysanodonta* species, which have three alternating primary and three secondary cords intercalated, but we are reluctant to erect a new genus for this species.

Thysanodonta chauvereauensis nov. sp. is a curious little species. It is the smallest shelled calliostomid in the Assemblage I deposits. A small patch of the honeycomb surface sculpture is preserved just above the suture (Pl. 63, fig. 1c). The most notable character in this species is the drastic change in sculpture between the first teleoconch whorl, which is unicarinate, and the later whorls, which are straight-sided and predominated by two strong abapical cords. The sculptural transition on the second teleoconch whorl is rapid. Sculpture on the last teleoconch whorl is rather variable; 1-3 beaded cords lie above the upper of the two stronger abapical cords that can be almost as strong as the abapical cords to rather weak. Equally, the basal sculpture is variable, composed of raised narrow cords, which can be subobsolete or missing mid-base. *Thysanodonta chauvereauensis* differs from all its antipodean congeners (*i.e.* *T. aucklandica* Marshall, 1988, *T. wairua* Marshall, 1988, *T. boucheti* Marshall, 1988, *T. eucosmia* Marshall, 1995, *T. festiva* Marshall, 1995, *T. cassis* Vilvens & Maestrati, 2006, *T. diadema* Vilvens & Maestrati, 2006, *T. pileum* Vilvens & Maestrati, 2006) in being smaller shelled and in having the two abapical cords more strongly developed.

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

Family Liotiidae Gray, 1850
Genus *Pareuchelus* Boettger, 1907

Type species (by original designation) – *Euchelus excellens* Boettger, 1907, Miocene, Romania.

1907 *Pareuchelus* Boettger, p. 186.

***Pareuchelus lecointreae* (Dollfus & Dautzenberg, 1899)**
Plate 64, figs 1-3

1854 *Delphinula Radiata* Millet, p. 157 (*nomen nudum*).

1865 *Delphinula radiata* Millet, p. 584 (*non* Kiener, 1838).

*1899 *Turbo lecointreae* Dollfus & Dautzenberg, p. 218, pl. 9, figs 5, 6 (*nom. nov. pro. Delphinula radiata* Millet 1865; *non* Kiener, 1838).

1938 *Leptothyra? Lecointreae* [*sic*] – Peyrot, p. 37.

1949 *Turbo lecointreae* Dollfus & Dautzenberg, 1899 – Glibert, p. 77.

1964 *Pareuchelus lecointreae* Dollfus et Dautzenberg, 1899 – Brébion, p. 129, pl. 3, fig. 17.

Material and dimensions – Maximum height 9.5 mm, width 8.5 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0032 (1), 2016/0103/0033 (5), LC (3). **Sceaux-d'Anjou:** NHMW 2016/0103/0035 (4), RGM.1309528 (3); RGM.1309584 (1); RGM.1309617 (1), RGM.1347851 (3), LC (6), FVD (6). **Renauleau:** NHMW 2016/0103/1423-1424 (2), NHMW 2016/0103/0034 (14), LC (50), FVD (15). **Beugnon:** RGM.1309529 (1); RGM.1309530 (1); RGM.1309531 (2); RGM.1309740 (2), LC (1).

Discussion – *Pareuchelus lecointreae* (Dollfus & Dautzenberg, 1899) is similar to the older *P. fossariopsis* Cossmann & Peyrot, 1917, but this species from the Atlantic lower Miocene Aquitanian of France has fewer spiral cords (6 vs. 7), which are stronger. In the middle Miocene Paratethys *P. excellens* Boettger, 1906 has only four spiral cords that are even stronger, *P. heres* Boettger, 1906 seems to have the same number of cords as *P. fossariopsis*. The holotype is incomplete (Zilch, 1934, pl. 4, fig. 55) and difficult to separate from the French lower Miocene species, however, it differs from *P. lecointreae* in the same way as *P. fossariopsis*; fewer and stronger spiral cords.

In *P. lecointreae* the primary axials are often interrupted by the spirals and are not continuous axially (see Pl. 64, fig. 1a). One interesting sculptural feature, which is probably a generic character, is that there are anything between two and six secondary axials between the primary axials that are only developed over the cords and are short, not extending into the interspaces. The number of these secondary axial riblets increases abapically.

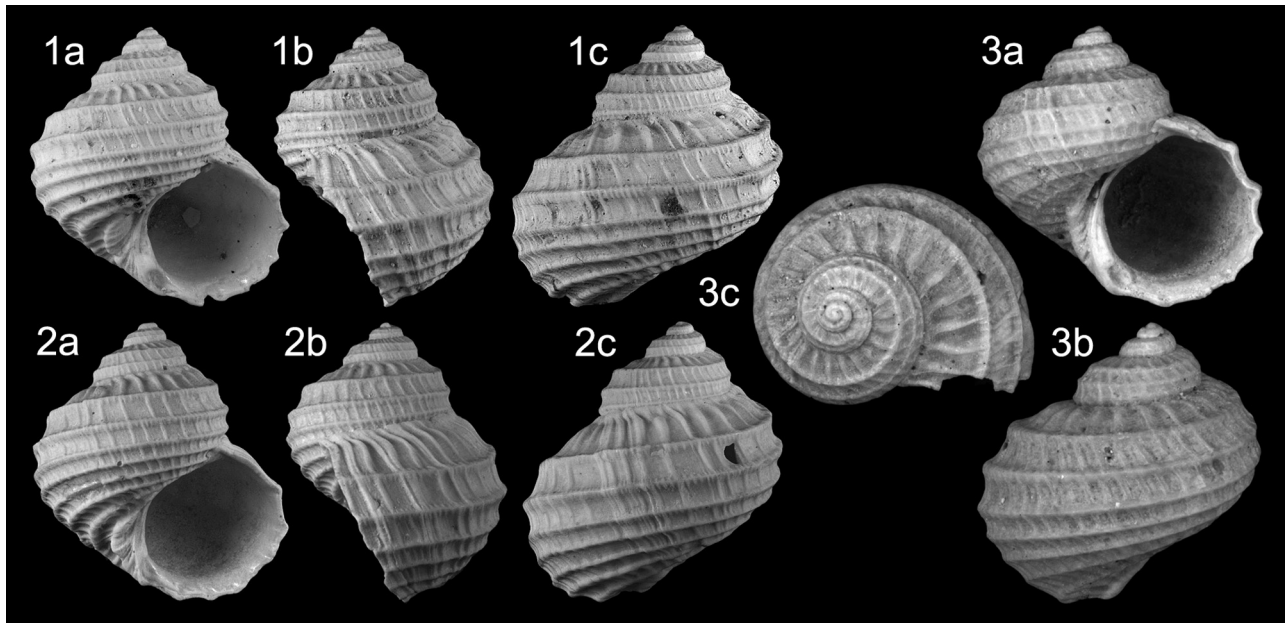


Plate 64. *Pareuchelus lecointreae* (Dollfus & Dautzenberg, 1899); 1. NHMW 2016/0103/1423, height 7.2 mm, width 6.6 mm; 2. NHMW 2016/0103/1424, height 7.2 mm, width 6.5 mm. Renauleau; 3. NHMW 2016/0103/0032, height 9.5 mm, width 8.5 mm. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Millet (1854) recorded this species only from the Assemblage I locality of Sceaux-d'Anjou, but it is widespread in the deposits; Brébion (1964, p. 130) added Thorigné, St-Clément-de-la-Place and Beaulieu, to which we add Renauleau.

Trochus sublimbatus d'Orbigny, 1852 from the Mediterranean Pliocene has similar sculpture, but the similarity is superficial. It belongs in the genus *Danilia* Brusina, 1865 (placed in Seguenzoidea: Chilodontidae). *Danilia* species are solid-shelled, *Pareuchelus* Boettger, 1907 have thin shells. The aperture in *Danilia* bears a labial varix, which is denticulate within, whereas the outer lip in *Pareuchelus* is thin, lacking a labial varix, and smooth within, so that specimens with a complete aperture are scarce.

Distribution – Middle Miocene: Atlantic (Langhian) Loire Basin, France (Peyrot, 1938). Upper Miocene: Atlantic, Tortonian, NW France (Millet, 1854, 1865; Brébion, 1964).

***Pareuchelus dautzenbergi* nov. sp.**

Plate 65, fig. 1

Type material – Holotype RGM.1309551, height 5.6 mm, width 5.1 mm; paratype 1 NHMW 2016/0103/1592, height 6.0 mm, width 5.8 mm; paratype 2 NHMW 2016/0103/1593, height 4.6 mm, width 4.5 mm; paratype 3 NHMW 2016/0103/1594, height 3.5 mm, width 3.6 mm.

Other material – Maximum height 4.6 mm (incomplete), diameter 6.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/1595 (3 juveniles), LC (1), FVD (2).

Sceaux-d'Anjou: RGM.1309782 (1); RGM.1309783 (1), RGM.1347997 (1), LC (1), FVD (2).

Etymology – Named after Philippe Dautzenberg (1849-1935), Belgian malacologist, in recognition of his enormous contribution to the field. *Pareuchelus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pareuchelus* species of small size, with a relatively tall turbiniform shell, highly sculptured teleoconch whorls bearing narrow elevated cords of primary and secondary strength and crowded axial lamellae, scabrous of finely beading axials; spirals bearing twice as many axials as interspaces between spirals, convex last whorl bearing 8-10 strong cords.

Description – Shell small, relatively elevated turbiniform. Protoconch paucispiral, composed of about 1.5 whorls, with large nucleus. Teleoconch of four convex whorls with periphery above abapical suture. Suture deeply impressed, narrowly canaliculated. First teleoconch whorl with three elevated spiral cords. On second whorl fourth cord develops on subsutural platform. On penultimate whorl further weaker cords above and below suture and single secondary cord between 1st and 2nd primary cords. Last whorl inflated, convex bearing 8-10 strongly developed, narrow, elevated cords plus secondary cords in some interspaces. The most adapical one or two primary spirals turned upwards, lower three turned downwards.

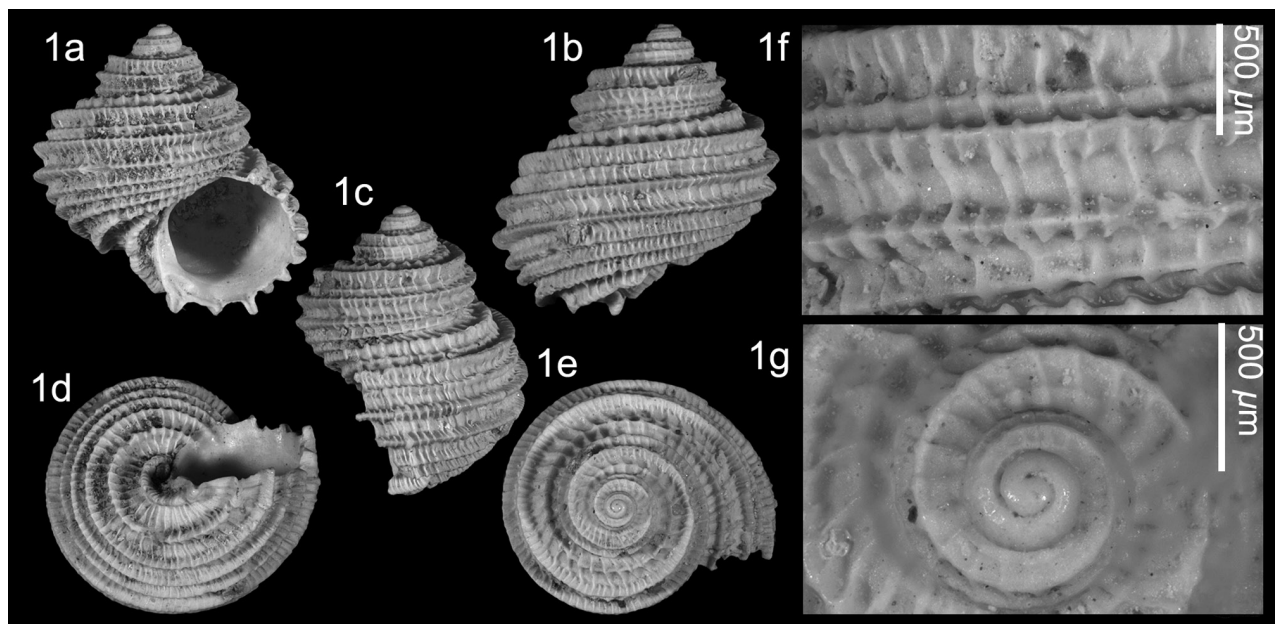


Plate 65. *Pareuchelus dautzenbergi* nov. sp.; 1. **Holotype** RGM.1309551, height 5.6 mm, width 5.1 mm; La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Axial sculpture of continuous, crowded lamellae, scabrous over, or finely beading spiral cords. In interspaces between ribs, cords bear a further spiral that disappears in the interspaces between cords, so that cords bear twice as many ribs as interspaces. Base not delimited, bearing narrow umbilical chink. Aperture ovate, outer lip rounded, edge crenulated by spiral sculpture, smooth within. Peristome complete. Columellar callus thickened abapically bearing small ridge bordering siphonal canal. Parietal callus thin, erect over umbilical chink.

Discussion – This species seems to have been overlooked and lumped together with *Pareuchelus lecointreae* (Dollfus & Dautzenberg, 1899) by all workers, including ourselves until late in the preparation of this monograph. It differs from *P. lecointreae* in being smaller with a more elevated spire, in having more numerous primary spiral cords with secondaries developed in some of the interspaces; *P. lecointreae* does not develop secondary spirals. The difference in number of spirals is not just due to a greater development of secondaries, but is evident from the first teleoconch whorl, which only has two spirals in *P. lecointreae*, three in *Pareuchelus dautzenbergi* nov. sp. The two species also differ in their axial sculpture, which consists of far more crowded, but less prominent and less interrupted axials in *P. dautzenbergi*. This is particularly evident on the subsutural platform. Furthermore, the secondary axial sculpture (see above under *P. lecointreae*) in *P. dautzenbergi* differs in only having one secondary axial between the spirals that is longer and extends a short distance into the interspaces. *Pareuchelus fossariopsis* Cossmann & Peyrot, 1917 from the Atlantic lower Miocene Aquitanian of France has even fewer spiral cords (6 vs. 8–10). *Pareuchelus dautzenbergi* is found together with *P. lecointreae* at Sceaux-d'Anjou

and St-Clément-de-la-Place, although less frequent. At Renauleau, where the genus is most abundant, we have only found *P. lecointreae*.

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

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

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

1968 *Dikoleps* Høisaeter, p. 47.

Dikoleps cutleriana (Clark, 1849)

Plate 66, fig. 1

1849 *Skenea Cutleriana* Clark, p. 424.

2016a *Dikoleps cutleriana* (Clark, 1849) – Ceulemans *et al.*, p. 73, pl. 10, fig. 1 (*cum syn.*).

Material and dimensions – Maximum diameter 1.3 mm, height 1.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0020 (1), NHMW 2016/0103/0021 (50+), RGM.1309558 (11), RGM.1309645 (10), RGM.1347961 (2), LC (5). **Sceaux-d'Anjou**: RGM.1309628 (10), LC (2). **Renauleau**: NHMW 2016/0103/1400 (29), LC (5).

Discussion – We see no significant difference between the extant specimens and those from St-Clément-de-la-Place. This is the stratigraphically oldest record for

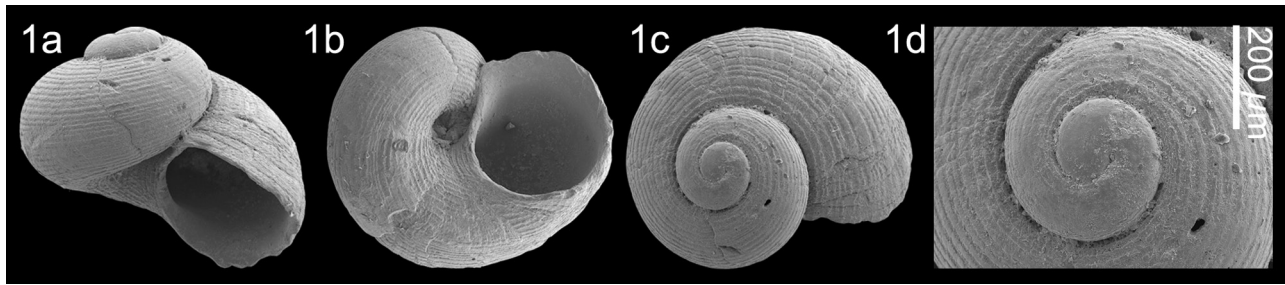


Plate 66. *Dikoleps cutleriana* (Clark, 1849); 1. NHMW 2016/0103/0020, diameter 1.3 mm, height 1.1 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Dikoleps cutleriana (Clark, 1849). The genus is known in the Atlantic of France since the upper Oligocene; *Dikoleps sublaevis* Lozouet, 1999 differs in having a smooth surface, without any spiral sculpture and *D. aldradensis* Lozouet, 1999 from the lower Miocene has spiral sculpture restricted to the base.

For further discussion see Ceulemans *et al.* (2016a, p. 73).

Distribution – Upper Miocene: Atlantic, Tortonian, NW France (Ceulemans *et al.*, 2016a). Lower Pliocene: NW France (Ceulemans *et al.*, 2016a); Luchtbal Sand, Belgium (Marquet & Landau, 2006). Present-day: Atlantic, SW England (Fretter & Graham, 1977) southwards into Mediterranean, Corsica (van Aartsen *et al.*, 1984).

***Dikoleps insulsa* nov. sp.**

Plate 67, fig. 1

Type material – Holotype 2016/0103/1590, height 460 µm, diameter 960 µm; paratype 1 NHMW 2016/0103/1591, height 510 µm, diameter 1.0 mm.

Other material – Known from type series only.

Etymology – Latin ‘*insulsus*, -a, -um’, adjective meaning boring, referring to the lack of shell characters. *Dikoleps* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Dikoleps* of small size, with smooth paucispiral protoconch, teleoconch of 1.5 whorls, devoid of sculpture, except for occasional growth lines accentuated towards aperture, convex, non-delimited base, broad, smooth, deep umbilicus, columellar and parietal calluses only slightly thickened.

Description – Shell minute, planorbid. Protoconch of one smooth whorl, with large nucleus, ($dp = 180 \mu\text{m}$, $dn = 120 \mu\text{m}$). Junction with teleoconch marked by scar. Teleoconch of 1.5 depressed, strongly convex whorls, smooth, except for occasional growth lines becoming accentuated towards

aperture. Suture linear, impressed. Last whorl depressed, strongly convex. Base not sharply delimited, convex, bearing wide, smooth, deep umbilicus. Aperture ovate, prosocline in profile, outer lip simple, Peristome complete, with only weakly tickened columellar and parietal callus.

Discussion – Although we are fairly certain this is a ske-neiid, we struggle to assign it to a genus. We have placed it provisionally in *Dikoleps* Høisaeter, 1968, which have depressed to strongly depressed shells and can lack spiral sculpture on the dorsum. However, its European congeners reviewed by Rubio *et al.* (2004) all have umbilical ribs, although in *D. nitens* (Philippi, 1844) they can be much reduced (see Rubio *et al.*, 2004, p. 118, figs 3, 4). *Dikoleps insulsa* nov. sp. further differs from all of its European congeners in having an even more depressed shell. *Cirsonella* Angas, 1877 species are also smooth, but less depressed and have an umbilical callus pad. *Moelleriopsis* Bush, 1897 species also have similarly planorbid shells, but the protoconch has fine spiral sculpture and the umbilicus is keeled. Two relatively deep-water European species described by Rubio & Rolán (2013) under *Trenchia* Knudsen, 1964; *T. biangulata* and *T. anselmoi* differ in having an umbilical keel. We note that although originally described in Skeneidae, it is now transferred to Seguenzioidea [unassigned] (Bouchet *et al.*, 2013; WoRMS). *Skenea bogii* Chirli, 2004 from the Italian lower Pliocene also lacks spiral sculpture, but is less depressed, with more numerous whorls separat-

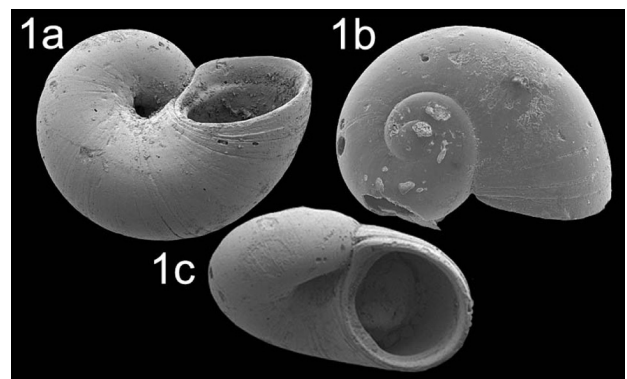


Plate 67. *Dikoleps insulsa* nov. sp.; 1. **Holotype** NHMW 2016/0103/1590, height 460 µm, diameter 960 µm (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ed by a deeper suture, and more accentuated axial growth lines. *Skenea pelagia* Nofroni & Valenti, 1987 from the present-day Mediterranean is similar in shape, especially the character of the base and umbilicus, but differs in having spiral sculpture on the teleoconch.

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

Genus *Leucorhynchia* Crosse, 1867

Type species (by monotypy) – *Leucorhynchia caledonica* Crosse, 1867, present-day, New Caledonia.

1867 *Leucorhynchia* Crosse, p. 319.

Leucorhynchia rotellaeformis (Grateloup, 1832)

Pl. 68, fig. 1

- *1832a *Delphinula rotellaeformis* Grateloup, p. 203.
- 1845 *Delphinula rotellaeformis* Grat. – Grateloup, pl. 12.
- 1854 *Delphinula Plicatella* Millet, p. 156.
- 1856 *Delphinula rotellaeformis* Grat. – Hörnes, p. 473, pl. 46, fig. 6.
- 1865 *Delphinula plicatella* Millet – Millet, p. 584.
- 1917 *Leucorhynchia rotellaeformis* (Grateloup) – Cossmann & Peyrot, p. 205, pl. 6, figs 42-44.
- non 1954 *Leucorhynchia rotellaeformis* Grat. – Strausz, p. 8, pl. 9, fig. 161 (= *Leucorhynchia zboroviensis* Friedberg, 1928).
- non 1966 *Leucorhynchia rotellaeformis* Grateloup (1832) 1840 – Strausz, p. 47, pl. 50, figs 10-15 (= *Leucorhynchia zboroviensis* Friedberg, 1928).
- 1964 *Leucorhynchia rotellaeformis* Grateloup, 1832 – Brébion, p. 125, pl. 3, fig. 16.
- 1975 *Leucorhynchia rotellaeformis* (Grateloup, 1840 [sic]) – Bahuk, p. 52, pl. 5, fig. 9.

Material and dimensions – Maximum diameter 3.3

mm, height 1.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0027 (1), 2016/0103/0028 (26), RGM.1309641 (2), LC (10). **Sceaux-d'Anjou**: NHMW 2016/0103/0030 (22), RGM.1309679 (20), RGM.1309758 (9), RGM.1347959 (2), RGM.1348008 (2), LC (15). **Renauleau**: NHMW 2016/0103/0029 (50+), LC (50+), FVD (50+). **Beugnon**: NHMW 2016/0103/0031 (8).

Discussion – This is undoubtedly the same species described by Millet as *Delphinula plicatella*: ‘Plicatella, Millet. – Sceaux. – Renauleau. – Cette espèce a quelque analogie avec les *Delphinula callifera*, Desh., et *D. canalifera*, Lamk.; mais les petits plis rayonnants qui partent de l’ombilic dans notre espèce, sont suffisants pour la faire distinguer (Millet, 1854, p. 156)’. The specimen figured (Pl. 68, fig. 1) illustrated the spiral sculpture that was not commented on by Cossmann & Peyrot (1917).

Leucorhynchia miorotelloides Sacco, 1896 was described from the lower Miocene Proto-Mediterranean of Italy. It is difficult to compare with the small figures given by Sacco (1896a, pl. 4, fig. 67) and the syntype illustrated by Ferrero Mortara *et al.* (1894, pl. 50, fig. 7), which is poorly preserved. Sacco’s description (1896a, p. 53) does not help either, as he admits this may just be a form of *L. rotellaeformis*. We refrain from synonymising the two, as the columellar callus seems to be even more strongly developed in the Italian shell, but more material would be required to be certain. *Leucorhynchia zboroviensis* Friedberg, 1928 from the middle Miocene Paratethys of Poland, is quite different, with an angular periphery and a wider umbilicus bounded by a raised periumbilical cord. *Leucorhynchia iricolor* Boettger, 1907 described from the middle Miocene of Kostež, is probably a synonym of *L. rotellaeformis* as suggested by Baluk (1975, p. 53), but we have not seen specimens from the type locality. Today the genus in the Atlantic has a more southern distribution with three species described from West Africa (Rolán & Rubio, 2012). Millet (1854, 1865) recorded this species from the Assemblage I localities of Sceaux-d’Anjou and Renauleau, to which Brébion (1964, p. 126) added Beaulieu and we add St-Clément-de-la-Place.

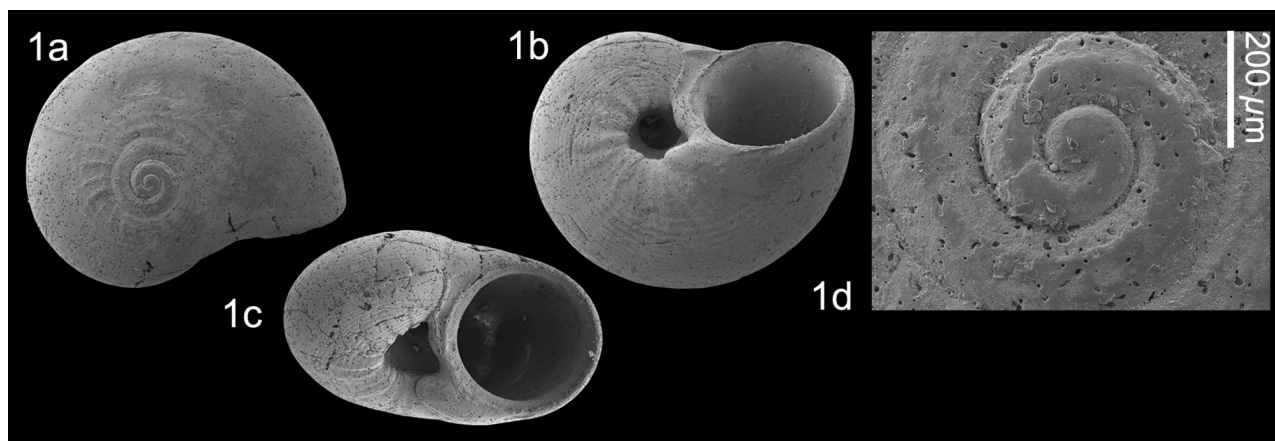


Plate 68. *Leucorhynchia rotellaeformis* (Grateloup, 1832); 1. NHMW 2016/0103/0027, diameter 3.3 mm, height 1.9 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Distribution – Lower Miocene: Atlantic (Burdigalian), Aquitaine Basin, France (Cossmann & Peyrot, 1917). Middle Miocene: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1917); Paratethys, Austria (Hörnes, 1856), Poland (Baluk, 1975). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854; Brébion, 1964).

Genus *Lodderena* Iredale, 1924

Type species (by original designation) – *Liotia minima* Tension-Woods, 1878, present day, South Australia.

- 1924 *Lodderena* Iredale, p. 182, 233.
 1958 *Cyclostremiscus* (*Pachystremiscus*) Olsson & McGinty, p. 52. *Type species* (by original designation): *Pachystremiscus pulchellus* Olsson & McGinty, 1958, present-day, Caribbean.

***Lodderena redferni* nov. sp.**

Plate 69, figs 1-2

Type material – Holotype NHMW 2016/0103/1462, diameter 1.2 mm, height 645 μm ; paratype 1 NHMW 2016/0103/1463, diameter 1.3 mm, height 625 μm , **St-Clément-de-la-Place**. Paratype 2 NHMW 2016/0103/1611, diameter 1.3 mm, height 650 μm , **Renauleau**.

Other material – Known only from type series.

Etymology – Named after Colin Redfern of Boca Raton, Florida (USA) in recognition of his work on the genus.

Lodderena gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Lodderena* species of minute size, with quadricarinate last whorl, carinae raised and wavy, lacking mid-basal cord, finely rugose surface, rugae strengthening towards aperture, and moderately wide, deep umbilicus delimited by further wavy cord.

Description – Shell minute, almost planispiral. Protoconch paucispiral, composed of just over one whorl, with deformed nucleus (dp = 170 μm , dn = 65 μm). Teleoconch of 1.5 quadricarinate whorls, separated by deeply canalliculated suture. Carinae formed by raised wavy cords; adapical carina placed mid-dorsum, abapical carina delimiting base, with two further slightly closer-spaced carinae placed at periphery either side of mid-line, fifth weaker carina delimiting moderately wide, deep umbilicus. Mid-basal cord absent; spiral sculpture absent. Whorl profile between carinae concave. Surface finely rugose; rugae coarser on base adjacent to aperture. Aperture round, peristome complete, outer lip simple.

Discussion – *Lodderena* species have shells characterised by being planispiral or almost planispiral, spirally and/or axially striated, often with one or more prominent peripheral keels, an almost round aperture and a paucispiral protoconch with a deformed nucleus (Moolenbeek, 1996). Warén (1992, p. 155) placed the present-day

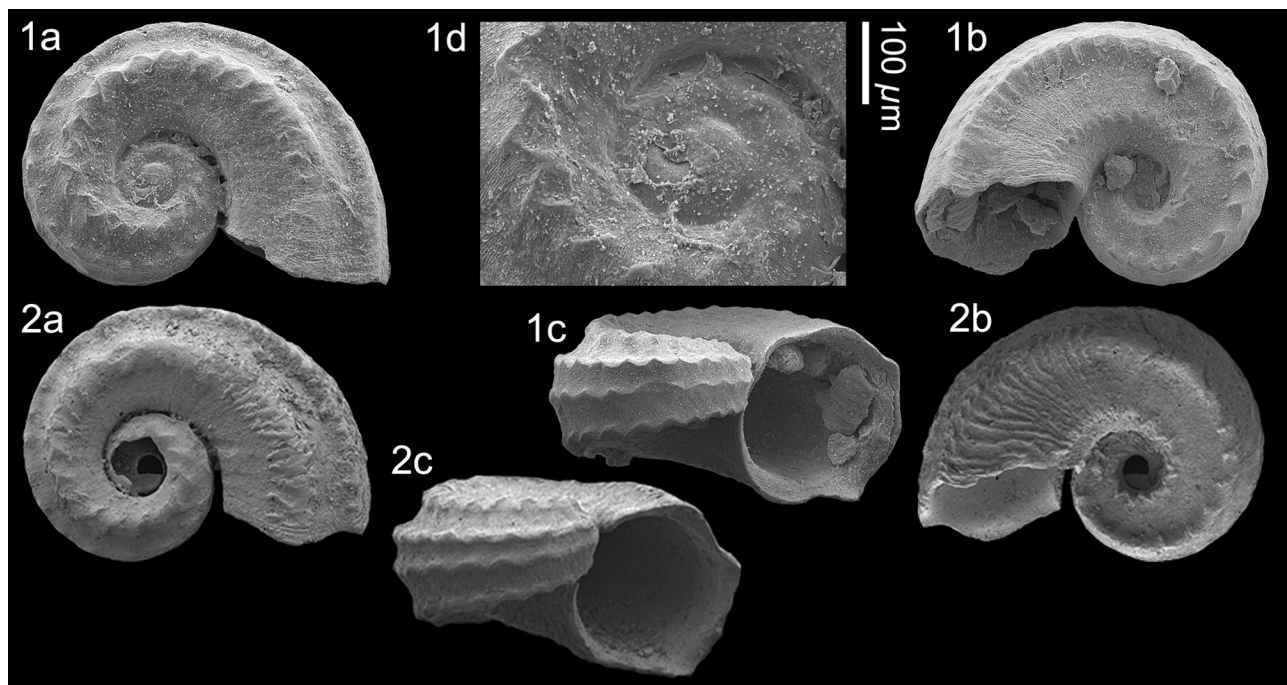


Plate 69. *Lodderena redferni* nov. sp.; 1. **Holotype** NHMW 2016/0103/1462, diameter 1.2 mm, height 645 μm ; 1d, detail of protoconch (SEM image); 2. **Paratype 1** NHMW 2016/0103/1463, diameter 1.3 mm, height 625 μm (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Mediterranean *Cyclostrema catenoides* in the genus *Lodderena*, but it was transferred to *Skenea* Fleming, 1825 by WoRMS (Gofas, 2015). The new species from France is undoubtedly a *Lodderena* species and the first confirmed fossil record for the genus in Europe. It is characterised by its quadricarinate last whorl, the carinae formed by wavy lines. *Lodderena redferni* nov. sp. is uncommon and so far only found at St-Clément-de-la-Place. We note that the outer lip is described as simple, non-thickened. This is unusual for the genus and might indicate that the two specimens at hand are not fully mature.

The French Miocene species is most similar to some of the present-day Caribbean species, such as *L. ornata* (Olsson & McGinty, 1958), also recorded in the Cape Verde Archipelago by Rolán (2005), which also has wavy carinae, but it differs in having two further cords, one placed between the apex and the mid-dorsal cord and a second placed mid-base, and the surface is covered by fine spiral cords. Another present-day Caribbean species; *Lodderena pulchella* (Olsson & McGinty, 1958), also has a quadricarinate periphery to the last whorl, plus a raised central basal cord, but the cords are linear and not wavy, the axial sculpture is much stronger than in *L. redferni* and the outer lip is thickened by varix. *Lodderena janetmayae* Rubio, Rolán & Redfern, 1998 from the Bahamas is similar in number of carinae, which are also wavy, but differs in having the abapical cord placed mid-base and having axial ribs between the two peripheral cords. *Lodderena bunnelli* Redfern & Rolán, 2005 from the Bahamas is quite different with a honeycomb pattern at the periphery.

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

Genus *Parviturbo* Pilsbry & McGinty, 1945

Type species (by original designation) – *Parviturbo reheri* Pilsbry & McGinty, 1945, present-day, Florida, USA.

***Parviturbo rubioi* nov. sp.**

Plate 70, figs 1-2

Type material – Holotype NHMW 2016/0103/0026, diameter 940 μ m, height 840 μ m; paratype 1 NHMW 2016/0103/1469, diameter 1.1 mm, height 980 μ m; paratype 2 RGM.1309642, diameter 930 μ m, height 830 μ m.

Other material – Maximum diameter 1.1 mm, height 980 μ m. **St-Clément-de-la-Place:** NHMW 2016/0103/0712 (1).

Etymology – Named after Federico Rubio of Valencia, Spain in recognition of his excellent review of the genus. *Parviturbo* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Parviturbo* species of small size, with relatively elevated shell, moderately dense regularly reticulated surface pattern consisting of three spiral cords on first whorl, five on last whorl and 18 axial ribs on first whorl, 21 on last, in which axial and spiral elements are of equal strength, and strong periumbilical cord.

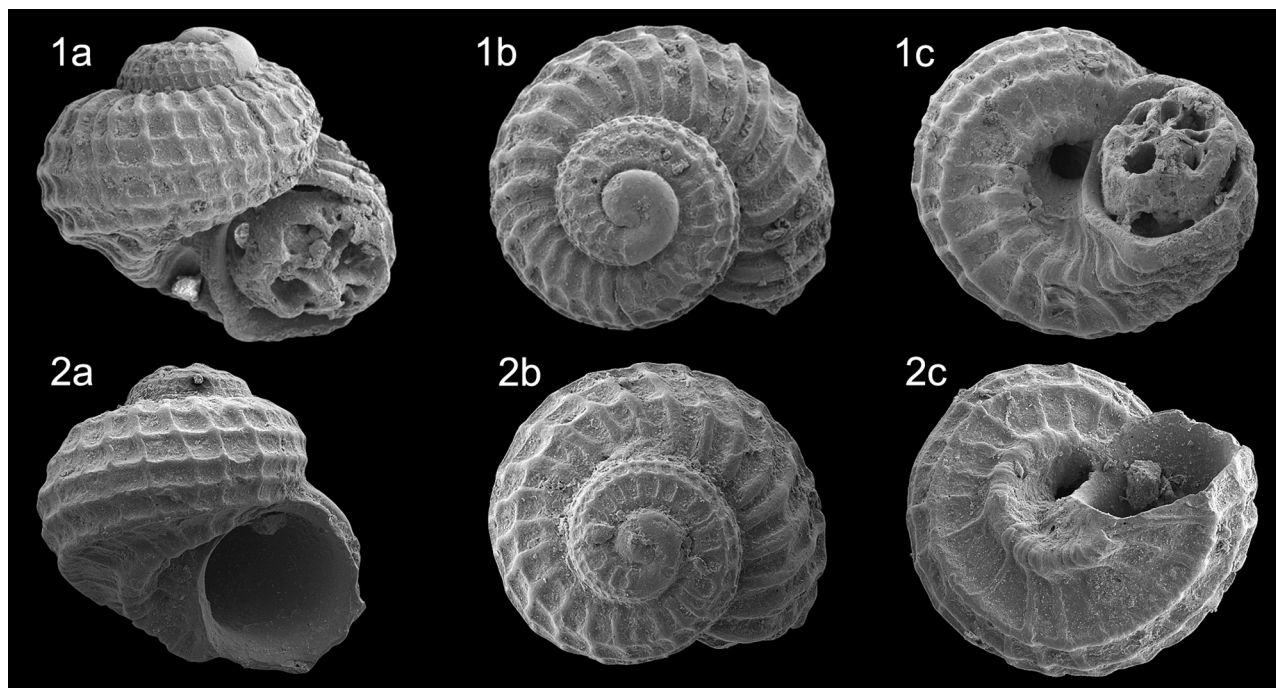


Plate 70. *Parviturbo rubioi* nov. sp.; 1. **Holotype** NHMW 2016/0103/0026, diameter 940 μ m, height 840 μ m (SEM image); 2. **Paratype 1** NHMW 2016/0103/1469, diameter 1.1 mm, height 980 μ m (SEM image). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell minute, turbiniform. Protoconch of just over one smooth whorl, with large nucleus ($dp = 250 \mu\text{m}$, $dn = 95 \mu\text{m}$). Junction with teleoconch sharp, marked by beginning of spiral sculpture. Teleoconch of 1.8 convex whorls, separated by impressed suture. Three spiral cords on spire whorl, five on last whorl, about one-quarter width of their interspaces. Axial sculpture of 18 prosocline ribs on first whorl, 21 on last whorl, equal in width to spiral sculpture, forming evenly reticulated surface pattern. Interspaces slightly concave, bearing irregular micropustules. Last whorl convex, bearing five subequal spiral cords, plus stronger peribasal and strongest periumbilical cord. Base deeply umbilicate, bearing conspicuous growth lines within. Aperture rounded, outer lip simple, columella thickened, slightly reflected at base.

Discussion – *Parviturbo rubioi* nov. sp., with its reticulated surface sculpture in which neither the spiral nor axial elements are strongly overwhelming, is typical of the Eastern Atlantic species group as illustrated by Rubio *et al.* (2015, p. 171). It is most similar to the extant *P. rolandi* Engl, 2001 from the Canary Islands, but this species has only two spiral cords on the spire whorl as opposed to three in the French shell and the axial ribs are thinner and more numerous than in *P. rubioi*. Other European species with regularly reticulated surface sculpture are *P. elegantulus* (Philippi, 1844) from the Plio-Pleistocene to present day Mediterranean, which has finer reticulated sculpture with four spiral cords on the spire whorl; *P. alboranensis* Peñas & Rolán in Peñas *et al.* 2006, which has the same number of cords on the spire whorl, but the cords mid-whorl on the last whorl are zig-zag, leading to the interspaces being hexagonal honeycomb shaped; *P. ergasticus* Rubio, Rolán & Gofas in Rubio *et al.*, 2015 from the Bay of Biscay, which has much finer reticulated sculpture with more numerous ribs and cords. Several present-day European species such as *P. fenestratus* (Chaster, 1896) and *P. azoricus* Rubio, Rolán & Segers in Rubio *et al.*, 2015 are separated by their predominantly spiral sculpture.

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

Genus *Pseudorbis* Monterosato, 1884

Type species (by monotypy) – *Fossarus granulum* Brugnone, 1873, present day, Mediterranean.

1884 *Pseudorbis* Monterosato, p. 109.

***Pseudorbis beugnonensis* nov. sp.**

Plate 71, fig. 1

Type material – Holotype MNHN.F.A57703, height $720 \mu\text{m}$, width $770 \mu\text{m}$; paratype 1 NHMW 2016/0103/0273, height $710 \mu\text{m}$, width $750 \mu\text{m}$.

Other material – **Beugnon**: NHMW 2016/0103/0274 (20).

Etymology – Named after the type locality of Beugnon. *Pseudorbis* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pseudorbis* species of small size, with regularly globose shape, solid shelled, bearing sculpture of seven broad, strap-like cords on last whorl, and circular non-dilated aperture bordered by thick outer lip.

Description – Shell minute, solid, globose turbiniform. Protoconch paucispiral, of 1.5 smooth whorls, with a large rounded nucleus ($dp = 260 \mu\text{m}$, $dp = 85 \mu\text{m}$, $dpl = 170 \mu\text{m}$). Junction with teleoconch not sharply delimited. Teleoconch of 1.2 whorl separated by broadly canalliculated suture. Sculpture of broad, flattened, strap-like cords of equal strength, 2-3 times the width of their interspaces, three on first half teleoconch whorl. Last whorl globose, regularly convex, bearing seven spiral cords. Base continuous with dorsum, imperforate. Aperture circular, peristome complete, narrow. Outer lip thick, regularly rounded, not dilated, anal and siphonal canals not developed. Columella thickened, narrow, smooth.

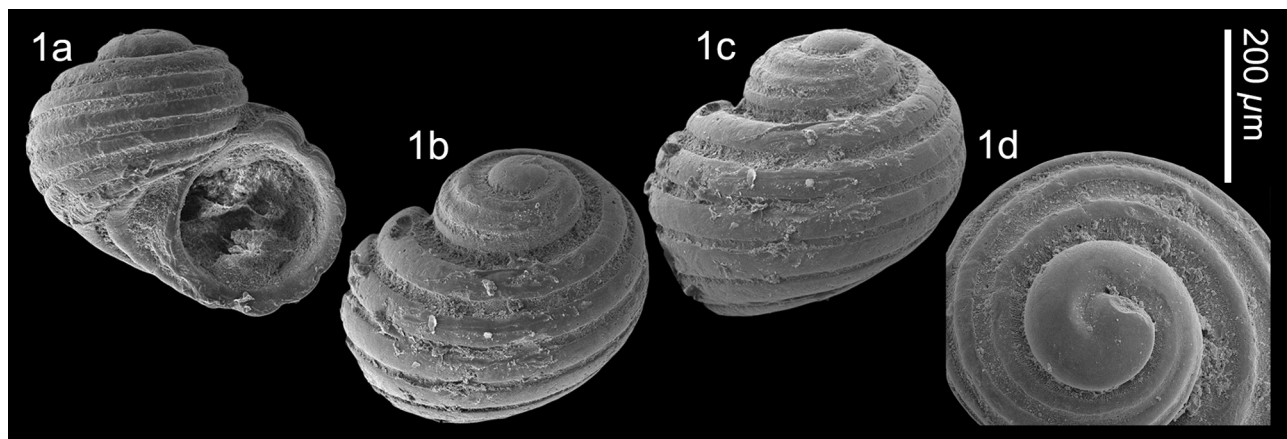


Plate 71. *Pseudorbis beugnonensis* nov. sp.: 1. **Holotype** MNHN.F.A57703, height $720 \mu\text{m}$, width $770 \mu\text{m}$; 1d, detail of protoconch (SEM image). Beugnon, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Pseudorbis beugnonensis* nov. sp. is easily separated from *Pseudorbis granulum* (Brugnone, 1873), with which it co-occurs, by its sculpture of broad, strap-like cords as opposed to the rather sharp cords seen in *P. granulum*. It is in much more similar to the stratigraphically slightly older middle Miocene *P. falunica* Lozouet, 1999 from the Loire Basin of France, which is also sculptured by broad cords, but in that species they are more numerous; five on the spire whorl, and 14 on the last whorl, including the basal cords. In *P. falunica* the apertural portion on the last whorl is dilated, whereas in *P. beugnonensis* it is not. *Pseudorbis carinifera* Lozouet 1999 from the Atlantic upper Oligocene of France differs from *P. beugnonensis* in the same characters as *P. granulum* (see above). *Pseudorbis jameonsis* Rubio & Babío, 1990 from the Canary Islands differs in having eight primary spiral cords mid-whorl, which are much narrower than in *P. beugnonensis*.

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

Pseudorbis granulum (Brugnone, 1873)

Plate 72, fig. 1

- *1873 *Fossarus granulum* Brugnone, p. 13.
- 1990 *Pseudorbis granulum* (Brugnone, 1873) – Rubio & Babío, p. 204, figs 1:1-5.
- 1992 *Pseudorbis granulum* (Brugnone, 1873) – Warén, p. 160, fig. 40E.
- 1994 *Pseudorbis granulum* (Brugnone, 1873) – Giannuzzi-Savelli *et al.*, figs 365, 366.
- 2015 *Pseudorbis granulum* (Brugnone, 1873) – Rubio *et al.*, p. 244, figs 45, 46A-G, 47A-E, 48A-H, 49A-F.

Material and dimensions – Maximum diameter 1.4 mm, height 1.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0017 (1), NHMW 2016/0103/0018 (50+), RGM.1309634 (50+), LC (8). **Sceaux-d’Anjou**: RGM.1309586 (2), RGM.1347974 (1). **Renauleau**: NHMW 2016/0103/1316 (15), LC (2). **Beugnon**: NHMW 2016/0103/0019 (14), LC (1).

Discussion – *Pseudorbis granulum* (Brugnone, 1873) is a very characteristic species, with its prominent spiral cords forming elevated carinae, six on the last whorl, with a further three on the base. The protoconch is paucispiral, consisting of just 1.25 whorls, with a large nucleus. The crest seen on the last quarter protoconch whorl (Pl. 72, fig. 1d) is also seen in the present-day specimen illustrated by Rubio & Babío (1990, p. 206, fig. 1:5). The only small difference between the French fossil shell and that illustrated by Rubio & Babío (1990) is that it lacks the very fine axial folds seen adjacent to the crest. The authors describe these as ribs, although in our opinion they are not true ribs. We consider this difference insignificant. *Pseudorbis jameonsis* Rubio & Babío, 1990 from the Canary Islands differs in having eight primary spiral cords mid-whorl.

Lozouet (1999, p. 12) described *P. carinifera* from the Atlantic upper Oligocene of France. This species is almost identical to *P. granulum*, with which it was not compared in the original description. Rubio *et al.* (2015) stated that ‘the number of spiral cords of *P. carinifera* is intermediate between *P. granulum* and *P. jameonsis* (2015, p. 250). This is not correct. The number of cords is the same: six primaries on the last whorl, three weaker ones on the base. Judging from the single shell illustrated from Saint-Paul-lès-Dax, the cords on the Oligocene shell are lower and the coiling seems regular, whereas in *P. granulum* the spire is slightly tilted in respect to the last whorl, so that the suture is more oblique. The cords in this species group seem to increase in strength over time. Lozouet (1999) noted that in the Atlantic southwestern France lower Oligocene specimen from Gaas were weaker sculptured than the upper Oligocene shells and that the lower Miocene ones were similar in sculpture to the upper Oligocene ones; these are all considered *P. carinifera* (Lozouet, 1999). We note that by the upper Miocene Tortonian the sculpture is the same as that seen in the extant *Pseudorbis granulum*. As far as we are aware, this is the first fossil record for the species.

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (this paper). Present-day: Atlantic, Canary Islands (Rubio & Babío, 1990) to Senegal (Rubio *et al.*, 2015), Mediterranean (Warén, 1992).

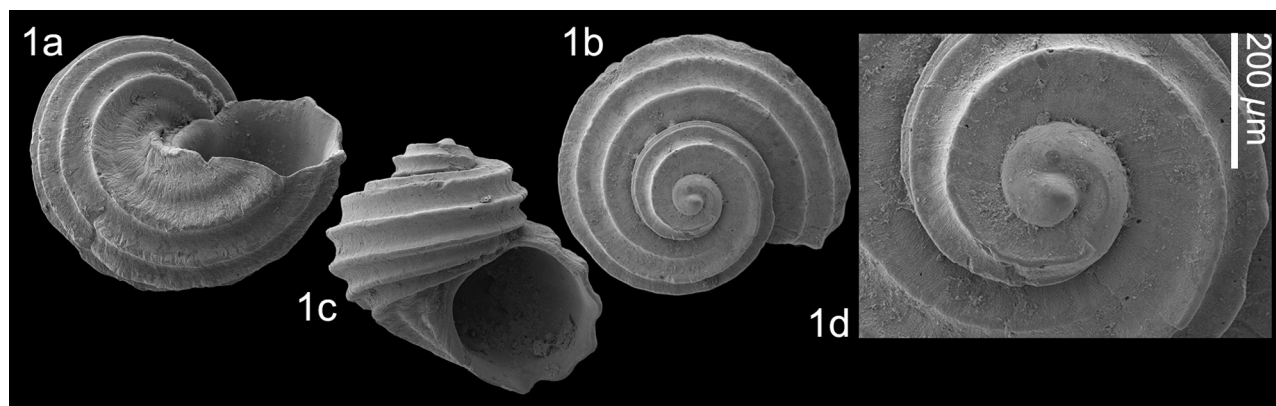


Plate 72: *Pseudorbis granulum* (Brugnone, 1873); 1. NHMW 2016/0103/0017, diameter 1.4 mm, height 1.3 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Skenea* Fleming, 1825

Type species (by subsequent designation, Gray, 1847) – *Helix serpuloides* Montagu, 1808, present-day, British Isles.

1825 *Skenea* Fleming, p. 246.

1827 *Delphinoidea* Brown, p. 32. *Type species* (by subsequent designation, Gray, 1847b): *Helix unispiralis* Montagu, 1803, present-day, British Isles.

***Skenea dautzenbergi* (Glibert, 1949)**

Plate 73, fig. 1

1949 *Circulopsis dautzenbergi* Glibert, p. 71, pl. 5, fig. 1.

Material and dimensions – Maximum diameter 1.6 mm, height 1.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0022 (1), 2016/0103/0023 (50+), RGM.1309553 (15), RGM.1309561 (6), RGM.1309624 (50+), LC (10). **Sceaux-d’Anjou**: RGM.1347975 (2), **Renauleau**: NHMW 2016/0103/0024 (42), LC (10). **Beugnon**: NHMW 2016/0103/0025 (16).

Revised description – Shell small, planorbis. Protoconch of one smooth whorl, with large nucleus (dp= 190 μ m, dn = 110 μ m). Junction with teleoconch marked by fine growth lines and appearance of single fine cord just above suture. Teleoconch of 2.2 depressed, strongly convex whorls, separated by impressed suture. On second half of first teleoconch whorl further spiral cords appear on abapical half of whorl; adapical half remains smooth, except for fine spiral line at shoulder. Last whorl depressed, strongly convex, bearing fine spiral sculpture below shoulder and on base. Base bearing wide umbilicus bordered by peri-umbilical cord, three strong cords run within umbilicus. Aperture ovate, prosocline in profile, outer lip simple. Peristome complete, flattened.

Discussion – This species is superficially similar to the lower Pliocene to present-day European *Moelleriopsis messanensis* (Seguenza, 1876), which occurs in the lower

Pliocene Assemblage III localities of NW France. Indeed, in Ceulemans *et al.* (2016a, p. 74) the Tortonian Assemblage I localities of northwestern France were included in the distribution of that species. However, close inspection of the specimens under SEM imaging shows them not to be a *Moelleriopsis* species, but a *Skenea* species. The protoconch has no spiral sculpture and the peristome is flattened. In our opinion this is the same species as described by Glibert (1949) under the name *Circulopsis dautzenbergi*. Although the original description does not mention any spiral sculpture on the teleoconch, this is only visible under SEM. We therefore consider it useful to include a revised description.

Skenea dautzenbergi (Glibert, 1949) is characterised by its fine spiral sculpture on the abapical half of the last 1.5 teleoconch whorls and the few, but strong, cords running in the umbilicus. There is a suggestion of some micro-pustules on the second half protoconch whorl adjacent to the suture, but it is too abraded to be certain. The French fossil species differs from the type species *S. serpuloides* (Montagu, 1808), from the present-day eastern Atlantic and Mediterranean *S. pelagia* Nofroni & Valenti, 1987 and *S. giemellorum* Romani, Bogi & Bartolini, 2015 in that these three species have stronger spiral sculpture, which covers the entire teleoconch surface and the umbilical cords are not strongly developed. We note that whilst the generic description of *Skenea* given by Warén (1992, p. 155) describes the protoconch as perfectly smooth, in *S. giemellorum* it is sculptured by a couple of spiral threads. *Skenea dautzenbergi* is most similar to the French Atlantic upper Oligocene *S. indubitabilis* Lozouet, 1999, which also has stronger periumbilical keels than the present-day European species, but in that species the teleoconch is smooth, devoid of spiral sculpture and four cords run within the umbilicus as opposed to three (periumbilical keel not included) in *S. dautzenbergi*. *Skenea multicostellata* Lozouet, 1999, also from the French Atlantic upper Oligocene, like the present-day species, has spiral sculpture covering the entire whorl surface.

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

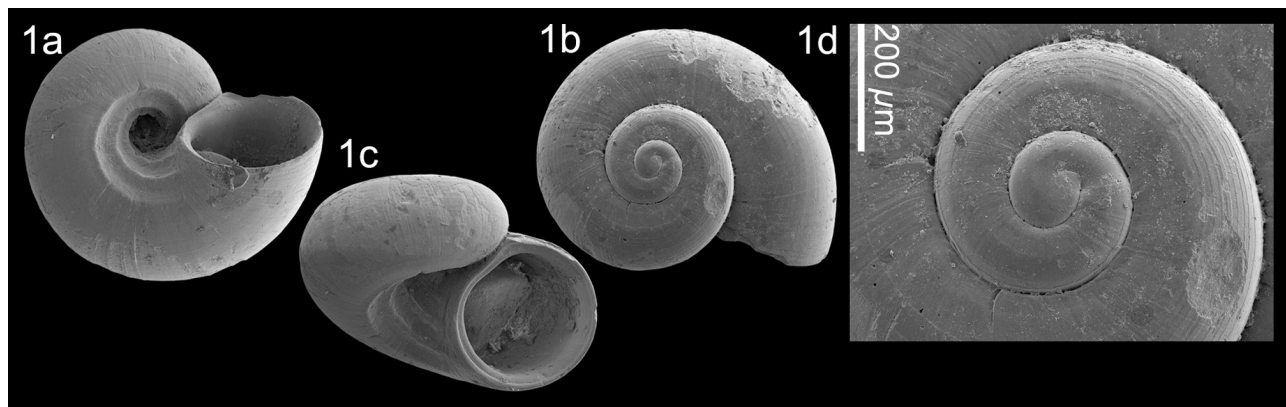


Plate 73. *Skenea dautzenbergi* (Glibert, 1949); 1. NHMW 2016/0103/0022, diameter 1.6 mm, height 1.1 mm; 1d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Skenea minuticostata* nov. sp.**

Plate 74, fig. 1

Type material – Holotype NHMW 2016/0103/0056, diameter 850 μ m; paratype 1 NHMW 2016/0103/0057, diameter 750 μ m; paratype 2 NHMW 2016/0103/0711, diameter 900 μ m; paratype 3 RGM.1309646; paratype 4 RGM.1309647.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/1395 (1), RGM.1309648 (1 fragment).

Etymology – Latin compound name from ‘*minutus*, -a, -um’, adjective, meaning small or tiny and ‘*costatus*, -a, -um’, adjective, meaning ribbed; reflecting the sculpture of very fine, close-set ribs. *Skenea* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Skenea* species of small size, with paucispiral protoconch bearing single cord mid-whorl, teleoconch last whorl angular at shoulder, periphery and base, angulations marked by broad cord interrupted by irregular, close-set axial ripple-like ribs that cover entire whorl and continue into deep umbilicus.

Description – Shell small, planorbid. Protoconch of one whorl, with large nucleus, bearing a single spiral cord mid-whorl (dp= 210 μ m, dn = 120 μ m). Junction with teleoconch marked by beginning of axial sculpture. Teleoconch of two depressed whorls, separated by deeply impressed suture. Sculpture on first whorl of two poorly delimited spiral cords placed below suture and at shoulder. Irregular ripple-like axial ribs radiate from cords, but leav-

ing mid-portion of whorl smooth. Abapically, axial ribs strengthen, broaden and become elevated, axial ribs coalesce mid-whorl, so that on second teleoconch whorl axial ribs extend across dorsum, elevated, roughly equal in width to their interspaces. Last whorl angled at shoulder, periphery and base, which are delimited by broad cords, interrupted by the irregular, elevated axial sculpture that extends onto base and into wide umbilicus. Aperture ovate, prosocline in profile, outer lip simple. Peristome complete.

Discussion – It is difficult to find any species that can be usefully compared in the European fossil and present-day faunas. The axial sculpture of ripple-like axial ribs is unique for the genus. It is most similar to some *Lodderena* Iredale, 1924 species such as the present-day species *L. ornata* (Olsson & McGinty, 1958), *L. omanensis* Moolenbeek, 1996 and *L. tanae* Moolenbeek, 1996 from Oman and *L. formosa* Powell, 1930 and *L. nana* Powell, 1930 from New Zealand have predominantly spiral sculpture, whereas in *Skenea minuticostata* nov. sp. the sculpture is predominantly axial. *Lodderena pachynepion* (Pilsbry & Olsson, 1945) from the Pacific coast of Colombia does have axial sculpture, but this is much less dense than in *S. minuticostata*. The most similar species we could find is *L. pulchella* Olsson & McGinty, 1958 from the present day Caribbean, which has very similar sculpture on the dorsum, but the axial ribs fade over the base and there is an extra inner cord on the base, absent in *L. minuticostata*. An undescribed extant *Lodderena* species from Mauritius illustrated on the website of the National Museum of Wales ([http://www.museumwales.ac.uk/curatorial/bio-syb/mollusca/research/interpretation/accessed 17.052016](http://www.museumwales.ac.uk/curatorial/bio-syb/mollusca/research/interpretation/accessed%2017.052016)) has very similar sculpture to the French Miocene species.

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

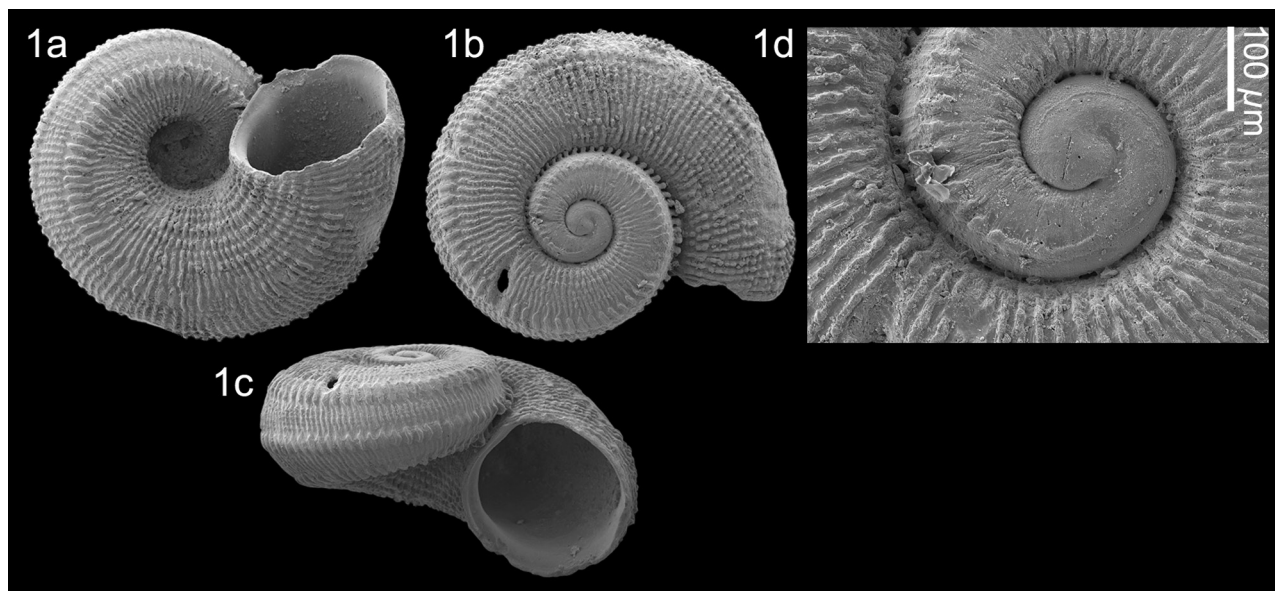


Plate 74. *Skenea minuticostata* nov. sp.: 1. **Holotype** NHMW 2016/0103/0056, diameter 850 μ m; 1d, detail of protoconch (SEM image). Le Grand Chauvreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

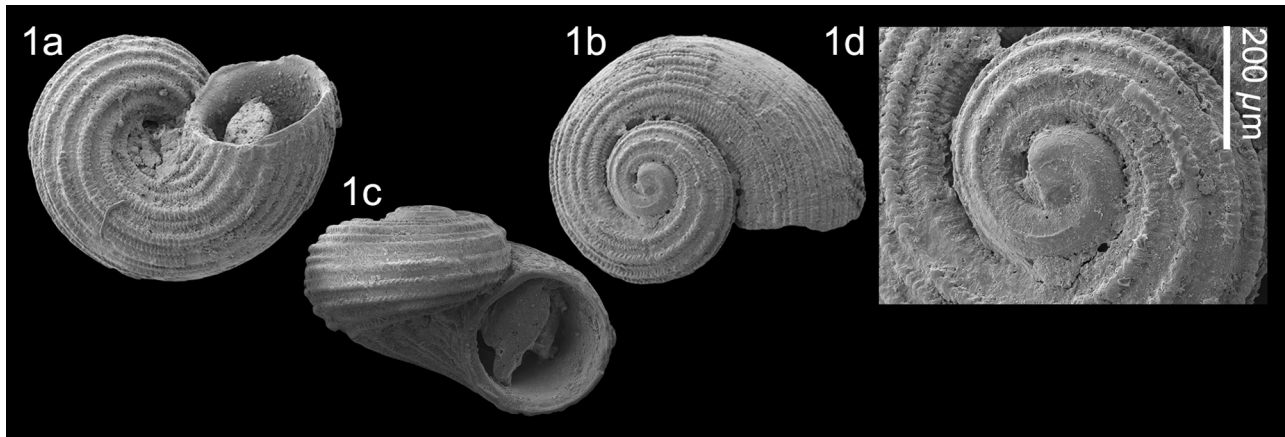


Plate 75. *Skenea wareni* nov. sp.; 1. **Holotype** MNHN.F.A57684, diameter 1.4 mm, height 950 µm; 1d, detail of protoconch (SEM image). Le Grand Chauvureau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Skenea wareni* nov. sp.**

Plate 75, fig. 1

Type material – Holotype MNHN.F.A57684, diameter 1.4 mm; height 950 µm; paratype 1 NHMW 2016/0103/0052; paratype 2 NHMW 2016/0103/0053; paratype 3 NHMW 2016/0103/0054; paratype 4 RGM.1309636; paratype 5 RGM.1309637; paratype 5 RGM.1309638.

Other material – **St-Clément-de-la-Place**: NHMW 2016/0103/0055 (11), RGM.1309639 (18 fragments), LC (3). **Re-nauleau**: NHMW 2016/0103/1399 (7), LC (2).

Etymology – Named after Anders Warén of the Zoologiska Institutionen, Göteborg (Sweden), in recognition to his enormous contributions to malacology, and especially skeneimorph gastropods. *Skenea* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Skenea* species of small size, with paucispiral protoconch bearing spiral threads, teleoconch bearing strong spiral cords crossed by lamellar growth lines, giving surface beaded or scabrous appearance, sculpture continuing onto base, broad umbilicus.

Description – Shell small, planorbid. Protoconch of one whorl, with large nucleus, bearing irregular spiral threads (dp = 240 µm, dn = 140 µm). Junction with teleoconch marked by the beginning of three strong spiral cords placed adjacent to each suture and at shoulder, crossed by close-set lamellar growth lines, which cut cords, giving them finely beaded or scabrous appearance. Teleoconch of 2.6 depressed, strongly convex whorls, separated by deeply impressed suture. After 0.75 teleoconch whorls secondary cords appear in interspaces, rapidly gaining in strength, with further tertiary cords developing in interspaces on last half whorl. Entire teleoconch surface cov-

ered in raised lamellar growth lines, giving interspaces between beaded cords scabrous appearance. Last whorl depressed, strongly convex, bearing about 12 beaded spiral cords of subequal strength; alternate strength mid-whorl. Base bearing wide umbilicus, sculptured by prominent beaded cords of alternating strength. Aperture ovate, prosocline in profile, outer lip simple, Peristome complete.

Discussion – We had initially placed *Skenea minuticos-tata* nov. sp. and *Skenea wareni* nov. sp. in the genus *Lodderena* Iredale, 1924. Warén (1992, p. 155) considered the genus *Lodderena* to include skeneimorph gastropods with spirally striated shell with three or more scaly periumbilical ribs [cords]. The present-day Mediterranean *Cyclostrema catenoides* Monterosato, 1877, which was placed in the genus *Lodderena* by Warén, is most like *S. wareni* but differs in having only the periumbilical cords strongly developed, the rest of the teleoconch surface is covered with fine, close-set spiral cords. Warén (1992) noted that the differences between *Lodderena* and *Skenea* species were small and that they might turn out to be congeneric. Indeed, *L. catenoides* was placed in the genus *Skenea* Fleming, 1825 by WoRMS (Gofas, 2015). We therefore follow WoRMS in placing these species in *Skenea* and use *Lodderena* in a more restricted sense following Rubio *et al.* (1998). *Skenea wareni* is similar to the type species of *Skenea*, *S. serpuloides* (Montagu, 1808), but the latter does not have stronger periumbilical cords and the axial sculpture is not lamellar.

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

Genus *Skeneoides* Warén, 1992

Type species (by original designation) – *Delphinula exilissima* Philippi, 1844, present-day, Italy.

1992 *Skeneoides* Warén, p. 156.

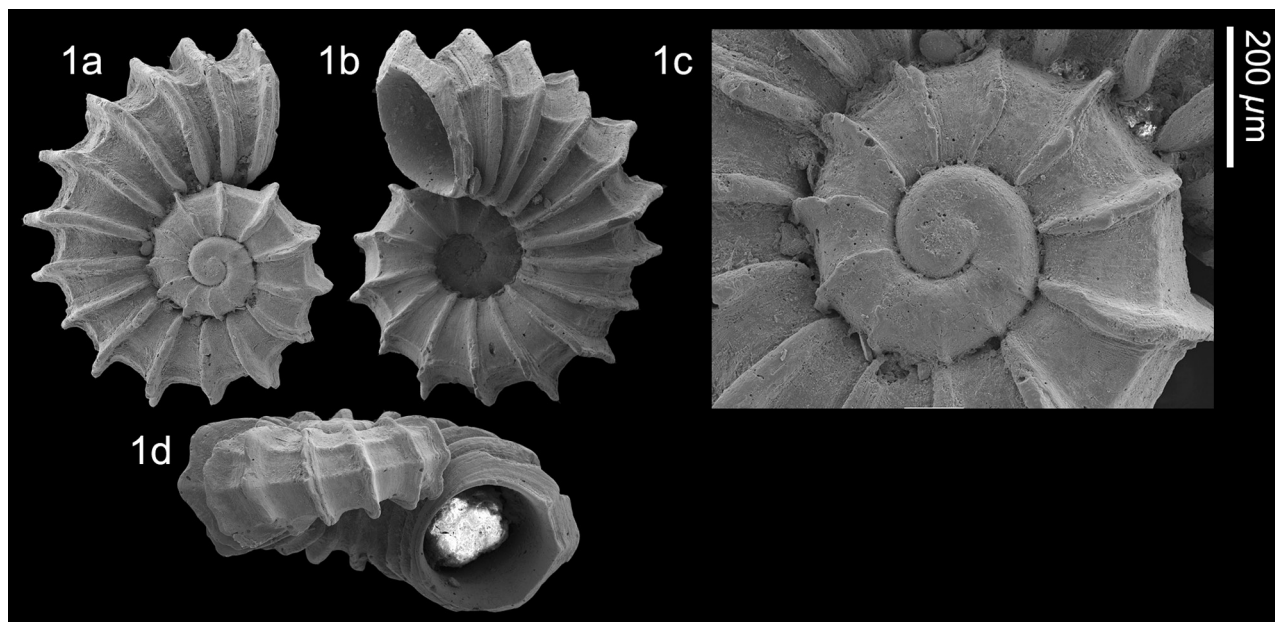


Plate 76. *Skeneoides crassistriata* Lozouet, 1999; 1. NHMW 2016/0103/0013, diameter 1.8 mm, height 1.1 mm; 1c, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Skeneoides crassistriata* Lozouet, 1999**

Plate 76, fig. 1

1999 *Skeneoides crassistriata* Lozouet, p. 12, pl. 7, figs 1-4.

Material and dimensions – Maximum diameter 1.9 mm, height 1.1 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0013 (1), NHMW 2016/0103/0014 (10), RGM.1309640 (5), LC (2). **Renauleau:** NHMW 2016/0103/0015 (4). **Beugnon:** NHMW 2016/0103/0016 (14).

Discussion – *Skeneoides crassistriata* Lozouet, 1999 is a striking species, characterised by the extremely strongly developed and elevated axial ribs. It is most similar to the present-day Mediterranean *S. jeffreysii* (Monterosato, 1872), but this species has weaker primary axial ribs, secondary ribs in the interspaces and about five spiral cords mid-whorl. *Skeneoides exilissima* (Philippi, 1844), also extant in the Mediterranean, again has weaker, more numerous primary ribs and stronger spiral cords delimiting the shoulder and base. *Skeneoides tenuistriata* Lozouet, 1999 from the Oligocene of France has fine reticulated surface sculpture. This species was described based on material from the middle Miocene of Ferrière-Larçon, Indre-et-Loire, France.

We note that ICZN (1999a) Art. 30.1.4.4 rules that genus names ending *-oides* are masculine, and accordingly that the name should be *crassistriatus*. But there is an exception; that when treated as feminine in the original description it should remain so. Warén (1992, p. 156) nominated *Delphinula exilissima* Philippi, 1844 as type species for *Skeneoides*, and used the combination *Skeneoides exilissima*, meaning that he considered *Skeneoides* to be feminine. Therefore, Lozouet (1992) was quite cor-

rect in keeping the trivial name for his new species feminine.

Distribution – Middle Miocene: Atlantic (Langhian) Loire Basin (Lozouet, 1999). Upper Miocene (Tortonian): Atlantic, NW France (this paper).

Family Phasianellidae Swainson, 1840
Subfamily Tricoliinae Woodring, 1928
Genus *Tricolia* Risso, 1826

Type species (by subsequent designation, Gray, 1847b) – *Turbo pullus* Linnaeus, 1758, present-day, Mediterranean.

- 1826 *Tricolia* Risso, p. 122.
- 1847a *Thicolia* Leach in Gray, p. 271. Incorrect subsequent spelling.
- 1847b *Thicolea* Gray, p. 144. Incorrect subsequent spelling.
- 1847b *Tricolea* Gray, p. 144. Incorrect subsequent spelling.
- 1852 *Eudora* Leach in Gray, p. 147, 199. Type species (by monotypy): *Eudora varians* Leach in Gray, 1852, present-day, Europe. Junior homonym of *Eudora* Péron & Lesueur, 1810 [Cnidaria] and several others.
- 1853 *Chromotis* H. & A. Adams, p. 19. Type species (by monotypy): *Phasianella neritina* Dunker, 1846, present-day, South Africa.
- 1884a *Tricoliella* Monterosato, p. 110. Type species (by subsequent designation, Pilsbry, 1888): *Turbo pullus* Linnaeus, 1758, present-day, Mediterranean. Junior objective synonym of *Tricolia*.

- 1891 *Steganomphalus* Harris & Burrows, p. 112. Type species (by typification of replaced name): *Eudora varians* Leach in Gray, 1852, present-day, Europe. *Nom. nov. pro Eudora* Leach in Gray, 1852, non Péron & Lesueur, 1810 [Cnidaria].
- 1920 *Epheriella* Pallary, p. 48. Type species (by original designation): *Epheriella algoidea* Pallary, 1920, present-day, Morocco.
- 1973 *Eutricolia* Nordsieck, p. 10. Type species (by original designation): *Turbo speciosus* Megerle von Mühlfeld, 1824, present-day, Mediterranean.

***Tricolia pullus* s.l. (Linnaeus, 1758)**

Plate 77, figs 1-6

- *1758 *Turbo pullus* Linnaeus, p. 1233.
- 1854 *Phasianella Turbinoidea* Lamk. – Millet, p. 158 (non Lamarck, 1804).
- 1925 *Phasianella pulla* var. *pulchella* Récluz – Harmer, p. 870, pl. 65, fig. 26.
- 1964 *Tricolia pullus* Linné, 1766 [sic] – Brébion, p. 136, pl. 3, figs 22-23.
- 2003 *Tricolia pullus pullus* (Linnaeus, 1758) – Landau et al., p. 34, pl. 8, figs 1, 2 (cum syn.).
- 2004 *Tricolia pullus* (Linné, 1758) – Chirli, p. 42, pl. 13, figs 10-13, pl. 14, figs 1-5.
- 2010 *Tricolia pullus* (Linnaeus, 1758) – Sosso & Dell'Angelo, p. 19, p. 30 unnumbered fig. bottom right.

Material and dimensions – Maximum height 10.3 mm, width 5.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0518-0524 (7), NHMW 2016/0103/0525 (50+), RGM.1309569 (3), RGM.1309570 (50+), RGM.1309574 (30 juveniles), RGM.1347889 (50+), LC (50), FVD (50+).

Sceaux-d'Anjou: RGM.1309581 (13), RGM.1309583 (1 adult + 3 juveniles), RGM.1347853 (50+), RGM.1347956 (26), RGM.1348021 (21), LC (10). **Renauleau**: NHMW 2016/0103/1482 (10), LC (10), FVD (3). **Beugnon**: RGM.1309582 (41 adults and subadults).

Discussion – In the present-day faunas there are two subspecies living off the shores of continental Europe. *Tricolia pullus pullus* (Linnaeus, 1958) found in the Mediterranean, up to the Straits of Gibraltar and *T. pullus picta* (Da Costa, 1778), which is predominantly an Atlantic subspecies, ranging from the British Isles to the north, southwards to Morocco. In the western Mediterranean transitional morphologies can be found (Gofas, 1982). Usually the Atlantic subspecies is thinner shelled, with the upper part of the whorls slightly more flattened, with a zigzag colour pattern predominating, especially on the base of the last whorl.

The Assemblage I specimens from St-Clément-de-la-Place illustrated here (Pl. 77, figs 1-6) cover the entire range of shell shape and pattern illustrated by Gofas (1982, figs 1-13) for Mediterranean and Atlantic forms, with globose and more slender forms, striped and spotted forms, and we would hesitate to say if they are of the *pullus* or *picta* morphotype. It is possible that in the upper Miocene this distinction was not present and that the ancestral form exhibited both morphotypes. Despite several attempts at SEM imaging to illustrate the protoconch, none of the five specimens examined had a clearly delimited protoconch/teleoconch boundary. We therefore provisionally consider the Assemblage I population to be *T. pullus sensu lato*. We note that specimens from Renauleau are much larger, up to 10 mm in height.

The middle Miocene Loire Basin shell illustrated by Glibert (1949, p. 78, pl. 4, fig. 16) as *Tricolia millepunc-*

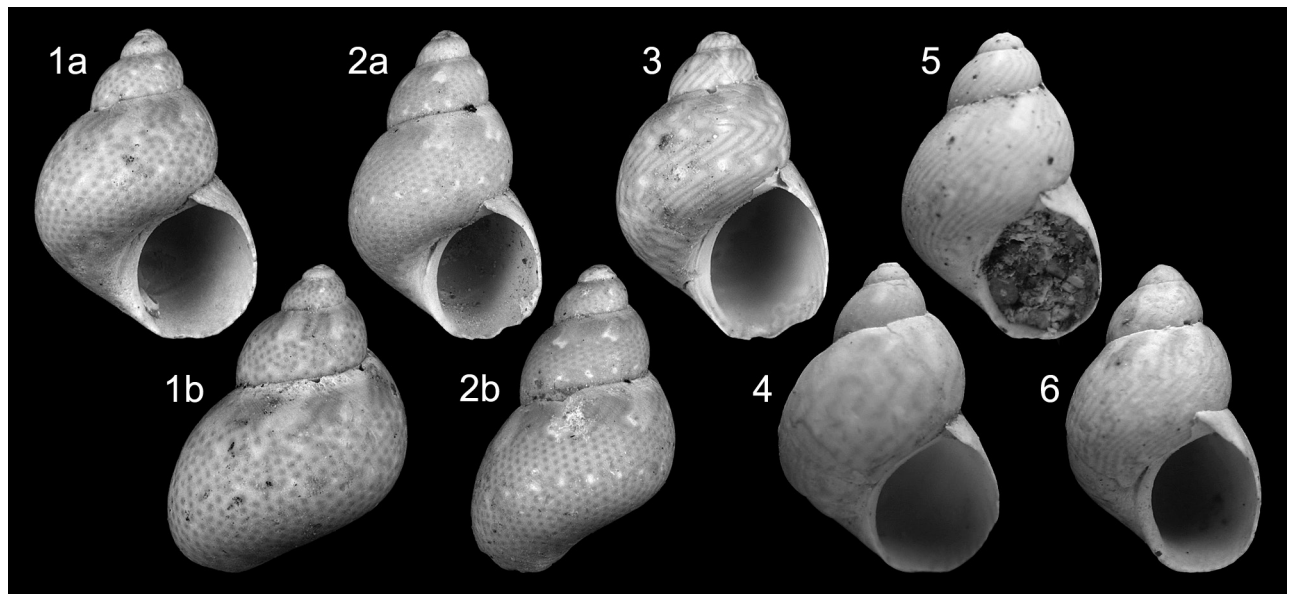


Plate 77. *Tricolia pullus* (Linnaeus, 1758); 1. NHMW 2016/0103/0518, height 4.2 mm; 2. NHMW 2016/0103/0519, height 5.3 mm; 3. NHMW 2016/0103/0520, height 4.5 mm; 4. NHMW 2016/0103/0521, height 4.3 mm; 5. NHMW 2016/0103/0522, height 4.4 mm; 6. NHMW 2016/0103/0523, height 4.3 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

tata (Benoist, 1873) is umbilicate and therefore probably a distinct species. The Loire Basin shell identified by the same author as *T. eichwaldi* (Hörnes, 1855) is also probably correct, and differs from *T. pullus* in having a relatively expanded last whorl, low spire and a concave subsutural collar (see also Landau *et al.*, 2013, p. 34). The Pliocene to present-day Mediterranean *T. tenuis* (Michaud, 1829) differs from *T. pullus* in having a higher spire, flatter whorls and a predominance of dotted pattern, with the flammules restricted to area immediately below the suture.

Brébion (1964, p. 137) recorded this species from Assemblage I (Renauleau, Thorigné, Sceaux-d'Anjou, St-Clément-de-la-Place, Beaulieu).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964). Lower Pliocene: central Mediterranean, Tunisia (Fekih, 1975), Italy (Pavia, 1975; Chirli, 2004; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona, Spain (Landau *et al.*, 2003); central Mediterranean, Italy (Sacco, 1896a). Lower Pleistocene: Atlantic, St Erth, England (Harmer, 1925). Pleistocene: western Mediterranean, Balearic Islands, (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1916; Taviani *et al.*, 1998). Present-day: western coasts of British Isles, south into the Mediterranean, intertidal to 35m deep in the north, in the Mediterranean often found in *Posidonia* fields in shallow water (Poppe & Goto, 1991).

Remarks

In this work on the Patellogastropoda and Vetigastropoda of the upper Miocene Tortonian Assemblage I localities (*sensu* Van Dingenen *et al.*, 2015) 76 species are recorded, of which 26 are new to science, six are homonyms and receive replacement names and five are left in open nomenclature. This is an important increase in the diversity compared to the 44 species recorded by Brébion (1964). We were able to identify all the vetigastropods recorded by Brébion except for four:

Calliostoma cf. *conulum* [sic] Linnaeus, 1758 (1964, p. 82, pl. 2, fig. 1). Recorded at Renauleau (1) and Sceaux-d'Anjou (2), the specimen illustrated is poorly preserved and only half the height of present-day specimens. This record is doubtful and requires confirmation.

Calliostoma hybridum Millet, 1854 (1964, p. 89, pl. 2, fig. 10). This is a *nomen nudum*, later formally described by Millet (1865, p. 583). Unfortunately this is a junior homonym of *Trochus hybridus* Linnaeus, 1758. Recorded from Renauleau (2) and Sceaux-d'Anjou (2), we were unable to find any specimens that we could ascribe to this species. The specimen illustrated by Brébion might be a form of *Calliostoma gratiosum* (Millet, 1865).

Calliostoma couffoni Brébion (1964, p. 90, pl. 2, fig. 11) *nomen nudum*. Despite being recorded from numerous Assemblage I deposits by Brébion, we have not found any specimens that fit this species.

Gibbula (Colliculus) varia var. *monodontoides* Millet, 1854 (1964, p. 108, pl. 3, figs 1-2). This is a *nomen nudum*, later formally described and validated by Millet (1865, p. 582). This species seems to be abundant at St-Michel, which was not sampled and Apigné, which is a Messinian Assemblage II locality. Hopefully we will come across this species later in the series.

We highlight the first description of a member of the subfamily Thysanodontinae in the European faunas and the first fossil record, with the description of *Thysanodonta chauvereauiensis* nov. sp. Marshall (1988) described the subfamily as having a vicariant distribution in South Africa, Australia, New Zealand and New Caledonia. Subsequent reports and additions of new species have not increased this geographic distribution (Marshall, 1995; Vilvens & Maestrati, 2006). The description of the subfamily in Europe suggests a wider distribution, and it is quite possible further members remain unrecognised or described as *Calliostoma* species.

A full synthesis of the Assemblage I fauna will be given at the end of the series, but already some preliminary observations are worthy of discussion. The Assemblage I vetigastropod fauna is remarkable in several respects. As far as we are aware, it is the most speciose European Neogene gastropod assemblage known, with 76 species representing 33 different genera/subgenera. In contrast with this specific diversity, almost no species attains a height greater than a couple of centimetres. Even genera usually represented by medium sized shells such as *Diodora*, *Gibbula* and *Calliostoma* are represented in Assemblage I by small species or dwarf forms of species found in other assemblages. The composition of the fauna suggests shallow water environment, littoral zone and the presence of genera such as *Patella*, *Tectura*, *Diodora*, *Gibbula*, *Jujubinus*, and *Calliostoma* amongst others, and the abundance of specimens in these genera, suggest a hard bottom environment, which are usually under-represented in the fossil record.

The fauna is also highly endemic, with 48 of the 76 (63%) species known only from the northwestern French Assemblage I localities (Fig. 2). Of these 75 species only 9 (12%) survived into the lower Pliocene Assemblage III fauna of northwestern France. Thirty-eight (51%) also occur in the earlier middle Miocene Langhian assemblage of the Loire Basin, but relationships with other European basins are weak; six (8%) also occur in the Miocene-present-day North Sea Basin, 14 (19%) in the Mediterranean and one (1.3%) in the Pleistocene of St. Erth (Cornwall, England).

Amongst the vetigastropods, the generic composition is similar to that seen today; a few genera are extinct, such as *Lucapinella*, *Paroxystele* and *Pareuchelus*. There are a few elements suggesting thermophilia; the genus *Leucorhynchia* occurs today in a more southern distribution, found off the coast of West Africa, and the species *Haliotis tuberculata coccinea* Reeve, 1846 and *Gibbula fanulum* (Gmelin, 1791).

Further remarks will be made as the series develops.


| Species | Geographical distribution | | | | | Stratigraphical distribution | | | | | | | |
|---|---|---|---|---|-----|------------------------------|--------|-------|----------|-------|-------------|-------|-----|
| |  | | | | | Miocene | | | Pliocene | | Pleistocene | | Hol |
| | 1 | 2 | 3 | 4 | A/M | Lower | Middle | Upper | Lower | Upper | Lower | Upper | |
| <i>Patella protea</i> Doderlein, 1862 | | | ● | ● | A | | | ■ | | | | | |
| <i>Tectura virginea</i> (Müller, 1776) | ● | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Diodora graeca</i> (Linnaeus, 1758) | ● | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Diodora multifida</i> (Deshayes, 1830) | | | ● | | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Diodora sancticlementensis</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Emarginula adriatica</i> Costa, 1830 | | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Emarginula imbricata</i> Millet, 1865 | | | ● | | A | ■ | ■ | ■ | | | | | |
| <i>Emarginula octaviana</i> Coen, 1839 | | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Emarginula rosea</i> Bell, 1824 | ● | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Lucapinella clypeata</i> (Grateloup, 1828) | | | ● | ● | A | ■ | ■ | ■ | | | | | |
| <i>Haliotis</i> cf. <i>tuberculata coccinea</i> Reeve, 1846 | | | ● | | A | | | ■ | | | | | |
| <i>Scissurella transylvanica</i> Reuss, 1860 | | | ● | ● | A | ■ | ■ | ■ | | | | | |
| <i>Sinezona geigeri</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Anatoma redoniana</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Clanculus</i> (s.s.) <i>brebioni</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Clanculus</i> (<i>Clanculopsis</i>) <i>baccatus</i> (Defrance, 1824) | | | ● | | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Clanculus</i> (<i>Clanculopsis</i>) <i>sancticlementensis</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Clanculus</i> (<i>Clanculopsis</i>) <i>umbilicovadus</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus coronatus</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus</i> aff. <i>exasperatus</i> (Pennant, 1777) | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus proximus</i> (Millet, 1865) | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus</i> cf. <i>proximus</i> (Millet, 1865) | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus redoniensis</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus sceauxensis</i> nov. sp. | | | ● | | A | | | ■ | | | | | |
| <i>Jujubinus striatus</i> (Linnaeus, 1758) | ● | | ● | ● | A | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| <i>Colliculus biangulatus</i> (Eichwald, 1830) | | | ● | | A | ■ | ■ | ■ | | | | | |
| <i>Colliculus insignis</i> (Millet, 1854) | | | ● | | A | ■ | ■ | ■ | | | | | |

Figure 2. 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). (Continued next pages).

| Species | Geographical distribution | | | | | Stratigraphical distribution | | | | | | | |
|---|---------------------------|---|---|---|--------|------------------------------|--------|-------|-------|-------|-------|-------|-----|
| | 1 | 2 | 3 | 4 | 5/6 | Lower | Middle | Upper | Lower | Upper | Lower | Upper | Hol |
| <i>Gibbula brebioni</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Gibbula clanculiforma</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Gibbula conicomagus</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Gibbula fanulum</i> (Gmelin, 1791) | | | ● | ● | Ⓐ Ⓜ | | | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Gibbula marianae</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Gibbula provosti</i> Ceulemans, Van Dingenen & Landau, 2016 | | | ● | | Ⓐ | | | ■ | ■ | | | | |
| <i>Gibbula sagus</i> (Defrance, 1828) | | | ● | | Ⓐ | ■ | ■ | ■ | | | | | |
| <i>Gibbula striatellata</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Paroxystele trochiformis</i> (Millet, 1865) | | | ● | | Ⓐ | ■ | ■ | ■ | | | | | |
| <i>Phorcus gallicophorcus</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Bolma granosa</i> (Borson, 1821) | | | ● | ● | Ⓐ Ⓜ | ■ | ■ | ■ | ■ | ■ | | | |
| <i>Bolma</i> cf. <i>meynardi</i> (Michelotti, 1847) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma alternatum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma baccatum</i> (Millet, 1865) | | | ● | | Ⓐ | ■ | ■ | ■ | | | | | |
| <i>Calliostoma biangulatum</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma contractum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma gibbuliforme</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma echinatum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma gratiosum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma lamellatum</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma michaeli</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma microgemmatum</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma milletigranum</i> nov. nom. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma mitorulosum</i> nov. nom. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma miotumidum</i> nov. nom. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma planospirum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma quaggaoides</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma pagodulum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma presselierense</i> nov. sp. | | | ● | | | | | ■ | | | | | |
| <i>Calliostoma spinosum</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |

| Species | Geographical distribution | | | | | Stratigraphical distribution | | | | | | | |
|--|---------------------------|---|---|---|-----|------------------------------|--------|-------|-------|-------|-------|-------|-----|
| | 1 | 2 | 3 | 4 | 5/6 | Lower | Middle | Upper | Lower | Upper | Lower | Upper | Hol |
| <i>Calliostoma umbellum</i> (Millet, 1865) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma verrucosum</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Calliostoma vibrayanum</i> (Dollfus & Dautzenberg, 1886) | | | ● | | Ⓐ | | ■ | ■ | | | | | |
| <i>Calliostoma</i> cf. <i>zizyphinum</i> (Linnaeus, 1758) | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Thysanodonta chauvereauensis</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Pareuchellus lacointreae</i> (Dollfus & Dautzenberg, 1899) | | | ● | | Ⓐ | | ■ | ■ | | | | | |
| <i>Pareuchellus dautzenbergi</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Dikoleps cutleriana</i> (Clark, 1849) | ● | | ● | ● | Ⓐ | | | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Dikoleps insulsa</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Leucorhynchia rotellaeformis</i> (Grateloup, 1832) | | | ● | | Ⓐ | | ■ | ■ | | | | | |
| <i>Lodderena redferni</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Parviturbo rubioi</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Pseudorbis beugnonensis</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Pseudorbis granulum</i> (Brugnone, 1873) | | | ● | ● | Ⓐ | | | ■ | ■ | ■ | ■ | ■ | ■ |
| <i>Skenea dautzenbergi</i> (Glibert, 1949) | | | ● | | Ⓐ | | ■ | ■ | | | | | |
| <i>Skenea minuticostata</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Skenea wareni</i> nov. sp. | | | ● | | Ⓐ | | | ■ | | | | | |
| <i>Skeneoides crassistriata</i> Lozouet, 1999 | | | ● | | Ⓐ | | ■ | ■ | | | | | |
| <i>Tricolia pullus</i> s.l. (Linnaeus, 1758) | ● | ● | ● | | Ⓐ | | | ■ | ■ | ■ | ■ | ■ | ■ |

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