The upper Miocene gastropods of northwestern France, 4. Neogastropoda

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In this paper we review the Neogastropoda of the Tortonian upper Miocene (Assemblage I of Van Dingenen *et al.*, 2015) of northwestern France. Sixty-seven species are recorded, of which 18 are new: *Gibberula ligeriana* nov. sp., *Euthria presselierensis nov. sp., Mitrella clava* nov. sp., *Mitrella ligeriana* nov. sp., *Mitrella miopicta* nov. sp., *Mitrella pseudoinedita* nov. sp., *Mitrella pseudoblonga* nov. sp., *Mitrella pseudoturgidula* nov. sp., *Sulcomitrella sceauxensis* nov. sp., *Tritia turtaudierei* nov. sp., *Engina brunettii* nov. sp., *Pisania redoniensis* nov. sp., *Pusia* (*Ebenomitra*) *brebioni* nov. sp., *Pusia* (*Ebenomitra*) *pseudoplicatula* nov. sp., *Pusia* (*Ebenomitra*) *renauleauensis* nov. sp., *Pusia* (*Ebenomitra*) *sublaevis* nov. sp., *Episcomitra s.l. silvae* nov. sp., *Pseudonebularia sceauxensis* nov. sp. *Fusus strigosus* Millet, 1865 is a junior homonym of *F. strigosus* Lamarck, 1822, and is renamed *Polygona substrigosa* nom. nov. *Nassa* (*Amycla*) *lambertiei* Peyrot, 1925, is considered a new subjective junior synonym of *Tritia pyrenaica* (Fontannes, 1879).

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

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al*., 2014, 2016a, b, 2018; Van Dingenen *et al*., 2014, 2015, 2016; Landau *et al*., 2017, 2018, 2019): Gastropods of the order Neogastropoda in the Assemblage I deposits of Van Dingenen *et al*. (2015) of the Tortonian upper Miocene age are revised.
In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded 90 Neogastropoda species from Assemblage I deposits, some of which were described as new. However, as the thesis was never published, these names do not comply with article 13 of the ICZN code (1999) and must be considered *nomina nuda*.

Geological setting and material and methods

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

Abbreviations:

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

Systematics

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

Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Family Cystiscidae Stimpson, 1865
Subfamily Persiculinae G. A. Coovert & H. K. Coovert, 1995

Genus *Gibberula* Swainson, 1840

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

1840 *Gibberula* Swainson, p. 323.

For generic synonymy see Van Dingenen *et al*. (2017, p. 36).

***Gibberula ligeriana* nov. sp.**
Plate 1, figs 1-3

Type material – Holotype MNHN.F.A70513, height 6.0 mm, width 3.9 mm; paratype 1 MNHN.F.A70514, height 5.9 mm, width 4.0 mm; paratype 2 NHMW 2016/0103/0830, height 6.6 mm, width 4.5 mm; paratype 3 NHMW 2016/0103/0831, height 6.1 mm, width 4.1 mm; paratype 4 NHMW 2016/0103/0834, height 6.0 mm, width 4.0 mm, paratype 7 RGM.1349126, height 5.4 mm, width 3.7 mm, **St-Clément-de-la-Place**; paratype 5 RGM.1349115, height 5.8 mm, width 3.9 mm; paratype 6 RGM.1349116, height 6.0 mm, width 3.9 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 6.7 mm, width 4.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0832 (50+), RGM.1349127 (6), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0833 (50+), RGM.718127 (50+), RGM.1347919 (42), RGM.1349185 (5), RGM. 1349186 (50+), RGM.1349235 (6), RGM.1349285 (17), RGM.1352240 (15), LC (5), FVD (50+).

Etymology – Named after the '*Golfe Ligérien*', the name of the bay in which the species lived. *Gibberula* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Gibberula* species of large size for genus, cylindrical shell shape, strongly thickened, alate outer lip, strongly denticulate within, seven columellar plications, second plication from base significantly stronger, from which extends outwards a groove and ridge delimiting base from siphonal fasciole.

Description – Shell large for genus, solid, cylindrical-ovate, with a relatively wide, strongly depressed spire. Protoconch covered by callus. Teleoconch of about two whorls, suture superficial. Last whorl more than 95% total height, convex, maximum diameter situated just above mid-height, weakly constricted at base. Surface smooth and glossy, with only faint growth striae. Aperture narrow, elongate, weakly curved, slightly wider abapically. Outer lip strongly thickened, somewhat alate adapically, extending almost to the apex, abapically extending beyond tip of siphonal fasciole, bearing 14-19 well-developed denticles within, those placed on abapical portion slightly stronger; anal canal narrow; siphonal canal short, open, deeply notched. Columella weakly convex, bearing seven plications, two abapical plications more strongly developed, second plication significantly stronger, thereafter folds decreasing in size adapically. Two abapical plications extend externally over columella, thickly callused, forming small abapical callus pad. Parietal callus moderately well developed, expanded over venter, bearing small vertical parietal pad in most specimens. Siphonal fasciole flattened, delimited from base by shallow groove and ridge extending from just above second plication.

Discussion – *Gibberula ligeriana* nov. sp. is the largest *Gibberula* species in Assemblage I, and one of the two largest European Neogene species. It is also remarkably constant in shape and in its apertural armature. The only species with which it can be confused is *G. miliaria* (Linnaeus, 1758), with which it co-occurs in Assemblage I. The two are similar in maximum size, although on average *G. ligeriana* is slightly larger than the average *G. miliaria*. In Assemblage I *G. miliaria* does not reach a height greater than 4.3 mm (see below), which makes them easy to separate. The most important differences are the alate adapical part of the outer lip in *G. ligeriana*

Plate 1. *Gibberula ligeriana* nov. sp.; 1. **Holotype** MNHN.F.A70513, height 6.0 mm, width 3.9 mm; 2. **Paratype 1** MNHN.F.A70514, height 5.9 mm, width 4.0 mm; 3. **Paratype 2** NHMW 2016/0103/0830, height 6.6 mm, width 4.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

that almost extends to the apex; in *G. miliaria* the outer lip is not alate and the insertion is at or below the suture, and the greater number of columellar folds (7 in *G. ligeriana* vs 4-6 in *G. miliaria*). The apertural dentition is also stronger than in most specimens of *G. miliaria*. We have re-examined Glibert's (1952a) record of *G. miliaria* in the middle Miocene Loire Basin of France and, based on both his figure (1952a, pl. 12, fig. 8) and material at hand we agree that this is *G. miliaria*. The only possible difference is that the French fossil shells have slightly coarser teeth within the outer lip than extant *G. miliaria*. Landau *et al*. (2006a) discussed several congeners from the upper Pliocene, lower Piacenzian of the Estepona Basin of southern Spain. The only species with an alate outer lip is *G. pilarae* Muñiz Solís, 1996, but this is a much smaller species with a triangular shell profile. *Gibberula jriae* (Sacco, 1890) from the Pliocene Mediterranean also has seven columellar plications, but it is smaller (3.6-5.0 mm; see Chirli, 2002, pl. 10, figs 1-12), less inflated, and does not have an alate outer lip.

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

***Gibberula miliaria* (Linnaeus, 1758)**
Plate 2, figs 1-3

*1758	*Voluta miliaria* Linnaeus, p. 730.
1964	*Gibberula miliaria* Linné, 1766 – Brébion, p. 533.
2017	*Gibberula miliaria* (Linnaeus, 1758) – Van Dingenen *et al*., p. 37, pl. 3, fig. 6 (*cum syn*.).

Material and dimensions – Maximum height 4.3 mm, width 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0835-0837 (3), NHMW 2016/0103/0838 (50+), RGM. 1349128 (6), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0842 (50+), RGM.718128 (50+), RGM. 1349184 (36), RGM.1349189 (3), RGM.1349236 (9), RGM. 1349286 (50+), RGM.1352241 (45), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1376 (10).

Description – Specimens of *Gibberula miliaria* (Linnaeus, 1758) from Assemblage I are relatively small. The spire is low; the outer lip inserts at the level of the suture, is denticulate in all specimens, and the columella bears 5-6 folds, weakening adapically. The only difference with extant *G. miliaria* is that the French fossil shells have slightly coarser teeth within the outer lip, but we consider this insufficient to erect a new species.
Gibberula miliaria is similar to the Pliocene Mediterranean *G. proxima* Landau, La Perna & Silva, 2006 from the Estepona Basin, Spain, but the latter is broader-shelled, with the shoulder placed higher, *G. miliaria* is more slender and regularly cylindrical in shape, and the labial varix is thicker, especially abapically in *G. proxima*.
The presence of this species in the Pliocene Mediterranean and Iberian coast has not been confirmed in the recent literature (Chirli, 2002; Landau *et al*., 2006a; Silva *et al*., 2011). We have not included older references, which need to be confirmed. For further discussion see Silva *et al*. (2011) and Van Dingenen *et al*. (2017).
Brébion (1964, p. 503) recorded this species from Assemblage I localities (Renauleau, Thorigné, Sceaux d'Anjou, St-Clément-de-la-Place, St-Michel, Beaulieu), Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Le Girondor), and Assemblage IV (Gourbesville). In the distribution we have only included the Assemblage I-III records. The others will be confirmed in subsequent papers.

Distribution – Middle Miocene: Atlantic (Langhian), NW France (Glibert, 1952a). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al*., 2017). Present-day: Mediterranean and adjacent Atlantic (Gofas, 1987).

***Gibberula philippii* (Monterosato, 1878)**
Plate 3, figs 1-3

*1878	*Marginella philippi* [*sic*] Monterosato, p. 109. (*nom. nov. pro. Marginella minuta* Philippi, 1844 *non* Pfeiffer, 1840 = *Gibberula pfeifferi* Faber, 2004; *non Marginella minima* Gray, 1826).
1964	*Gibberula philippi* [*sic*] Monterosato, 1878 – Brébion, p. 534, pl. 13, figs 15-17.
2017	*Gibberula philippii* (Monterosato, 1878) – Van Dingenen *et al*., p. 37, figs 713-714 (*cum syn*.).

Material and dimensions – Maximum height 3.2 mm,

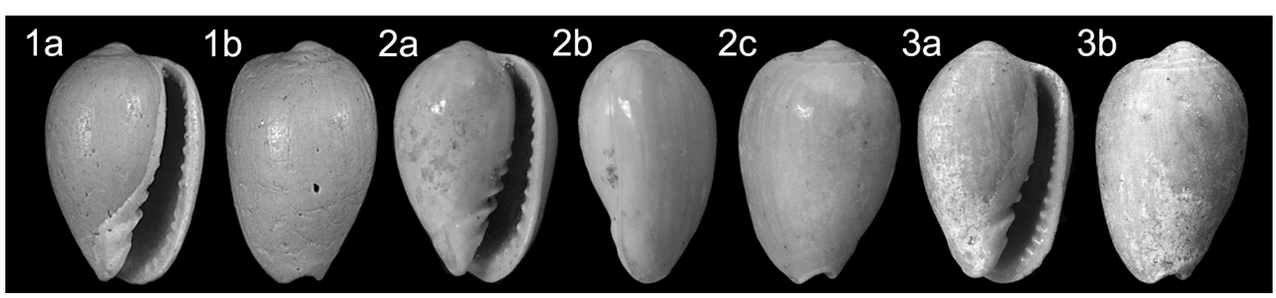


Plate 2. *Gibberula miliaria* (Linnaeus, 1758); 1. NHMW 2016/0103/0835, height 4.3 mm, width 2.7 mm; 2. NHMW 2016/0103/0836, height 4.1 mm, width 2.5 mm; 3. NHMW NHMW 2016/0103/0837, height 4.2 mm, width 2.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

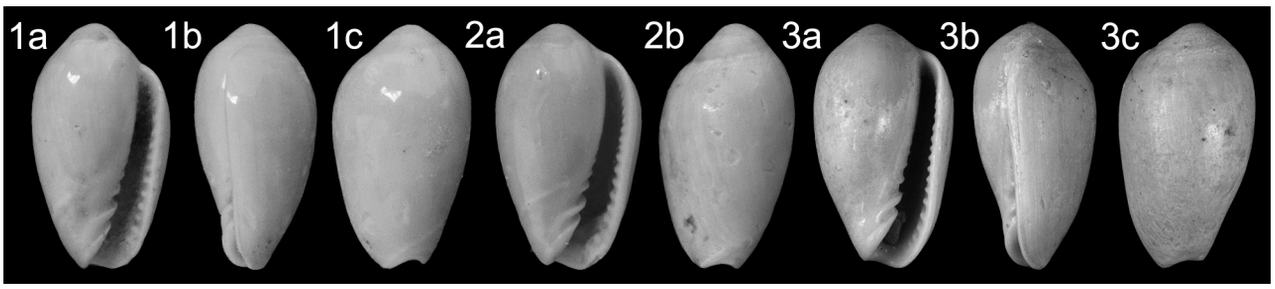


Plate 3. *Gibberula philippii* (Monterosato, 1878); 1. NHMW 2016/0103/0839, height 3.2 mm, width 1.8 mm; 2. NHMW 2016/0103/0840, height 3.1 mm, width 1.7 mm; 3. NHMW 2016/0103/1377, height 3.1 mm, width 1.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

width 1.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0839-0840 (2), NHMW 2016/0103/1377 (1), NHMW 2016/0103/0841 (24), RGM.1349129 (8), LC (9), FVD (9). **Sceaux-d'Anjou**: RGM.734982 (25), RGM.1352535 (1), LC (6).

Discussion –The fossil specimens from Assemblage I agree with the description and figures given by Gofas (1987) for the species, and unlike the specimens from Assemblage III, relatively strong denticulation is developed at the inner edge of the outer lip in all specimens. *Gibberula philippii* (Monterosato, 1878) is easily separated from *G. miliaria* (Linnaeus, 1758), with which it co-occurs in the Assemblage I deposits, by its smaller size, more slender shell shape, relatively high spire and low insertion of the outer lip.
Like *G. miliaria*, the presence of this species in the Pliocene Mediterranean and Iberian coast has not been confirmed in the recent literature (Chirli, 2002; Landau *et al*., 2006a; Silva *et al*., 2011). We have not included older references, which need to be confirmed.
Brébion (1964, p. 503) recorded this species from the middle Miocene Loire Basin (La Beurelière), Assemblage I localities (Thorigné, St-Clément-de-la-Place, St-Michel), Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Palluau), and Assemblage IV (Gourbesville). In the distribution we have only included the Assemblage I-III records. The others will be confirmed in subsequent papers.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al*., 2017). Present-day: Mediterranean and adjacent Atlantic (Gofas, 1987).

Superfamily Volutoidea Rafinesque, 1815
Family Volutidae Rafinesque, 1815
Subfamily Scaphellinae Gray, 1857
Genus *Euroscaphella* Van Dingenen, Ceulemans, & Landau, 2014

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

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

Note – Van Dingenen *et al*. (2014, p. 12) argued that the Old World scaphellids form a distinct group from the New World species, and erected the genus *Euroscaphella* Van Dingenen, Ceulemans, & Landau, 2014. *Euroscaphella* differs from *Scaphella* (*s.str.*) Swainson, 1832 and its subgenus *Clenchina* Pilsbry & Olsson, 1953 in not having axial sculpture on the early teleoconch whorls, and in having no siphonal fasciole and probably no colour pattern, and from the subgenus *Aurinia* H. Adams & A. Adams, 1853 by again not having axial sculpture or colour pattern and having well developed columellar folds. Although the number of columellar folds is similar in *Scaphella* and its subgenera to that in *Euroscaphella*, and in both they become more oblique abapically, there is a subtle difference in their shape. The folds in New World *Scaphella* species are highly asymmetrical; the anterior face is much less steep than the posterior face, giving the folds a ratcheted appearance. This is not so in *Euroscaphella*, in which the folds are elevated and symmetrically rounded.

Euroscaphella cf. *miocenica* (Fischer & Tournouër, 1879)

Plate 4, fig. 1

cf.*1879 *Voluta miocenica* Fischer & Tournouër, p. 50.
1964 *Scaphella miocenica* [*sic*] Fischer & Tournouër – Brébion, p. 515.
2014 *Euroscaphella* cf. *miocenica* (Fischer & Tournouër, 1879) – Van Dingenen *et al*., p. 14, pl. 1, figs 11-13 (*cum syn*.).

Material and dimensions – Maximum height 83.2 mm, width 33.4 mm. **St-Clément-de-la-Place**: RGM.794200 (1 complete adult), RGM.1349074 (2 apical fragments), RGM.1349077 (2 fragments), FVD (1 complete adult), LC (1 large fragment + 7 juveniles). **Sceaux-d'Anjou**: RGM.739222 (1 juvenile), RGM.1349065 (14 small fragments), RGM.1349066 (2 large fragments); RGM.1349067 (1 complete adult + 1 fragment), RGM.1349270 (2 fragments). **Renauleau**: FVD (3 juveniles, 3 apical fragments,

Plate 4. *Euroscaphella* cf. *miocenica* (Fischer & Tournouër, 1879); 1. RGM.794200, height 66.9 mm, width 26.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

6 large fragments), LC (10 fragments + 5 juveniles).

Discussion – Two well-preserved shells from Saint-Clément-de-la-Place and a third from Sceaux-d'Anjou, are the only complete adult scaphelline shells available from Assemblage I. The teleoconch is indistinguishable from that of *Euroscaphella miocenica*, characterised by its solid shell, relatively broad, inflated, strongly shouldered last whorl, which is moderately strongly constricted at the base, in contrast to *E. namnetensis* Van Dingenen, Ceulemans & Landau, 2014 from Assemblage III, in which it is hardly constricted. However, the Assemblage I shell differs from middle Miocene Langhian specimens of *E. miocenica* in being much smaller (66.9 mm height as opposed to about 100 mm in *E. miocenica*) and in having a smaller protoconch, with a diameter of only 5.4 mm as opposed to 7.7-7.9 in *E. miocenica*. However, this size difference must be interpreted with caution as protoconch size may vary in volutes.
Both *E. miocenica* and *E. namnetensis* have a well developed palatal callus, whereas all other *Euroscaphella* species have a thin outer lip without any internal callus. It is possible that *E. namnetensis* evolved from *E. miocenica*, as both share a relatively solid shell, the same number of columellar folds, a flattened protoconch and the development of a palatal callus. The specimens from Saint-Clément-de-la-Place shows the teleoconch features of *E. miocenica* and the protoconch size of *E. namnetensis*. These specimens could represent either a 'dwarf' *E. miocenica* or a transitional form between the two species. More adult material would be necessary in order to further determine this species.
Brébion (1964, p. 516) reported *E. miocenica* from several Assemblage I localities (St-Michel, Beaulieu, Contigné) and added other as '*formes douteuses*' (Sceaux-d'Anjou, St-Clément-de-la-Place, Thorigné, Renauleau).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964; Van Dingenen *et al*., 2014).

Family Cancellariidae Forbes & Hanley, 1851
Subfamily Cancellariinae Forbes & Hanley, 1851
Genus *Brocchinia* Jousseaume, 1887

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

1887 *Brocchinia* Jousseaume, p. 221.

***Brocchinia auriculoides* (Millet, 1854)**
Plate 5, figs 1-9

*1854 *Cancellaria Auriculoides* Millet, p. 160.
1865 *Cancellaria auriculoides* Millet, p. 586.
1964 *Narona* (*Brocchinia*) *mitraeformis* Brocchi, 1814 – Brébion (*partim*), p. 531, (*non Voluta mitraeformis* Brocchi, 1814, *non* Lamarck, 1811 = *Brocchinia depressiplicata* Sacco, 1894) (*non* Assemblage III records; pl. 13, figs 12, 13 = *Brocchinia pigeonblancensis* Van Dingenen, Ceulemans & Landau, 2017).

2006b *Brocchinia auriculoides* (Millet, 1854) – Landau *et al*., p. 83, pl. 8, figs 1, 2.

Material and dimensions – Maximum height 9.4 mm, width 4.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1267-1275 (9), 2016/0103/1276 (50+), RGM.1349172 (9), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0927 (50+), RGM.718129 (50+), RGM.734981 (9), RGM.1348915 (19), RGM.1349164 (2), RGM.1349179 (3), RGM.1349246 (43), RGM.1349260 (10), RGM. 1349276 (3), RGM.1352214 (50+), RGM.1352237 (4), RGM.1352427 (15), LC (30), FVD (50+).

Original description – '[Cancellaria] Auriculoides*, Millet. – Thorigné, Sceaux. – Coquille allongée, de la taille ou grosseur d'un grain d'orge, marquée de côles longitudinales et de très fines stries qui les traversent; portant deux dents ou plis, rarement trois, a la columelle. On rencontre des individus sans côtes, qui pourraient à la rigueur constituer une variété*' (Millet, 1854, p. 160).

Revised description – 'Cancellaria auriculoïdes*, Millet. Coq. petite, ovale, très-allongée, composée de 7 tours de spire, peu bombés et portant de grosses côtes verticales ou obliques, mais souvent nulles sur le dernier tour; tous sont trés-finement striés transversalement. Ouverture semi-lunaire, munie de deux petits plis columellaires. Longueur: 13-14 millimètres; diamètre: 15 millimètres. Th. Sc. Elle présent des individus de taille inférieure, sans côtes et qui ne constituent qu'une simple variété*' (Millet, 1865, p. 586).

Discussion – The plethora of *Brocchinia* Jousseaume, 1887 species recognised to be present in the European Neogene deposits were summarised by Van Dingenen *et al*. (2017, p. 40). As stressed by Millet (1854, p. 160; 1865, p. 586), the Assemblage I species *Brocchinia auriculoides* (Millet, 1854) is extremely variable; the series illustrated shows broader and more slender forms, specimens with no columellar folds, two or three folds, axial sculpture present throughout or weakening on later whorls, and the smaller form mentioned by Millet (1865, p. 586) without any axial sculpture (Pl. 5, figs 3, 4). Despite the great variability seen in the Assemblage I specimens, we consider the Assemblage III form a separate species, *B. pigeonblancensis* Van Dingenen, Ceulemens & Landau, 2017, which differs in being larger, but thinner shelled, with a higher spire and in having the axial ribs much broader and somewhat nodular mid-whorl. In most specimens of *B. pigeonblancensis* the axial ribs continue relatively strongly at least onto the first half of the last whorl, whereas in most specimens of *B. auriculoides* the axial ribs weaken much earlier on the second or third teleoconch whorl. The spiral sculpture is weak in both species, but even more so in *B. pigeonblancensis*. Both species have a paucispiral protoconch of 1.5-1.75 smooth whorls, with a large nucleus, suggesting non-planktotrophic development, and we note the shape and diameter of the protoconch is somewhat variable.
Cossmann (1899, p. 20) described *B. rissoiaeformis* from the Upper Pliocene-Pleistocene Assemblage IV locality of Gourbesville. The holotype is poorly preserved, but the specimen illustrated by Brébion (1964, p. 532, pl. 13,

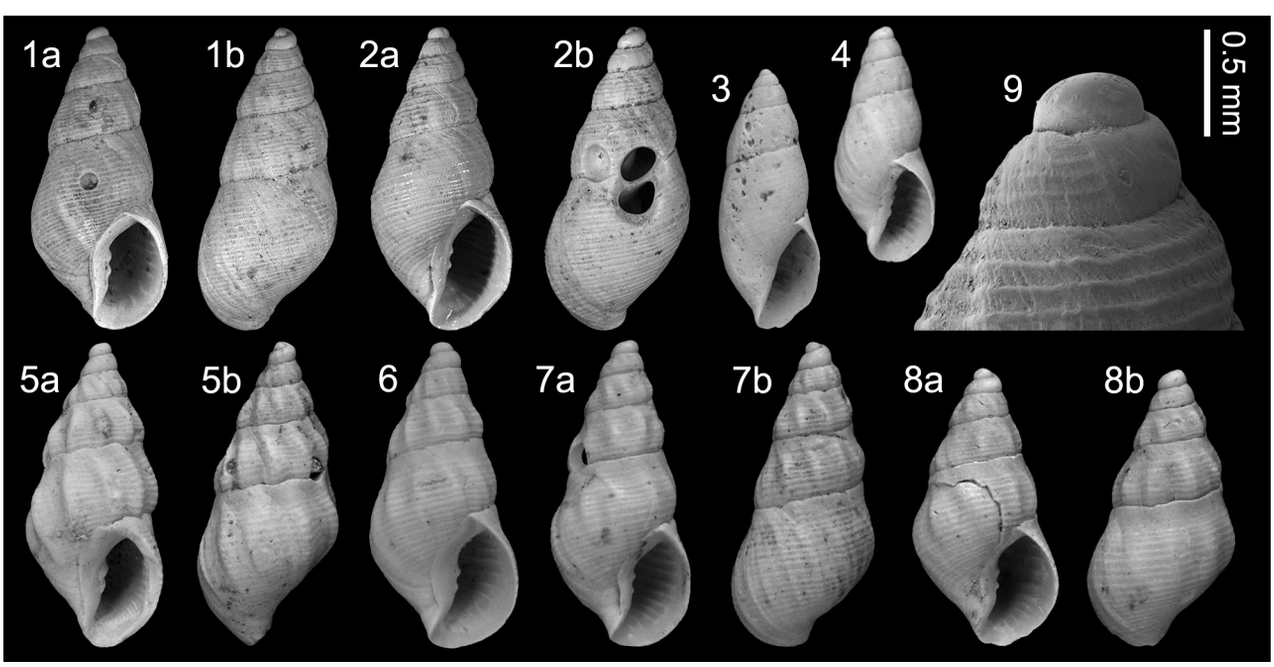


Plate 5. *Brocchinia auriculoides* (Millet, 1854); 1. NHMW 2016/0103/1267, height 9.1 mm, width 3.9 mm; 2. NHMW 2016/0103/1268, height 7.9 mm, width 3.6 mm; 3. NHMW 2016/0103/1269, height 6.9 mm, width 2.5 mm; 4. NHMW 2016/0103/1270, height 5.5 mm, width 2.1 mm; 5. NHMW 2016/0103/1271, height 9.2 mm, width 4.0 mm; 6. NHMW 2016/0103/1272, height 8.3 mm, width 3.5 mm; 7. NHMW 2016/0103/1273, height 8.2 mm, width 3.6 mm; 8. NHMW 2016/0103/1274, height 7.1 mm, width 3.5 mm; 9. NHMW 2016/0103/1275, height 5.3 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fig. 14) from the type locality shows a rather small (height 7 mm), squat species, with a protoconch composed of two whorls, about 12 spiral cords and no axial sculpture. For further discussion and comparison with other European congeners see Van Dingenen *et al*. (2017, p. 41).
Brébion (1964, p. 532) recorded *Narona* (*Brocchinia*) *mitraeformis* from numerous assemblages in northwestern France, but in view of the discussion above we consider only the Assemblage I (Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, St-Michel) records as *B. auriculoides*. We note, however, that we have not found this species at Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964; Landau *et al*., 2006b).

Genus *Contortia* Sacco, 1894

Type species (by original designation) – *Cancellaria contorta* de Basterot, 1825, Miocene, France.

1894 *Contortia* Sacco, p. 48.

***Contortia beraudiana* (Millet, 1854)**
Plate 6, fig. 1

*1854 *Cancellaria Beraudiana* Millet, p. 160.
1865 *Cancellaria Beraudiana* Millet – Millet, p. 586.
1964 *Cancellaria* (*Merica*) *beraudiana* Millet, 1854 – Brébion, p. 519, pl. 13, fig. 3.
1964 *Cancellaria* (*Merica*) *beraudiana* var. *couffoni* Brébion, p. 521, pl. 13, fig. 4 (*nomen nudum*).

Type material – Syntypes: Sceaux-d'Anjou; lost (*fide* Brébion, 1964, p. 520).

Material and dimensions – Maximum height 29.5 mm, width 21.0 mm (Brébion, 1964, p. 520). **St-Clément-de-la-Place**: NHMW 2016/0103/0923 (8 juveniles and fragments), RGM.1349144 (2 fragments), LC (3 adults + 20 juveniles). **Sceaux-d'Anjou**: NHMW 2016/0103/0925 (5), RGM.718131 (50+ juveniles), RGM.1349134 (11 fragments), RGM.1349234 (5 juveniles), RGM.1349289 (6 fragments), RGM.1352239 (3 juveniles). **Renauleau**: NHMW 2016/0103/1428 (1), LC (3 adults, 2 fragments + 15 juveniles), FVD (12 incomplete and fragments).

Original description – 'Beraudiana, *Millet. – Thorigné, Sceaux. – Cette espèce a quelques rapports avec le* C. evulsa*, Sow, mais elle est plus ventrue*' (Millet, 1854, p. 160).

Augmented description – 'Cancelleria Beraudiana, *Millet. Coq. assez grande, en ovale ventru et pointu au sommet, composée de 7 tours de spire arrondis, marqués de côtes verticales, croisées par de grosses stries, qui en passant sur chaque côte, y laissent une espèce de carène fortement prononcée. Le dernier tour, en outre, amplement dilaté, porte un bourrelet extérieur, sur lequel viennent aboutir les stries en question; l'ouverture, fortement élargie sur le bord droit, porte sur cette partie un rang de denticules qui en garnit toute l'étendue; le bord gauche renfoncé vers sa partie moyenne présente sur la columelle trois plis élevés, et en dehors de celle-ci une fente ombilicale seulement. Longueur: 25-27 millimètres; diamètre: 18-20 millimètres. Sceaux. Rare. Cette espèce a quelques rapports avec le* C. evulsa, *Sow.*' (Millet, 1865, p. 586).

Discussion – *Contortia beraudiana* (Millet, 1854) is large for the genus and has a very distinctive shell, with its strongly inflated last whorl and expanded outer lip that both become rapidly constricted towards the base. The protoconch is paucispiral, composed of just under 1.5 smooth whorls, with a large nucleus. Most specimens at hand are juveniles and subadults, but one large adult (Pl. 6, fig. 1) and various fragments of the outer lip show that in fully adult specimens there is a stromboid notch on the outer lip placed just below mid-aperture, surrounded by a semicircular expansion from the lip margin. *Contortia callosa* (Hörnes, 1854) from the middle Miocene Paratethys and eastern Proto-Mediterranean also has a large inflated shell, but has more numerous and wider ribs, is hardly constricted at the base, so that the last whorl is evenly convex, and it has a low dome-shaped protoconch of 2.5 whorls (Harzhauser & Landau, 2012,

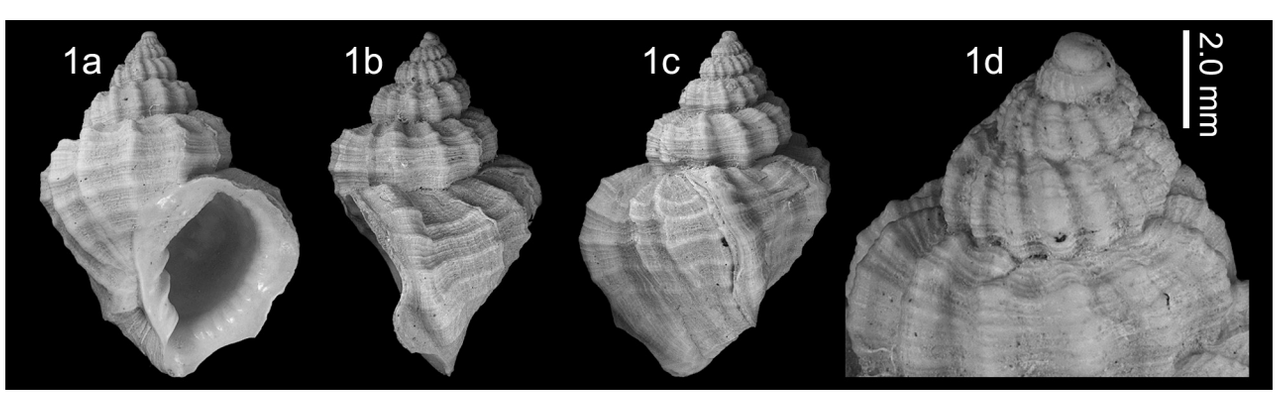


Plate 6. *Contortia beraudiana* (Millet, 1854); 1. NHMW 2016/0103/1428, height 25.1 mm, width 17.6 mm, 1d, detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

p. 21, fig. 3J). The Burdigalian shells from the Colli Torinesi in Italy, treated by Sacco (1894) as *Contortia callosa taurolaevior* and *C. c. tauroturrita*, differ strongly from the type in their sculpture. They lack the characteristic spiral cords and have broader and poorly defined axial ribs. In both forms the axial ribs are broader than in *C. beraudiana*.

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

***Contortia italica* (d'Ancona, 1872)**
Plate 7, figs 1-4

*1872	*Cancellaria italica* D'Ancona, p. 110 [230], pl. 12, figs 5a,b-6a,b.
1964	*Cancellaria* (*Merica*) *contorta* Basterot, 1825 – Brébion, p. 518.
1964	*Cancellaria* (*Merica*) *milleti* Brébion, p. 521, pl. 13, fig. 5 (*nomen nudum*).
2006b	*Contortia italica* (d'Ancona, 1872) – Landau *et al*., p. 65, pl. 1, figs 4-9 (*cum syn*.).
2008	*Contortia italica* (d'Ancona, 1872) – Brunetti *et al*., p. 58, figs 5A-H, 9B (*cum syn*.).
2008	*Contortia milleti* (Brébion, 1964, m. s.) – Brunetti *et al*., p. 60, figs 5I, L (*nomen nudum*).
2008	*Contortia strictoturrita* (Sacco, 1894) – Brunetti *et al*., p. 58, figs 5A-H, 9B (*cum syn*.).
2011	*Contortia italica* (d'Ancona, 1872) – Landau *et al*., p. 30, pl. 15, fig. 10.

Material and dimensions – Maximum height 18.5 mm, width 10.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0920-0921 (2), NHMW 2016/0103/0922 (2 + 10 juveniles), NHMW 2016/0103/0917-0918 (2), RGM.1349174 (11), LC (5 + 21 juveniles), FVD (8). **Sceaux-d'Anjou**: NHMW 2016/0103/0924 (5 juveniles), RGM.718132 (19 juveniles), RGM.739223 (23), RGM.1349162 (1 + 6 juveniles), RGM.1349135 (3), RGM.1349175 (1), RGM.1349233 (4 + 13 juveniles), RGM.1349240 (5), RGM.1349253 (2), RGM.1352203 (2), RGM.1352238 (3), RGM.1352552 (1), FVD (1). **Renauleau**: NHMW 2016/0103/0919 (1), LC (2 + 8 juveniles), FVD (1).

Discussion – The name *Cancellaria contorta* de Basterot, 1825 has been applied by numerous authors for medium-sized European *Contortia* species that are not conspecific (see Landau *et al*., 2006b; Brunetti *et al*., 2008; Harzhauser & Landau, 2012). *Contortia contorta* from the lower Miocene Burdigalian of the Aquitaine Basin of France have a multispiral dome-shaped protoconch of 2.5-3.0 whorls (Landau *et al*., 2006b, p. 66; Brunetti *et al*., 2008, fig. 7b). None of the *Contortia* specimens from Assemblage I have a multispiral protoconch. In the middle Miocene of the Loire Basin *C. ligeriana* (Glibert, 1952) differs in being smaller, squatter, with a wider apical angle and fewer, thicker axial ribs. Unfortunately, none of the specimens at hand have their protoconch preserved. Glibert (1952a, p. 366, pl. 11, fig. 11a) illustrated a second form from the Loire Basin, *C. contorta* forme *basteroti* Deshayes, 1860, which according to Peyrot (1928, p. 208) was just a juvenile of *C. contorta*, but according to Glibert was a dwarf race of *C. contorta*. We have not seen this form, but Peyrot said it was identical to *C. contorta*, for which he clearly described a multispiral protoconch.
Landau *et al*. (2006b, p. 66) stressed the importance of the protoconch type and recognised a single highly variable

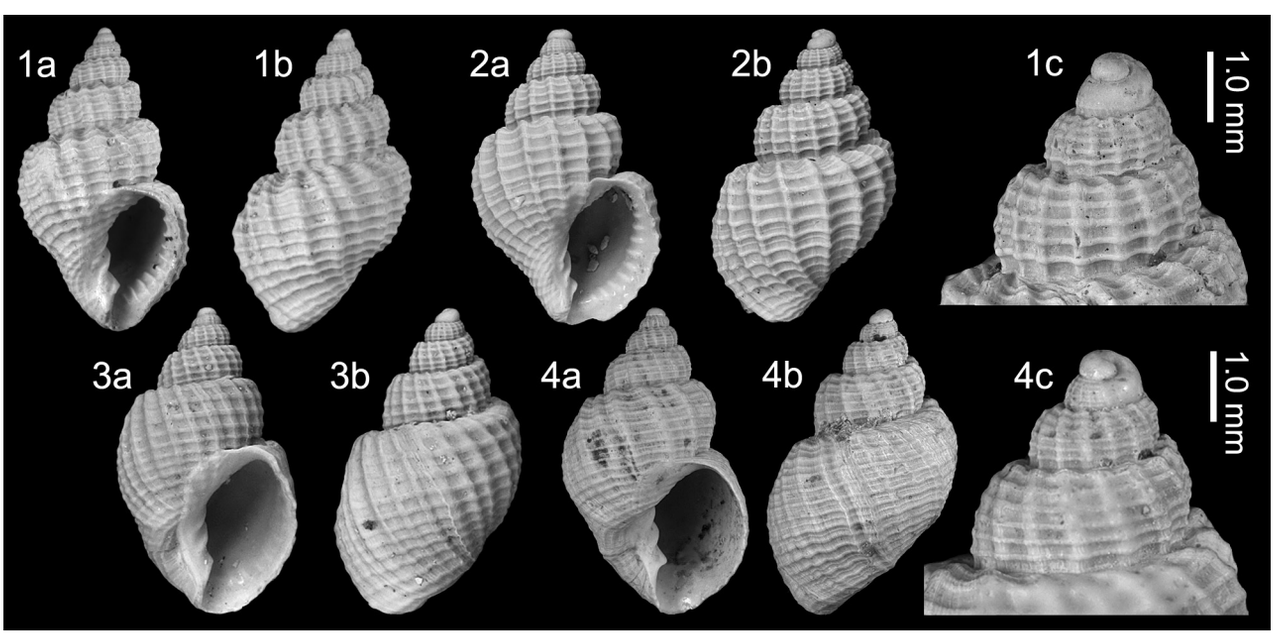


Plate 7. *Contortia italica* (d'Ancona, 1872); 1. NHMW 2016/0103/0917, height 14.1 mm, width 7.3 mm, 1c. detail of protoconch; 2. NHMW 2016/0103/0918, height 18.5 mm, width 10.0 mm. 3. NHMW 2016/0103/0920, height 12.9 mm, width 7.2 mm; 4. NHMW 2016/0103/0921, height 12.5 mm, width 6.8 mm, 4c. detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Pliocene species, *C. italica* (d'Ancona, 1872) (= *Cancellaria contorta* var. *altavillae* Libassi, 1859, p. 39, fig. 25; junior primary homonym of *C. altavillae* Aradas, 1846; not *C. labrosa* var. *altavillae* Libassi, 1859; = *Admetula malacitana* Vera-Peláez & Muñiz-Solís, 1995, p. 297, pl. 1, figs 1-13, pl. 2, figs 1-8).

Brunetti *et al.* (2008) separated the Mediterranean Pliocene forms into two species, *C. italica* and *C. strictoturrita* (Sacco, 1894), the latter differing from *C. italica* in being larger and thicker-shelled, with a narrower apical angle, with fewer axial ribs, more numerous spiral cords, a less nearly circular aperture and minor differences in the abapical columellar fold. The authors went on to point out a difference in protoconch size, which judging from their figures is about 20% in width, although only one protoconch of each form was illustrated.

Brunetti *et al*. (2008) placed *Admetula malacitana* Vera-Peláez & Muñiz-Solís, 1995 from the upper Pliocene Estepona Basin, Spain, which was synonymised with *C. italica* by Landau *et al*. (2006b), in the synonymy of *C. strictoturrita*. The Spanish specimens have an apical angle similar to that of *C. italica,* whereas those from the deeper Velerín carretera deposits are thin-shelled and those from the Velerín conglomerates are thicker shelled. Moreover, the protoconch of the Estepona shell is identical to that of *C. italica*. Brunetti *et al*. (2008, p. 60, figs 5I, L) illustrated a shell from Assemblage I and considered it a further species differing from *C. italica* in having a larger protoconch and denser and more regular spiral teleoconch sculpture.

Landau *et al*. (2013, p. 228) noted with scepticism the importance given by Brunetti *et al*. (2008) to the size of a paucispiral protoconch and gave some examples of reported intraspecific size differences in the literature. We have not come across any assemblage in which there are so many non-planktotrophic species, and what we note is that both the size and shape of a non-planktotrophic protoconch can be highly variable. Moreover, the series illustrated here shows quite considerable differences in teleoconch shape and sculpture. There is hardly a single constant character. The spire can be strongly scalate (Pl. 7, fig. 1), or less so (Pl. 7, fig. 4), the aperture denticulate within (Pl. 7, figs 1, 2), smooth or almost so (Pl. 7, figs 3, 4), the base bearing a strong siphonal fasciole (Pl. 7, figs 3, 4), or weak fasciole (Pl. 7, figs 1, 2), the sculpture can be regularly cancellate, without secondary sculpture (Pl. 7, fig. 2), similar to that seen in the specimen illustrated by Brunetti *et al*. (2008), but also rather irregular with secondaries intercalated in almost all the interspaces (Pl. 7, fig. 4), the number of ribs is variable, and the columellar callus can form a thickened rim (Pl. 7, fig. 3), or be hardly developed (Pl. 7, fig. 2). Intracapsular development, as is implied by the protoconch type, can lead to small variations in populations. We prefer to consider all these upper Miocene and Pliocene *Contortia* specimens with a paucispiral protoconch a single species.

Brébion (1964, p. 525) reported this species from numerous Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, Beaulieu, Renauleau), to which we add St-Clément-de-la-Place.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: western Mediterranean, Guadalquivir Basin, S. Spain (Landau *et al*., 2011); central Mediterranean, Italy (Chirli, 2002; Brunetti *et al*., 2008). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (Vera-Peláez & Muñiz-Solís, 1995; Landau *et al*., 2006b); central Mediterranean, Italy (Cavallo & Repetto, 1992; D'Ancona, 1872; Sacco, 1894; Glibert, 1960; Brunetti *et al*., 2008).

Genus *Scalptia* Jousseaume, 1887

Type species (by original designation) – *Cancellaria obliquata* Lamarck, 1822, present-day, Pacific.

1887 *Scalptia* Jousseaume, p. 213.

***Scalptia aspera* (Millet, 1865)**
Plate 8, figs 1-2

1856 *Cancellaria Acutangula* Faujas – Millet, p. 160 [*non Gulia acutangula* (Faujas, 1817)].
*1865 *Cancellaria aspera* Millet, p. 586.
1964 *Trigonostoma* (*Ventrilia*) *scrobiculata* Hörnes, 1856 [*sic*] – Brébion, p. 525, pl. 13, figs 6, 7 [*non Scalptia scrobiculata* (Hörnes, 1854)].

Type material – Syntypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 526).

Material and dimensions – Maximum height 18.5 mm, width 10.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0913-0914 (2), NHMW 2016/0103/0915 (15), RGM.1349136 (1), RGM.1349173 (3 + 6 juveniles), LC (6 + 20 juveniles), FVD (22). **Sceaux-d'Anjou**: NHMW 2016/0103/0916 (6), RGM.178130 (8 + 15 juveniles), RGM.1349070 (1 + 5 fragments), RGM.1349133 (15 fragments), RGM.1349169 (2 fragments), RGM.1349245 (8 fragments), RGM.1352220 (5 juveniles), LC (1), FVD (3). **Renauleau**: NHMW 2016/0103/1827 (1), LC (1 + 1 juvenile), FVD (1). **Beugnon**: RGM.1349120 (1 fragment).

Original description – 'Cancellaria aspera. *Millet. Coq. de moyenne taille, en ovale pointu et perforée à sa base, est composée de 7 tours de spire. Chaque tour, muni de côtes verticales angulaires et recouvrantes, et coupe transversalement par des filets plus rapprochés que ne le sont les côtes, presente à son sommet une rampe scalariforme, angulaire, dont les marches sont indiquées par le prolongement des côtes et qui forme sur son bord externe une crête à dents aiguës. Ouverture ovale, biangulaire, avec trois plis obliques sur la columelle. Longueur: 18-20 millimètres; diamètre: 10-11 millimètres. Th., Sc, Saint-Clément, Ren. – Ne pas confondra cette espèce avec l'*acutangula, *Fauj. qui ne lui ressemble qu'imparfaitement*' (Millet, 1865, p. 586).

Discussion – Millet's (1865, p. 586) original description

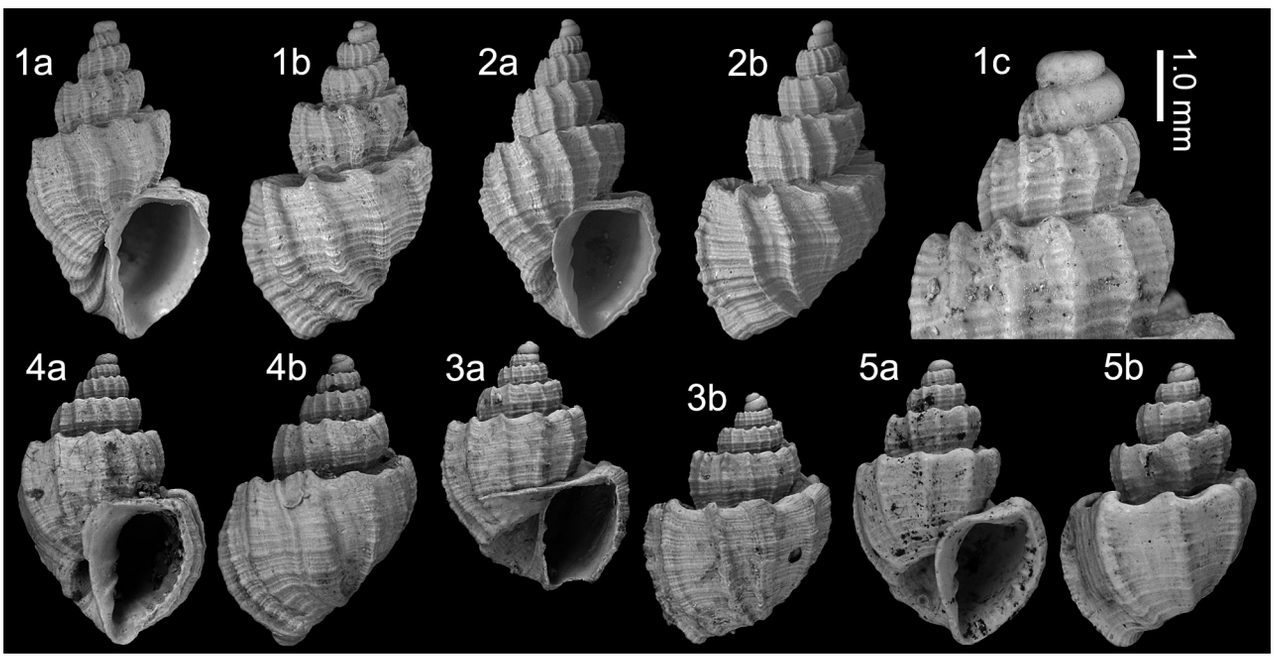


Plate 8. *Scalptia* and *Trigonostoma* species: *Scalptia aspera* (Millet, 1865); 1. NHMW 2016/0103/0913, height 14.1 mm, width 7.3 mm, 1c. detail of protoconch; 2. NHMW 2016/0103/0914, height 18.5 mm, width 10.0 mm; *Trigonostoma bellardii* De Stefani & Pantanelli, 1879; 3. NHMW 2016/0103/1870, height 15.0 mm, width 11.2 mm. *Trigonostoma benoisti* Peyrot, 1928; 4. NHMW 2016/0103/1868, height 17.8 mm, width 9.8 mm. 5. NHMW 2016/0103/1869, height 13.0 mm, width 8.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

is fairly accurate. We add that the protoconch is paucispiral, composed of two smooth whorls, with a medium sized nucleus and that the species is relatively thin-shelled compared with many of its congeners. Brébion (1964, p. 525) considered these French specimens conspecific with *Scalptia scrobiculata* (Hörnes, 1854) from the middle Miocene Paratethys, but that species is thicker-shelled, has a deeper sutural canal, coarser spiral sculpture, and has a multispiral protoconch (Harzhauser & Landau, 2012). The inside of the outer lip is smooth in most specimens, although some of the largest specimens have weak lirations within. *Scalptia spinosa* (Grateloup, 1827) from the lower Miocene Aquitanian of France differs in being solid-shelled, squatter, and having short spines developed at the sculptural intersections at the shoulder. Glibert (1952a, pl. 12, fig. 7) illustrated a specimen identified as *S. scrobiculata*. It is poorly preserved and incomplete, and whilst representing a *Scalptia* species, further identification is difficult. It seems to have stronger labial denticles than *S. aspera* (Millet, 1865), but this a highly intraspecifically variable character in cancellariids. Brébion (1964) also brought into synonymy *Trigonostoma benoisti* Peyrot, 1928 from the middle Miocene of France. We have not seen this species from its type locality in the Aquitaine basin, however, it seems thicker shelled than *S. aspera*, squatter, with an even wider subsutural platform, wider umbilicus and fewer axial ribs that form short spines at the shoulder, and a strongly lirate outer lip. A few specimens from Assemblage I are ascribed to that species (see below). Typical *S. aspera* is easy to separate, although some specimens could be considered intermediate. We provisionally prefer to separate the two forms, although Brébion might eventually be proved correct in synonymising them. *Trigonostoma benoisti* is extremely similar, and herein considered conspecific, with the shell from Assemblage III illustrated by Van Dingenen *et al.* (2017, pl. 4, fig. 6) as *Trigonostoma* sp. (see below).
Brébion (1964, p. 526) recorded *Scalptia aspera* from the Assemblage I localities of Renauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, Beaulieu and St-Michel. We have excluded his record for the Assemblage III locality of Le Pigeon Blanc, which is probably the species discussed above as *T. benoisti*.

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

Genus *Trigonostoma* de Blainville, 1827

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

1827 *Trigonostoma* de Blainville, p. 652.

***Trigonostoma bellardii* De Stefani & Pantanelli, 1879**
Plate 8, fig. 3

*1879 *Trigonostoma Bellardii* De Stefani & Pantanelli, p. 116.

2006b *Trigonostoma* (*Trigonostoma*) *bellardii* De Stefani & Pantanelli, 1879 – Landau *et al*., p. 67, pl. 2, figs 7-8 (*cum syn*.).
2011 *Trigonostoma bellardii* De Stefani & Pantanelli, 1879 – Landau *et al*., p. 30, pl. 15, fig. 11.
2011 *Trigonostoma bellardii* De Stefani & Pantanelli, 1879 – Brunetti *et al*., p. 114, figs 16F-L (*cum syn*.).

Material and dimensions – Height 15.0 mm, width 11.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1870 (1 incomplete juvenile).

Discussion – A single incomplete juvenile shell from St-Clément-de-la-Place represents this species, characterised by its dome-shaped multispiral protoconch, broad sutural platform and umbilicus. *Trigonostoma bellardii* De Stefani & Pantanelli, 1879 was fully discussed by Landau *et al*. (2006b, p. 67) and Brunetti *et al*. (2011, p. 115).

Distribution – Lower-middle Miocene: North Sea Basin, Belgium (Glibert, 1952b). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011); central Mediterranean, Italy (Sacco, 1894; Chirli, 2002; Brunetti *et al*., 2011). Upper Pliocene: North Sea Basin, Red Crag, England (Wood, 1874; Harmer, 1916), Oorderen Sands, Belgium (Nyst, 1878, 1881; Marquet, 1997); western Mediterranean, Estepona Basin, Spain (Landau *et al*., 2006b); central Mediterranean, Italy (Sacco, 1894; Caprotti & Vescovi, 1973; Malatesta, 1974; Cavallo & Repetto, 1992; Brunetti *et al*., 2011).

***Trigonostoma benoisti* Peyrot, 1928**
Plate 8, figs 4, 5

*1928 *Trigonostoma Benoisti* Peyrot, p. 245, pl. 14, fig. 31.
2017 *Trigonostoma* sp. – Van Dingenen *et al*., p. 42, pl. 4, fig. 6.

Material and dimensions – Height 13.0 mm, width 8.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1868 (1), NHMW 2016/0103/1869 (1), LC (1).

Discussion – Several specimens from St-Clément-de-la-Place Assemblage I are ascribed to *Trigonostoma benoisti* Peyrot, 1928, as is the single specimen illustrated in Van Dingenen *et al*. (2017, pl. 4, fig. 6) as *Trigonostoma* sp. from the lower Pliocene Assemblage III locality of Le Pigeon Blanc. That species was originally described from the middle Miocene Serravallian of the Aquitaine Basin of France. The only differences are that in the Aquitaine material the ribs form short spines at the shoulder not seen in our somewhat abraded material from northwestern France and the protoconch consists of just over two whorls, whereas Peyrot described the protoconch as having three smooth whorls. We have not seen specimens from the Aquitaine Basin and cannot verify Peyrot's description. The only species it can be confused with in the Mio-Pliocene of NW France is *Scalptia aspera* (Millet, 1865), which is compared above. *Trigonostoma parvotriangula* Sacco, 1894 from the Pliocene Mediterranean has similar axial sculpture composed of broad elevated ribs that form tubercles at the shoulder, but that species has a broader shell shape and a much wider umbilicus, which bears sculpture within.

Distribution – Middle Miocene: Atlantic (Serravallian), Aquitaine Basin, France (Peyrot, 1928). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al*., 2017).

Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815
Genus *Euthria* Gray, 1850

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

1850 *Euthria* Gray, p. 67

For generic synonymy see Van Dingenen *et al*. (2017, p. 24).

***Euthria presselierensis* nov. sp.**
Plate 9, figs 1, 2

1964 *Buccinulum* (*Euthria*) *costatum* var. *couffoni* Brébion, p. 424, pl. 10, figs 20, 21 (*nomen nudum*).

Type material – Holotype RGM.718090, height 21.9 mm, width 11.5 mm, **Sceaux-d'Anjou**. Paratype 1 NHMW 2016/0103/1315, height 12.7 mm, width 8.2 mm. **St-Clément-de-la-Place**.

Other material – Maximum height 45.0 mm, width 25.0 mm (*fide* Brébion, 1964, p. 424). **Sceaux d'Anjou**: RGM.1349098 (19 juveniles), RGM.1352223 (3 juveniles). **St-Clément-de-la-Place**: LC (2).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Euthria* species of small size, paucispiral protoconch, depressed coeloconoid spire, strongly globose last whorl, whorls with broad subsutural ramp, nine broad axial ribs below shoulder, weakening abapically, represented by small spinous tubercles at shoulder on

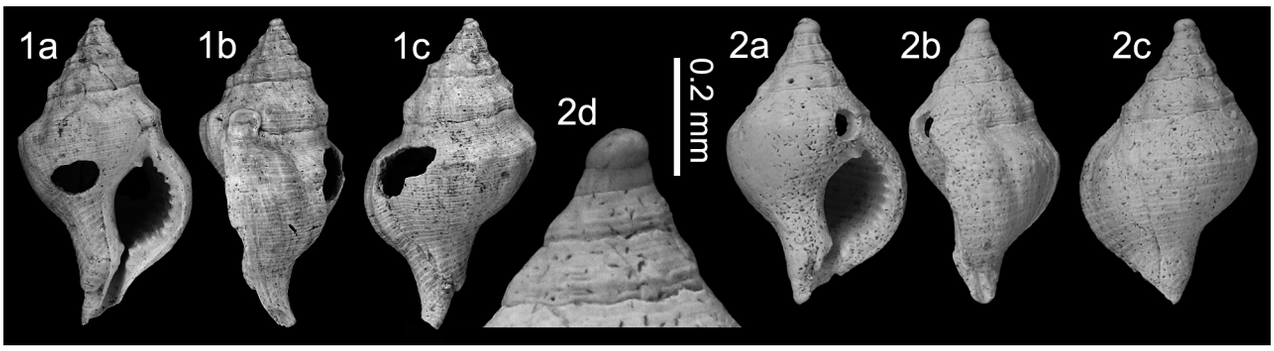


Plate 9. *Euthria presselierensis* nov. sp.; 1. **Holotype** RGM.718090, height 21.9 mm, width 11.5 mm; 2. **Paratype 1** NHMW 2016/0103/1315, height 12.7 mm, width 8.2 mm, 2d, detail of protoconch. La Presselière, Sceaux-d'Anjou. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

last whorl, weak spiral sculpture, aperture ovate, lirate within, moderately long siphonal canal.

Description – Shell small, globose, with depressed coeloconoid spire. Protoconch paucispiral, composed of 1.5 bulbous whorls, with large nucleus. Teleoconch of four depressed shouldered whorls, with broad, slightly concave subsutural ramp, shoulder placed about one-quarter shell height, periphery at abapical suture. Whorls separated by shallow suture. Sculpture of nine low, broad, rounded ribs developed only below shoulder, slightly spinous at shoulder, weakening abapically, subobsolete on last whorl. Spiral sculpture of narrow, low, close-set spiral cords of alternate strength developed over entire whorl. Last whorl weakly angled at about three-quarters whorl height, convex below, strongly constricted at base. Axial sculpture subobsolete, marked by weak spinous tubercles at shoulder. Aperture mid-size ovate; outer lip thickened by broad labial varix, densely lirate within, the lirae extending almost from lip edge to deep within aperture; anal sinus reduced to narrow groove; siphonal canal moderately long, open, narrow, straight, bent adaxially. Columella evenly excavated over entire length. Columellar callus thickened, forming narrow rim, with prominent parietal tooth and small tubercles abapically bordering siphonal canal.

Discussion – Two adult specimens are at hand, one from Sceaux-d'Anjou, one from Le Grand Chauvereau that fit the description and illustrations given by Brébion (1964, p. 424, pl. 10, figs 20, 21) for *Buccinulum* (*Euthria*) *costatum* var. *couffoni* (*nomen nudum*). That species is characterised by its small globose shell, with a low coeloconid spire and ribs that are only developed on the lower quarter of each whorl, below a broad, weakly concave subsutural ramp. The last whorl is strongly globose, the ribs represented by subobsolete tubercles at the shoulder. The entire surface is weakly sculptured by narrow cords of alternating strength. The outer lip bears close-set lirae that extend deep within the aperture and the evenly excavated columella bears a prominent parietal tooth and a tubercle at the edge of the siphonal canal. The protoconch is typical of that suggesting intracapsular development: composed of 1.5 bulbous whorls with a large nucleus. Brébion (1964) likened this species, and described it as what we would now consider subspecies of *E. costata* Bellardi, 1873, from the middle Miocene of Italy. They both have axial ribs that only develop on the abapical half of the whorl, but *E. costata* has a less depressed spire, which is not cyrtoconoid, and is less constricted at the base. We have not found a more recent illustration of Bellardi's species.
Brébion (1964) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and St-Michel, but it is extremely uncommon.

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

Euthria recurvata **(Millet, 1865)**
Plate 10, figs 1-4

1854	*Fusus Recurvatus* Millet, p. 162 (*nomen nudum*).
*1865	*Fusus recurvatus* Millet, p. 590.
1964	*Buccinulum* (*Euthria*) *recurvatum* Millet, 1854 [*sic*] – Brébion, p. 421, pl. 10, figs 17-18.

Type material – Syntypes: Thorigné and Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 422).

Material and dimensions – Maximum height 19.7 mm, width 8.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0803-0806 (5), NHMW 2016/0103/0807 (12), LC (20), FVD (14). **Sceaux-d'Anjou**: NHMW 2016/0103/0808 (3), RGM.718095 (7 + 50+ juveniles), RGM.1349061 (2 + 1 fragment), RGM.1349068 (2), RGM.1349268 (1 + 3 juveniles), RGM.1352235 (2 + 4 juveniles), RGM.1352531 (3 + 41 juveniles and fragments). **Renauleau**: NHMW 2016/0103/1415 (7), LC (7 adults + 13 juveniles), FVD (11).

Original description – 'Fusus recurvatus, *Millet. Coq. de moyenne longueur, aiguë au sommet, composée de huit à neuf tours de spire, peu bombés, séparés par une suture peu profonde et couverts de petites côtes verticales,*

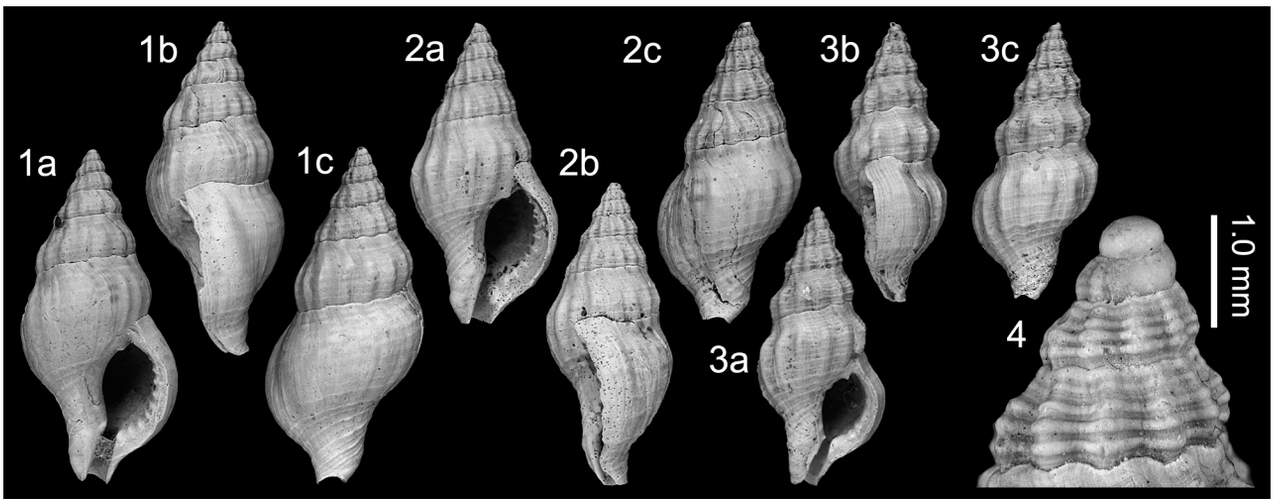


Plate 10. *Euthria recurvata* (Millet, 1865); 1. NHMW 2016/0103/0803, height 22.4 mm, width 9.7 mm; 2. NHMW 2016/0103/0804, height 18.5 mm, width 8.9 mm; 3. NHMW 2016/0103/0805, height 15.6 mm, width 6.9 mm; 4. NHMW 2016/0103/0806 (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

peu saillantes et très-rapprochées les unes des autres. Le dernier tour, presque lisse, présente une ouverture ovale, terminée par un canal court, ouvert, oblique et qui se relève en dessus; bord columellaire garni d'un rang de dents peu saillantes; bord droit bordé intérieurement d'un rang de dents bien prononcées, et en dehors d'un fort bourrelet arqué. Longueur: 28-30 millimètres; diamètre: 12-13 millimètres. Th., Sc. On rencontre des individus d'un tiers environ plus grands et plus forts que ceux du type de l'espèce; appartiennent-ils bien au F. recurvatus?' (Millet, 1865, p. 590).

Discussion – All members of the genus *Euthria* Gray, 1850 have paucispiral protoconchs, suggestive of non-planktotrophic development. Direct or lecithotrophic development favours high levels of speciation and endemism. Brunetti & Della Bella (2016) recently reviewed the representatives of the genus in the Italian Pliocene, and distinguished four separate species within what would previously have been considered the *E. cornea* (Linnaeus, 1758) species group. *Euthria recurvata* (Millet, 1865) belongs to what we informally call the *E. adunca* (Bronn, 1831) species group which differs in having axial sculpture on late teleoconch whorls. As with many Assemblage I species, it is small for the genus. The original description is accurate and highlights the variation is shell sculpture, in which the most gerontic specimens loose the axial ribs on the second half of the last whorl (Pl. 10, fig. 1). The protoconch consists of about 1.5 smooth whorls and is typical for the genus.
A similar species, *E. palumbina* Van Dingenen, Ceulemans & Landau, 2017 occurs in the lower Pliocene Assemblage III deposits of NW France. Apart from being larger than *E. recurvata* it differs in having fewer, broader axial ribs that weaken earlier, on the second half of the penultimate whorl. *Euthria adunca* (Bronn, 1831) from the Pliocene Mediterranean is larger still than *E. palumbina*, with even broader axial ribs, more angular whorls and a longer siphonal canal then either of species compared. *Euthria submarginata* (d'Orbigny, 1852) from the middle Miocene of the Loire Basin is also small, but squatter than *E. recurvata*, and has stronger and less numerous spiral cords that overrun the ribs forming elongated tubercles. *Euthria turonensis* Peyrot, 1938 described from the middle Miocene Loire Basin of France, but also recorded from the lower Pliocene Assemblage III of NW France (Van Dingenen *et al*., 2017, p. 26), differs from *E. recurvata* in having weakly, but regularly convex rather than subangular whorls, it lacks a well-defined subsutural ramp, the spiral cords are stronger, and the denticles placed within the outer lip are more numerous and extend into the aperture as lirae rather than being restricted to the inner edge of the bevelled outer lip.
Brébion (1964, p. 423) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place).

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

Family Colubrariidae Dall, 1904
Genus *Metula* H. Adams & A. Adams, 1853

Type species [by subsequent designation; Kobelt, 1876 (Rehder, 1943)] – *Buccinum clathratum* A. Adams & Reeve, 1850 (= *Metula amosi* Vanatta, 1913), present-day, Panamic Pacific.

1853 *Metula* H. Adams & A. Adams, p. 84.
1901 *Acamptochetus* Cossmann, p. 123. Type species (by original designation): *Murex mitraeformis* Brocchi, 1814, Pliocene, Italy.

1917 *Antimitra* Iredale, p. 329. Type species (by original designation): *Pleurotoma aegrota* Reeve, 1845, present-day, Philippines.
1943 *Antemetula* Rehder, p. 199. Type species (by original designation): *Buccinum metula* Hinds, 1844, present-day, Panamic Pacific.
1971 *Colubrarina* Kuroda & Habe in Kuroda, Habe & Oyama, p. 173. Type species (by original designation): *Antemetula* (*Colubrarina*) *metulina* Kuroda & Habe in Kuroda, Habe & Oyama, 1971, present-day, northern West Pacific.
1972 *Floritula* Olsson & Bayer, p. 921. Type species (by monotypy): *Metula roberti* Olsson, 1967, Pliocene, Florida.

***Metula tenuistriata* (Millet, 1865)**
Plate 11, figs 1-3

1854 *Buccinum Tenuistriatum* Millet, p. 165 (*nomen nudum*).
*1865 *Buccinum tenuistriatum* Millet, p. 596.
1964 *Acamptochetus tenuistriatus* Millet, 1854 [*sic*] – Brébion, p. 426, pl. 10, fig. 23.

Type material – Syntypes: Thorigné and Sceaux-d'Anjou, France; lost (*fide* Brébion, 1964, p. 427).

Material and dimensions – Maximum height 9.5 mm, width 3.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0899 (10), LC (3), FVD (6). **Sceaux-d'Anjou**: NHMW 2016/0103/0900 (1), NHMW 2016/0103/0901 (33), NHMW 2016/0103/1866-1867 (2), RGM.1348755 (2), RGM.718108 (50+), RGM.1349119 (10), RGM.1349151 (2), RGM.1349156 (2), RGM.1349183 (12 + 8 juveniles), RGM.1352548 (1), LC (4), FVD (17). **Renauleau**: NHMW 2016/0103/1430 (30), RGM.1348993 (5), LC (50+), FVD (41).

Original description – 'Buccinum tenuistriatum*, Millet. Coq. petite, ou de moyenne longueur, composée de 9 tours de spire, à peine bombés, couverts de stries qu'on ne peut voir qu'à l'aide d'une forte loupe; le dernier tour, qui à lui seul fait la moitié de la longueur de la coquille, présente sur le bord droit extérieur de l'ouverture un petit bourrelet qui se prolonge jusqu'à la partie supérieure du canal, qui est court et largement ouvert. L'ouverture, qui est allongée, présente quelques denticules sur la partie interne du bord droit. Longueur: 10 millimètres; diamètre: 3 millimètres. Sc., Th.*' (Millet, 1865, p. 596).

Discussion – *Metula tenuistriata* (Millet, 1865) is characterised by its slender fusiform shape, relatively tall, conical spire, weakly convex whorls separated by a superficial suture and fine spiral sculpture composed of crowded narrow low cords separated by shallow grooves. The spiral sculpture is somewhat more accentuated below the suture on the spire and over the base. The aperture is ovately elongate, the outer lip is flared abapically and bordered by a moderate lip callus, the columella callus is thickened, but narrow and the siphonal canal is relatively short for the genus, truncated, notched at the tip. Contrary to what Brébion reported (1964, p. 427) the protoconch is multispiral, composed of about three smooth whorls with a small nucleus (Pl. 11, fig. 1c). As seen in the series figured, there is little intraspecific variation; the last whorl is relatively taller in some specimens and the base more constricted, but otherwise they are similar in shape and sculpture.
The genus *Metula* is poorly represented in the European Neogene, and like most species found in the Assemblage I deposits, *M. tenuistriata* is much smaller than usual for the genus. *Metula mitraeformis* (Brocchi, 1814) from the Pliocene Mediterranean is much larger, with a longer siphonal canal and a paucispiral protoconch of 1.5 whorls. *Metula recta* (Sacco, 1904) from the lower to middle Miocene of Italy is also larger than *M. tenuistriata*, with a relatively shorter last whorl and aperture and more convex whorls than either of the other two species. *Metula submitraeformis* (D'Orbigny, 1852), widespread in the lower-middle Miocene North Sea Basin, eastern Atlantic, Paratethys and Mediterranean is large, like *M. mitraeformis*, but differs from that species in having a tall multispiral protoconch and finely reticulated early teleoconch whorls (see Landau *et al*., 2013, p. 167, pl. 53, fig. 17, pl. 79, fig. 11). *Metula reticulata* (Bellardi & Michelotti, 1840) from the lower to middle Miocene of the Turin Hills, Italy differs from all its European congeners in

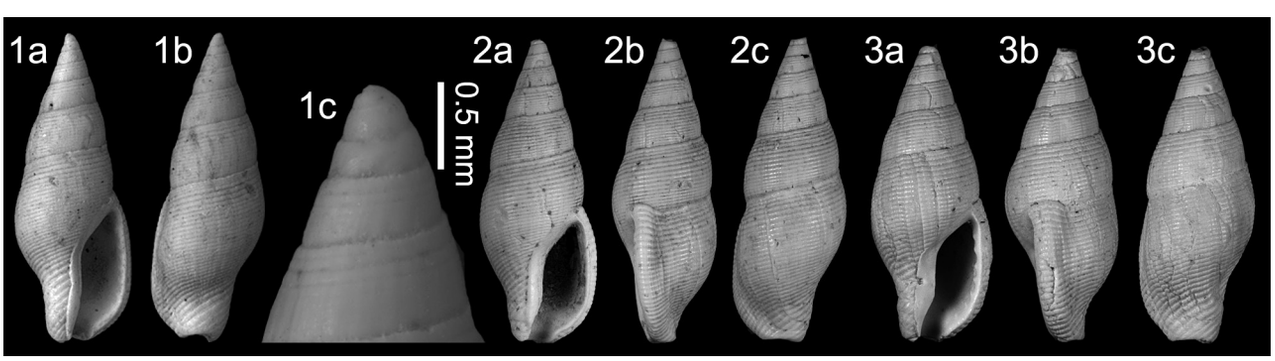


Plate 11. *Metula tenuistriata* (Millet, 1865); 1. NHMW 2016/0103/0899, height 7.4 mm, width 2.8 mm, 1c. detail of protoconch; 2. NHMW 2016/0103/1866, height 9.5 mm, width 3.7 mm; 3. NHMW 2016/0103/1867, height 7.3 mm, width 3.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

having finely reticulated surface sculpture on all teleoconch whorls, as the name would suggest (see Brunetti & Della Bella, 2016, fig. 15H, I). There are no other European taxa with which this shell can be confused.
Brébion (1964, p. 427) recorded this species from the upper Miocene Tortonian Assemblage I localities of Renauleau, Sceaux-d'Anjou and Thorigné, to which we add St-Clément-de-la-Place.

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

Family Columbellidae Swainson, 1840
Subfamily Columbellinae Swainson, 1840
Genus *Columbella* Lamarck, 1799

Type species (by monotypy) – *Voluta mercatoria* Linnaeus, 1758, present-day, Caribbean.

1799 *Columbella* Lamarck, p. 70.
1810 *Columbus* de Montfort, p. 591. Type species (by original designation): *Voluta mercatoria* Linnaeus, 1758, present-day, Mediterranean. Incorrect subsequent spelling or unjustified emendation of *Columbella* Lamarck, 1799. Junior homonym of *Columbus* Linnaeus, 1758 [Aves].
1815 *Peristera* Rafinesque, p. 145. Substitute name for *Columbella* Lamarck, 1799.
1816 *Colombella* Cuvier, p. 433. Incorrect subsequent spelling.

Note – The genus *Columbella* Lamarck, 1799 has been used rather indiscriminately in the fossil literature for inflated columbellids, however, true *Columbella* species can be recognised by having a narrow, elongated aperture, the outer lip is thickened internally in the midsection and there are two rows of columellar denticles, one placed at the columellar edge, the other, usually coarser and with fewer denticles, placed deep within the columella (K. Monsecour personal communication BL, 2019).

***Columbella globosa* Millet, 1865**
Plate 12, figs 1-3

1854 *Columbella Globosa* Millet, p. 164 (*nomen nudum*).
*1865 *Columbella globosa* Millet, p. 598.
1865 *Columbella picturata* Millet, p. 598.
1964 *Pterygia* (*Alia*) *globosa* Millet, 1854 [*sic*] – Brébion, p. 414, pl. 10, fig. 10.

Type material – Syntypes: Sceaux-d'Anjou, Thorigné, St-Michel or Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 415).

Material and dimensions – Maximum height 17.5 mm, width 9.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0856 (1), NHMW 2016/0103/0857 (14), LC (4), FVD (22). **Sceaux d'Anjou**: NHMW 2016/0103/0858-0859 (2), NHMW 2016/0103/0860 (14), RGM.734976 (50+), RGM.1349048 (16), RGM.1349059 (14 fragments), RGM.1349062 (2 + 6 fragments), RGM.1349227 (25 juveniles), RGM.1349230 (5 + 3 juveniles), RGM.1352251 (9), LC (2), FVD (8).

Original description – 'Columbella globosa, *Millet. Coq. moyenne, ovoïde, rétrécie à ses extrémités et légèrement striée à sa base; composée de 7-8 tours de spire, le dernier plus grand que tous les autres ensemble. Bord droit renflé intérieurement et couvert de petites lignes ou denticules saillantes, très-rapprochées les unes des autres; bord gauche lamellaire portant quelques dents peu prononcées. Longueur: 15-16 millimètres; diamètre: 9-10*

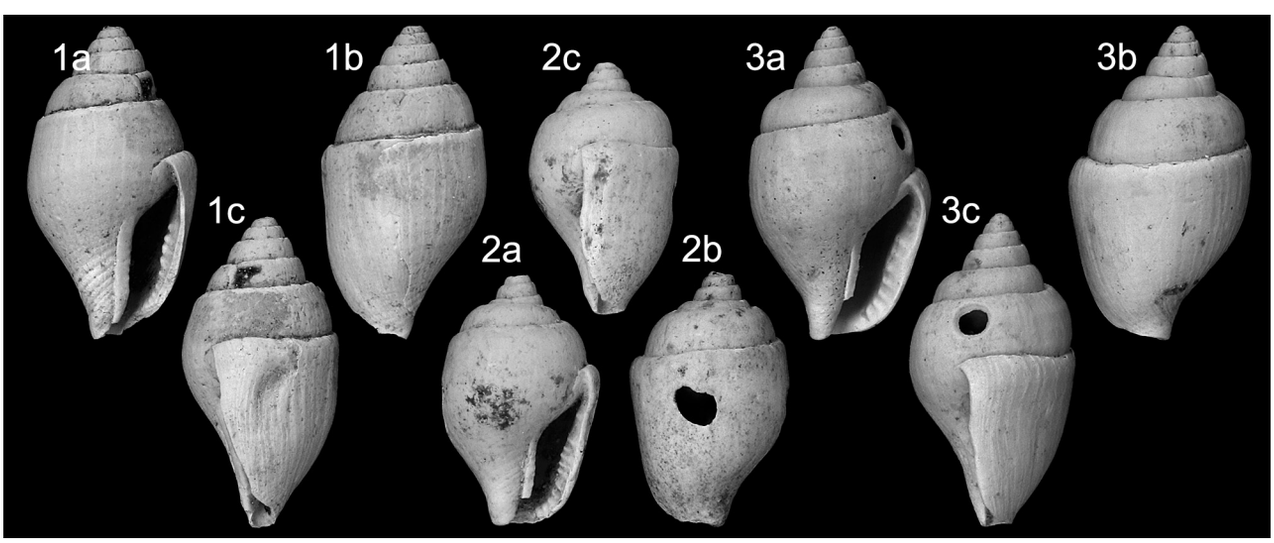


Plate 12. *Columbella globosa* Millet, 1865; 1. NHMW 2016/0103/0856, height 17.4 mm, width 9.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/0858, height 13.1 mm, width 8.3 mm; 3. NHMW 2016/0103/0859, height 15.5 mm, width 8.3 mm. La Presselière, Sceaux d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

millimètres. Sc, Th., Saint-Michel, Ren. On rencontre des individus dont la spire est très-courte' (Millet, 1865, p. 598).

Discussion – *Columbella globosa* Millet, 1865 is a curious species in which the early spire whorls increase in a regular fashion, but at the beginning of the penultimate whorl there is an abrupt increase in growth rate and whorl width, resulting in a shell with a low squat spire and strongly globose last two whorls. One specimen from Sceaux-d'Anjou has a somewhat higher coeloconoid spire than seen in the series illustrated. The surface of the last whorl has a subobsoletely rugose appearance; the aperture is narrow, with a denticulate outer lip; four central denticles are placed on a callus pad, developed internally mid-aperture, although this feature is less developed than in most of its congeners. The columellar callus forms a narrow rim, abapically thickened, and bears a row of denticles at the columellar edge and two broad, low denticles deep within. The protoconch is missing in all adult specimens, but one juvenile from Sceaux-d'Anjou and one from St-Clément-de-la-Place have their protoconch preserved, whichis paucispiral, composed of 1.5 smooth, globular whorls, suggestive of non-planktotrophic development.

Millet (1865) described a second form, *Columbella picturata*, from Genneteil, which was identical to *C. globosa*, except that the last whorl was even squatter and there were some traces of colour pattern. Colour pattern is not preserved in the material at hand, but the series illustrated (Pl. 12, figs 1-3) shows specimens with squat to very squat last whorls. As first revisers we choose *C. globosa*, which is an apt name for this species.

Columbella globosa differs from the Pliocene (?) to present-day *C. rustica* (Linnaeus, 1758) in having a more depressed spire, an even more globose last whorl and lacking spiral sculpture, although it must be said that both species are somewhat variable (see Giannuzzi-Savelli *et al*., 2003, figs 537-559 for variability in living *C. rustica*). Russini *et al*. (2017) showed that three extant eastern Atlantic species occur that could not be separated on teleoconch characters. The present-day *C. rustica* from the Mediterranean and Atlantic, southern Portugal to Senegal, has a paucispiral protoconch and is separated from the other two eastern Atlantic species, which both have multispiral protoconchs. Although a species with a similar teleoconch occurs in the Pliocene of the Mediterranean, none of the specimens at hand have their protoconch preserved. Chirli (2002, p. 3) described the protoconch of Italian Pliocene specimens as having 1.5 whorls, and we therefore consider it to be conspecific with *C. rustica*.

Columbella globosa is closely similar, and possibly descended from *C. curta* (Dujardin, 1837), from the middle Miocene Langhian of the Loire Basin, France. That species differs in having a less depressed spire, the increase in growth rate of the last two whorls is not as abrupt, so that the last two whorls and not as globose, the spire whorls are more convex, the suture deeper, and the aperture is wider than in *C. globosa*. We have not seen a specimen of *C. curta* and cannot confirm if it has the double row of columellar denticles. As discussed by Glibert (1952a, p. 319), the Paratethian Miocene references to *C. curta* (*i.e*. Hörnes, 1852; Friedberg, 1911; Kojumdgieva & Strachimirov, 1960) are not that species and were renamed *Columbella helvetica* Mayer, 1869. However, the earliest name for these shells was shown by Bałuk (1995) to be *Mitrella polonica* (Pusch, 1837), and we consider it to be a *Mitrella* species rather than a *Columbella*. Bałuk (1995) stressed the variability of the species and synonymised *Columbella helvetica* Mayer, 1869 with *Columbella turonica* Mayer, 1869. Glibert (1952a, p. 318) placed the shells illustrated by Hoernes & Auinger (1880, pl. 7, figs 15-20), from the middle Miocene Paratethys of Romania, in the synonymy of *C. curta* rather than of *M. polonica* as suggested by Bałuk (1995). These Romanian shells are probably not *C. curta* either, which is most likely endemic to the middle Miocene of the Loire Basin. Millet (1865, p. 598) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné, St-Michel, Renauleau and Genneteil, to which Brébion (1964, p. 415) added St-Clément-de-la-Place.

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

Genus *Zafrona* Iredale, 1916

Type species (by original designation) – *Columbella isomella* Duclos, 1840, present-day, Indo-Pacific.

1916a *Zafrona* Iredale, p. 32, 33.

***Zafrona arpula* (Michelotti, 1840)**
Plate 13, figs 1-4

*1840 *Buccinum arpula* Michelotti, p. 26.
1848 *Columbella corrugata* Bon. – Bellardi, p. 12, pl. 1, fig. 9 (*non Buccinum corrugatum* Brocchi, 1814).
1854 *Buccinum Festivum* Millet, p. 165 (*nomen nudum*).
1865 *Buccinum festivum* Millet, p. 597.
1880 *Columbella corrugata* Br. – Seguenza, p. 105, pl. 11, fig. 16 (*non Buccinum corrugatum* Brocchi, 1814).
1890 *Columbella* (*Anachis*) *corrugata* (Brocch.) – Sacco, p. 59, pl. 2, figs 81-83 (*non Buccinum corrugatum* Brocchi, 1814).
1925 *Anachis Lemoinei* Peyrot, p. 65, pl. 1, figs 70, 92.
non 1952a *Pyrene* (*Anachis*) *lemoinei* Peyrot, 1927 [*sic*] – Glibert, p. 317, pl. 9, fig. 1 (?turrid).
non 1952b *Pyrene* (*Anachis*) *corrugata* Brocchi, 1814 – Glibert, p. 99, pl. 7, fig. 16 (*non Buccinum corrugatum* Brocchi, 1814) [= *Costoanachis hosiusi* (Von Koenen, 1872)].
non 1964 *Anachis* (*Costoanachis*) *corrugata* Brocchi, 1814 – Anderson, p. 247, fig. 181 (*non Buccinum corrugatum* Brocchi, 1814) [= *Costoanachis hosiusi* (Von Koenen, 1872)].

1964 *Anachis corrugata* Bellardi, 1848 – Brébion, p. 405, pl. 9, figs 30, 31.

non 1972a *Anachis* (*Costoanachis*) *corrugata* (Brocchi, 1814) – Nordsieck, p. 76, fig. 105 (*non Buccinum corrugatum* Brocchi, 1814) [= *Costoanachis hosiusi* (Von Koenen, 1872)].

1992 *Anachis* (*Costoanachis*) *arpula* (Michelotti, 1840) – Cavallo & Repetto, p. 288, fig. 288.

Material and dimensions – Maximum height 9.8 mm, width 4.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0813-0814 (2), NHMW 2016/0103/1838-1839 (2), NHMW 2016/0103/0815 (50+), RGM.1348859 (22), RGM.1349075 (50+), RGM.1349076 (37 fragments), RGM.1349176 (5), RGM.1349177 (30 fragments), RGM. 1349216 (6), RGM.1349225 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0817 (50+), RGM.1348803 (27), RGM.1348913 (50+), RGM.718098 (50+), RGM.1349078 (50+), RGM.1349118 (50+), RGM. 1349228 (50+), RGM.1349265 (50+), RGM.1349272 (50+), RGM.1349282 (50+), RGM.1352195 (50+), RGM. 1352576 (5), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0816 (50+), RGM.1348994 (9), LC (50+), FVD (50+). **Beugnon**: RGM.1349125 (3).

Discussion – *Zafrona arpula* (Michelotti, 1840) is characterised by its multispiral protoconch with a small nucleus, suggestive of planktotrophic development, its relatively inflated, barrel-shaped last two whorls and sculpture consisting of close-set axial ribs that weaken abapically and crowded narrow spirals that cut the axials. The columella bears a row of 4-5 relatively sharp subhorizontal denticles at the outer edge and one broad fold or tooth at the inner edge close to the siphonal canal.

Recent authors have placed this species in the genus *Costoanachis* Sacco, 1890, however, the shell characters are closer to those of *Zafrona* Iredale, 1916, and it shape and sculpture are particularly similar to the present-day Caribbean *Z. pulchella* (de Blainville, 1829) and the Indo-Pacific type species *Z. isomella* (Duclos, 1840). Radwin (1977, p. 415) described members of the genus *Zafrona* as having two columellar folds. This does not seem to be a consistent generic character as most species have only one fold, sometimes a subobsolete second. The presence of one or two folds was also noted by García (2015, p. 49). As well as the row of sharp denticles at the columella edge, *Z. arpula* has a well-developed fold at the inner edge, as seen in *Zafrona* species. Radwin (1977, p. 415) also stated that the outer lip in *Zafrona* species was smooth within. García (2015, p. 49) noted that this was not the case in the western Atlantic species, nor is it in *Z. arpula*.

As can be seen from the series illustrated (Pl. 13, figs 1-4), *Z. arpula* is relatively constant in shape and sculpture. This species has often been referred to as *Anachis* or *Costoanachis corrugata* (Brocchi, 1814) (i.e. Sacco, 1890, p. 59; Brébion, 1964, p. 405; Landau *et al*., 2013, p. 188), an error initiated by Bellardi (1848, p. 12) who described and illustrated this species under the name *Columbella corrugata* Bon., but referred it to Brocchi (*Buccinum corrugatum*; 1814, p. 652, pl. 15, fig. 16), which is a nassariid. The name *Columbella corrugata* Bellardi, 1848 is also not available, as it is based on an incorrect identification. A closely similar species from the Miocene North Sea Basin was named *Columella pulchella* Nyst, 1861, but this is a junior homonym of *C. pulchella* Kiener, 1834. Janssen (1984) argued that the first available name for this species was *Tritonium hosiusi* Von Koenen, 1872. Despite the North Sea Basin and Atlantic/Mediterranean specimens being closely similar, comparing the NW French material with specimens at hand from the middle Miocene Berchem Formation (Heist-op-den-Berg, Belgium) and the Breda Formation (Miste, Winterswijk, The Netherlands) there are constant differences between the two populations. The North Sea Basin form is more slender, the suture slightly deeper and the whorls more convex, resulting in the last two whorls being less barrel-shaped, the axial sculpture is stronger, and most importantly the protoconch is comparatively larger, composed of four whorls as opposed to three in the NW French specimens. These differences are clearly seen in the specimens of *C. hosiusi* illustrated by Wienrich (2001, pl. 95, figs 4, 5). Therefore, we separate the North Sea Basin Miocene species *C. hosiusi*, which we place in *Costoanachis*.

We would agree with Brébion (1964, p. 406) that the

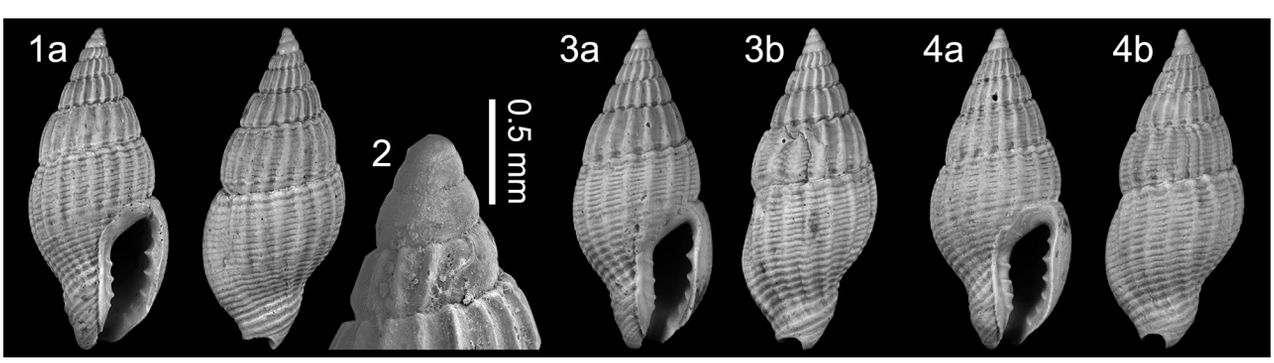


Plate 13. *Zafrona arpula* (Michelotti, 1840); 1. NHMW 2016/0103/0813, height 9.2 mm, width 3.7 mm; 2. NHMW 2016/0103/0814, height 7.8 mm, width 3.4 mm, detail of protoconch (SEM image); 3. NHMW 2016/0103/1838, height 8.7 mm, width 4.1 mm; 4. NHMW 2016/0103/1839, height 8.8 mm, width 4.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

specimen described as *Anachis lemoinei* Peyrot, 1925 from the middle Miocene Aquitaine Basin of France is a strongly sculptured variety of *Z. arpula*. However, the middle Miocene Loire Basin specimens identified as *Pyrene* (*Anachis*) *lemoinei* by Glibert (1952a, p. 317, pl. 9, figs 1, 2) are not this species, and might represent a turrid rather than a columbellid.
Brébion (1964, p. 406) recorded this species from the upper Miocene Tortonian Assemblage I localities of Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place and Les Pierres Blanches, to which we add Renauleau.

Distribution – Middle Miocene: Atlantic (Langhian and Serravallian), Aquitaine Basin (Peyrot, 1925). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Central Mediterranean, Italy (Bellardi, 1890). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (BL unpublished data); central Mediterranean, Italy (Bellardi, 1890; Cavallo & Repetto, 1992).

Subfamily Atiliinae Cossmann, 1901
Genus *Astyris* H. Adams & A. Adams, 1853

Type species (by subsequent designation; Cossmann, 1901) – *Columbella rosacea* Gould, 1840, present-day, NW Atlantic.

1853 *Astyris* H. Adams & A. Adams, p. 187.

***Astyris* (?) sp.**
Plate 14, fig. 1

Material and dimensions – Height 15.2 mm, width 6.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0902 (1).

Description – Shell of medium size and thickness, fusiform, with elevated spire. Protoconch not preserved. Five convex teleoconch whorls preserved, lacking shoulder, separated by shallow impressed suture. Sculpture very weak, consisting of subobsolete narrow flattened cords separated by shallow grooves, most clearly developed below the suture and irregular axial growth lines. Last whorl evenly convex, constricted at base, with spiral cords slightly stronger over siphonal fasciole and base. Aperture subquadrate, anal canal relatively shallow, siphonal canal medium length, open, twisted and dorsally reflected, notched at tip. Outer lip not thickened, bearing a row of short, weak, subequal denticles within inner edge. Columella smooth. Columellar and parietal callus forming very narrow callus rim. Siphonal fasciole poorly delimited from base, rounded.

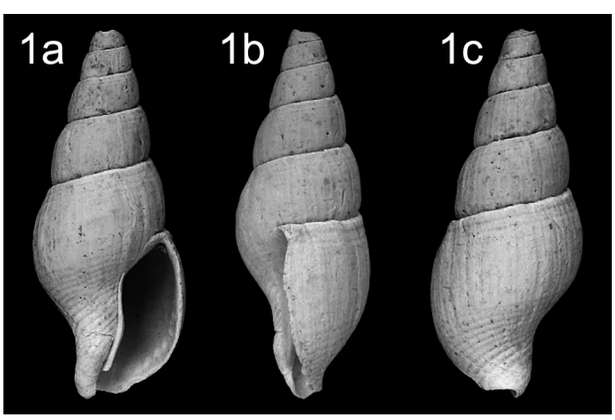


Plate 14. *Astyris* (?) sp.; 1. NHMW 2016/0103/0902, height 15.2 mm, width 6.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – A single specimen, missing its apex, is at hand of a columbellid without a thickened outer lip. Sculpture is much reduced, consisting of a few indistinct grooves just below the suture and weak cords on the siphonal canal and base. A row of small weak denticles are developed just within the edge of the outer lip. We provisionally place it in the genus *Astyris* H. Adams & A. Adams, 1853, which includes a group of relatively smooth columbellids without a thickened outer lip. The French fossil shell is similar to the type *Astyris rosacea* (Gould, 1840) from the NW Atlantic, but differs in having a taller last whorl, taller aperture and longer siphonal canal. We await further material to better characterise this species.

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

Genus *Costoanachis* Sacco, 1890

Type species (by subesquent designation; Pace, 1902) – *Costoanachis saccostata* Radwin, 1977 [= *Columbella* (*Anachis*) *turrita* Sacco, 1890, *non Columbella turrita* Sowerby, 1832], Miocene, Italy.

1890 *Costoanachis* Sacco, p. 57.

***Costoanachis terebralis* (Grateloup, 1834)**
Plate 15, figs 1-4

*1834b *Nassa terebralis* Grateloup, p. 271, no. 512.
1964 *Anachis terebralis* Grateloup, 1834 – Brébion, p. 407, pl. 9, fig. 32.
2013 *Costoanachis terebralis* (Grateloup, 1834) – Landau *et al*., p. 188, pl. 28, fig. 11, pl. 66, fig. 8, pl. 67, fig. 1 (*cum syn*.).

Material and dimensions – Maximum height 6.4 mm, width 2.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0809-0810 (2), NHMW 2016/0103/1840-1841 (2), NHMW 2016/0103/0811 (50+), RGM.1349080 (3), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0812 (22), RGM.1348914 (50+), RGM.718097 (50+), RGM.1349266 (50+), RGM.1352196 (50+), RGM.1352577 (5), LC (2), FVD (12). **Renauleau**: LC (2).

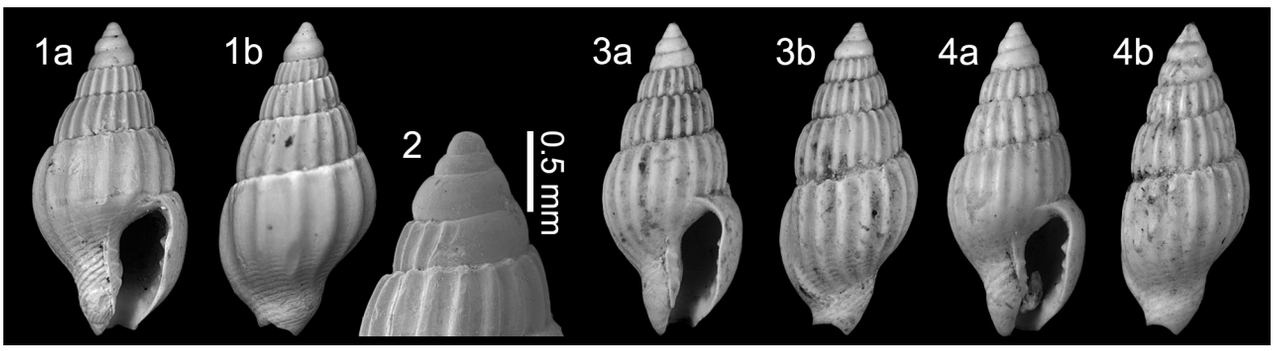


Plate 15. *Costoanachis terebralis* (Grateloup, 1834); 1. NHMW 2016/0103/0809, height 5.1 mm, width 2.7 mm; 2. NHMW 2016/0103/0810 (juvenile), detail of protoconch (SEM image); 3. NHMW 2016/0103/1840, height 6.2 mm, width 2.4 mm; 4. NHMW 2016/0103/1841, height 6.1 mm, width 2.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Costoanachis terebralis* (Grateloup, 1834) is superficially similar to *Zafrona arpula* (Michelotti, 1840), but differs in having a smaller shell, more closely set axial ribs and in the absence of spiral sculpture. The protoconch is multispiral, tall and dome-shaped, similar to that illustrated by other authors (Janssen, 1984, pl. 9, fig. 17; Wienrich, 2001, pl. 78, fig. 3; Landau *et al*., 2013, pl. 67, fig. 1), but like the eastern Proto-Mediterranean Karaman specimens, it does not show the microsculpture seen in the North Sea Basin specimens illustrated by Janssen (1984, pl. 9, fig. 17) and Wienrich (2001, pl. 78, fig. 3). The NW French shells are relatively constant in shape and sculpture (Pl. 15, figs 1-4); some shells are slightly more inflated than others and the rib density on the last whorl can vary. We see no constant difference between the Miocene Atlantic, Mediterranean and North Sea populations, apart from the protoconch microsculpture, and provisionally prefer to consider them a single species. For further discussion, see Landau *et al*. (2013, p. 188).
Brébion (1964, p. 407) recorded this species from the upper Miocene Tortonian Assemblage I localities of Sceaux-d'Anjou and Renauleau, to which we add St-Clément-de-la-Place.

Distribution – Lower Miocene: Atlantic (Aquitanian-Burdigalian), Aquitaine Basin, France (Peyrot, 1925; Lozouet *et al*., 2001). Lower-middle Miocene: North Sea Basin (upper Burdigalian-Langhian), Netherlands (van Voorthuysen, 1944; Nordsieck, 1972a; Janssen, 1984), Germany (Kautsky, 1925; Anderson, 1964; Wienrich, 2001). Middle Miocene: northeastern Atlantic (Langhian-Serravallian), Aquitaine Basin, France, (Peyrot, 1925), (Langhian), Loire Basin, France (Ivolas & Peyrot, 1900; Glibert, 1952a); Paratethys (Langhian-Serravallian): Poland (Bałuk, 1995), Vienna Basin, Austria (Hörnes, 1852; Hoernes & Auinger, 1880), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1962, 1966); eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964), Algarve Basin, Portugal (NHMW collection).

Genus *Mitrella* Risso, 1826

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

1826 *Mitrella* Risso, p. 247.

Note – The genus *Mitrella* Risso, 1826 as used here is interpreted rather widely and is unlikely to be monophyletic. There are several species groups that can be recognised based on shell characters, especially apertural characters, such as having a pinched outer lip, often associated with a thickened pad of callus within, or not, having a well-developed shallow anal sinus on the outer lip visible on lateral view, having subequal labial denticles or a predominant D1 or D2, and the presence or absence of parietal pad and tooth. However, numerous species occur that are difficult to place in one or other of the genera and subgenera proposed by past workers. We are unaware of any major molecular studies on columbellid gastropod phylogeny, and await these, hoping that they will shed some light on relationships. Until then we do not think it useful to give a generic synonymy.
Several mitrellid species in Assemblage I are impossible to separate reliably in the absence of their protoconch, forming species pairs, in which one member of the pair has a paucispiral and the other a multispiral protoconch, inferring different developmental modes (Oliverio 1996a, b, 1997). These are: *Mitrella oblonga* (Millet, 1865) / *M. pseudoblonga* nov. sp., *Mitrella inedita* (Bellardi *in* Sacco, 1890) / *M. pseudoinedita* nov. sp. and *Mitrella miopicta* nov. sp. / *M. pygmaea* (Bellardi *in* Sacco, 1890). Another possible species pair is *M. turgidula* (Brocchi, 1814) / *Mitrella pseudoturgidula* nov. sp., but *M. turgidula* does not occur in Assemblage I and there are small, but consistent, differences in teleoconch characters. The number of specimens counted for each locality only includes specimens in which the protoconch was intact. Therefore, for some localities such as Sceaux-d'Anjou, the number given is an enormous under-representation, as very few of the mitrellids at this locality have their protoconchs preserved.

***Mitrella borsoni* (Bellardi, 1848)**
Plate 16, figs 1-4

*1848	*Columbella Borsoni* Bellardi, p. 14, pl. 1, fig. 11.
1854	*Buccinum Pungens* Millet, p. 165 (*nomen nudum*).
1865	*Buccinum pungens* Millet, p. 595.
1964	*Mitrella* (*Atilia*) *borsoni* Bellardi, 1848 – Brébion, p. 401.
2013	*Mitrella borsoni* (Bellardi, 1848) – Landau *et al*., p. 189, pl. 28, fig. 12, pl. 67, fig. 2 (*cum syn*.).

Material and dimensions – Maximum height 10.8 mm, width 4.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0872-0874 (3), NHMW 2016/0103/0875 (50+), RGM.1349204 (50+), RGM.1352270 (7), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0876 (50+), RGM.718103 (50+), RGM.1349261 (7), RGM.1352211 (8), RGM.1352248 (50+), LC (20), FVD (50+). **Renauleau**: NHMW 2016/0103/0907 (17), LC (20), FVD (16).

Discussion – It has been suggested to us that this species should be placed in the genus *Columbellopsis* Bucquoy, Dautzenberg & Dollfus, 1882 (K. Monsecour personal communication BL, 2019), which was erected for a group of mitrellid species differing from *Mitrella* Risso, 1826 in having a more slender shell and a more constricted and elongated siphonal canal (Radwin, 1978, p. 332). It is certainly closely similar to the Mediterranean type species *Columbella minor* Scacchi, 1836. However, at present WoRMS considers *Columbellopsis* a synonym of *Mitrella* (MolluscaBase 2019a). As mentioned in the generic note we interpreted *Mitrella* rather widely until molecular evidence becomes available.
The specimens of *Mitrella borsoni* (Bellardi, 1848) from Assemblage I are very similar to those described by Landau *et al*. (2013, p. 189, pl. 28, fig. 12, pl. 67, fig. 2) from the middle Miocene Serravallian of the Karaman Basin of Turkey. Both populations have the spire whorls slightly less scalate than those of the syntype illustrated by Ferrero Mortara *et al*. (1981, pl. 57, fig. 11), but the shape of the last whorl and aperture are consistent with those of *M. borsoni*. As in the Karaman material, the protoconch is tall, multispiral, composed of about four strongly convex whorls (Pl. 16, fig. 4). This type of protoconch suggests planktotrophic development, which would favour the wide distribution reported for this species, which in the Miocene is found both in the Atlantic and Mediterranean. One detail we can add, based on the Assemblage I material, is a colour pattern of horizontally elongated blotches similar to that seen in several extant European species such as *M. bruggeni* Van Aartsen, Menkhorst & Gittenberger, 1984 and *M. broderipi* (G.B. Sowerby I, 1844). This is a common colour pattern within the genus.
Mitrella scalaris (Sacco, 1890) from the middle Miocene of Italy is of similar size and shape, but differs in having an outer lip that is more flared and somewhat alate adapically. *Mitrella vialensis* (Sacco, 1890) and *M. minima* (Sacco, 1890), both from the Pliocene of Italy, are also similar in shape but have a more contricted base. These two Pliocene species differ from each other in *M. minima* not having denticles within the outer lip. However, the labial denticles only develop in fully adult shells and it is possible that *M. minima* represents a subadult with a thickened outer lip, but without denticles yet developed. We have insufficient Italian material to clarify if they represent one or two species.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Peyrot, 1938; Glibert, 1952a); Proto-Mediterranean Sea (Serravallian), Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Messinian), NW France, France (Brébion, 1964), (Tortonian), Algarve Basin, Portugal (NHMW collection); Proto-Mediterranean Sea (Tortonian), Po Basin, Italy (Sacco, 1890).

***Mitrella clava* nov. sp.**
Plate 17, figs 1-4

Type material – Holotype MNHN.F.A66733, height 6.9 mm, width 2.8 mm; paratype 1 MNHN.F.A66734, height 5.8 mm, width 2.3 mm; paratype 2 NHMW 2016/0103/0896, height 7.0 mm, width 3.0 mm; paratype 3 NHMW 2016/0103/0897, height 6.7 mm, width 2.7 mm, paratype 4 RGM.1349192, height, 5.8 mm, width 2.4 mm,

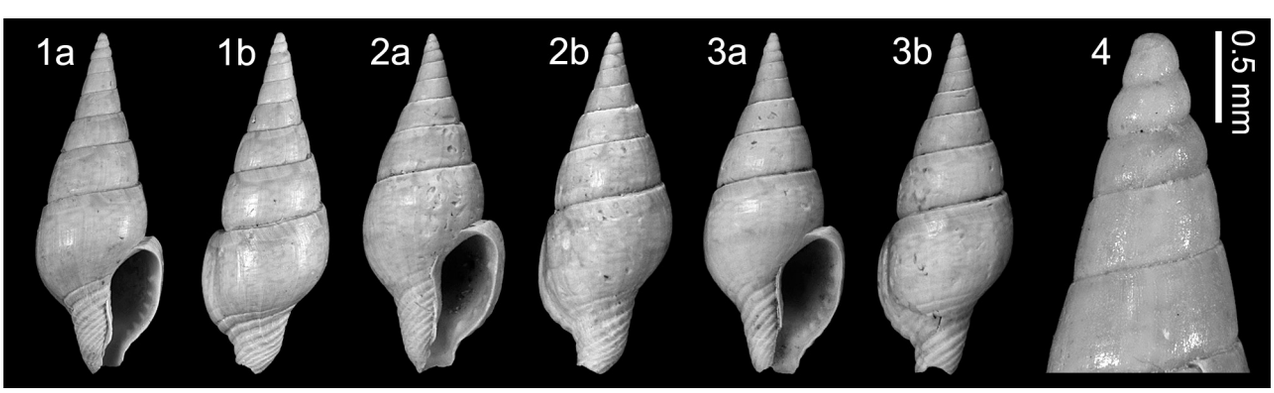


Plate 16. *Mitrella borsoni* (Bellardi, 1848); 1. NHMW 2016/0103/0872, height 9.4 mm, width 3.7 mm, 1c. detail of protoconch; 2. NHMW 2016/0103/0873, height 9.4 mm, width 3.7 mm; 3. NHMW 2016/0103/0874, height 9.2 mm, width 3.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

paratype 5 RGM.1349193, height 5.7 mm, width 2.3 mm; paratype 6 RGM.1349205, height 5.6 mm, width 2.4 mm.

Other material – Maximum height 7.7 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0898 (50+), RGM.1349127 (11), RGM.1349206 (5), RGM.1352265 (4), LC (50+), FVD (50+).

Etymology – Latin '*clava*, *-ae*', meaning club, cudgel, refecting the club-shaped shell shape. *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of small size, club-shaped, with regularly conical spire, paucispiral protoconch, spire whorls straight sided, last whorl moderately inflated, very short siphonal canal, aperture small, outer lip hardly thickened, wide U-shaped sinus abapically on outer lip, callus pad within, six stout denticles, columellar callus bearing four tubercles at inner edge.

Description – Shell small, solid, fusiform, with regular conical spire. Protoconch paucispiral, composed of two smooth bulbous whorls with large nucleus. Junction with teleoconch marked by prosocline scar. Teleoconch of six smooth whorls, straight-sided spire whorls, with periphery at abapical suture. Suture impressed. Last whorl moderately inflated, 57% total height, roundly angled at periphery placed mid-whorl, moderately constricted at base. Spiral cords over siphonal fasciole, not extending onto base. Aperture 36% total height, small, outer lip hardly thickened, broad, shallow U-shaped sinus adapically on lateral view,
bearing thickened callus pad within aperture below sinus, 4-6 stout denticles within, adapical ones on callus pad slightly stronger; siphonal canal very short, open, notched at tip. Columella excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing four rounded tubercles along inner edge; parietal callus hardly developed. Siphonal fasciole very short, broad.

Discussion – *Mitrella clava* nov. sp. is separated from all its Assemblage I congeners by its small, club-shaped shell, straight sided spire whorls, small aperture with only 4-6 tubercular denticles within and very short siphonal canal. *Mitrella transiens* (Bellardi *in* Sacco, 1890) from the upper Miocene of Italy is similar in having flat spire whorls, but differs in being twice the size and in having a longer siphonal canal. The holotype figured by Ferrero Mortara *et al.* (1981, pl. 57, fig. 2) seems to also have a small callus within the outer lip and a similar number of labial denticles. We have not seen this species and cannot comment on its protoconch. The present-day Mediterranean and adjacent Atlantic *M. scripta* (Linnaeus, 1758) has a similar shape and a paucispiral protoconch, but that species is at least twice the size of *M. clava*, the spire whorls are slightly more convex and the siphonal canal is longer. The number of denticles within the outer lip seems similar, but the callus pad within the outer lip is hardly developed in *M. scripta*.

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

***Mitrella erythrostoma* (Bellardi, 1848)**
Plate 18, figs 1-3

*1848	*Columbella erythrostoma* Bellardi, Bonelli m.s., p. 9, pl. 1, figs 4-5.
1981	*Columbella* (*Mitrella*) *erythrostoma* Bellardi, 1848, Bonelli m.s. – Ferrero-Mortara *et al*., p. 183, pl. 57, fig. 12.
2017	*Mitrella erythrostoma* (Bellardi, 1848) – Van Dingenen *et al*., p. 27, pl. 1, fig. 9 (*cum syn*.).

Material and dimensions – Height 13.6 mm, width 5.6 mm. **Sceaux d'Anjou**: NHMW 2016/0103/1807 (1), NHMW 2016/0103/1851-1852 (2), NHMW 2016/0103/1853 (2), RGM.718087 (1), RGM.1349112 (2), RGM.1349167 (1), RGM.1352254 (3).

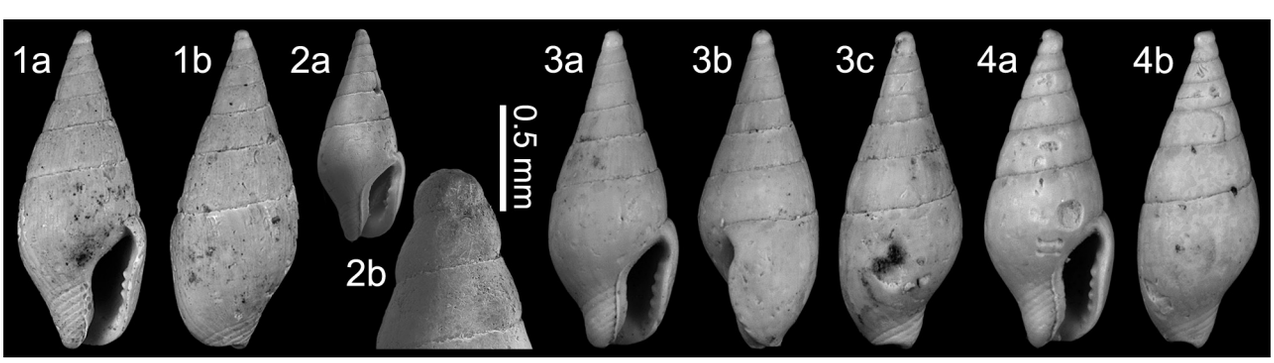


Plate 17. *Mitrella clava* nov. sp.; 1. **Holotype** MNHN.F.A66733, height 6.9 mm, width 2.8 mm; 2. **Paratype 1** MNHN.F.A66734, height 5.8 mm, width 2.3 mm (SEM image), 2b. detail of protoconch; 3. **Paratype 2** NHMW 2016/0103/0896, height 7.0 mm, width 3.0 mm; 4. **Paratype 3** NHMW 2016/0103/0897, height 6.7 mm, width 2.7 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

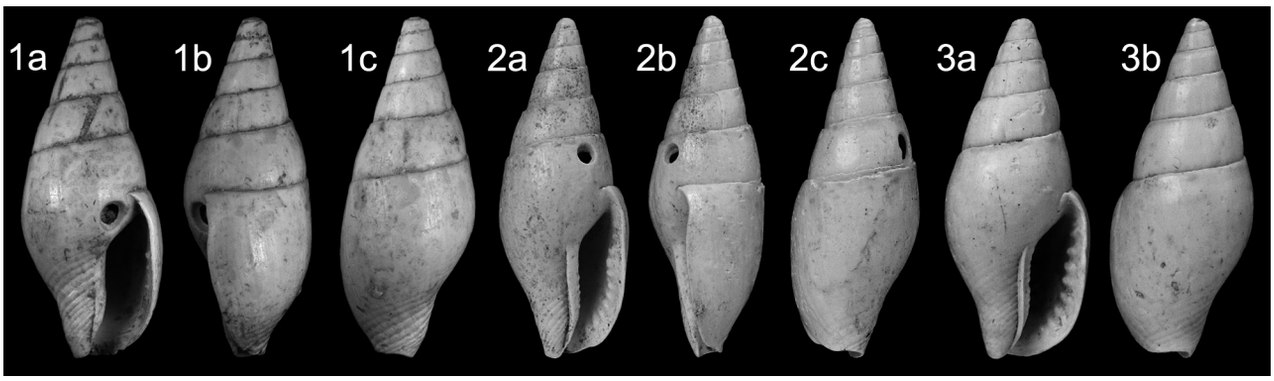


Plate 18. *Mitrella erythrostoma* (Bellardi, 1848); 1. NHMW 2016/0103/1807, height 13.6 mm, width 5.6 mm; 2. 1. NHMW 2016/0103/1851, height 24.2 mm, width 7.2 mm; 3. NHMW 2016/0103/1852, height 14.8 mm, width 6.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Mitrella erythrostoma* (Bellardi, 1848) is a relatively large-shelled mitrellid, characterised by its weakly convex spire whorls, its moderately inflated last whorl, elongated aperture, with the outer lip pinched inwards just above mid-height, bearing teeth along its entire inner edge, more strongly developed on the pinched section, its poorly callused inner lip and short siphonal canal. In the European assemblages this species is found from the middle Miocene to the upper Pliocene along the European Atlantic frontage and the Mediterranean, and was recorded from lower Pliocene Assemblage III of NW France (Van Dingenen *et al*., 2017, p. 28).
In Assemblage I this species is uncommon and occurs only at Sceaux-d'Anjou. The shell is only about half the size for specimens from other localities, but this is not unusual in Assemblage I. There is considerable variability between the specimens, with some specimens more slender than usual and the last whorl less inflated, and subsequently less constricted at the base (Pl. 18, figs 1, 2). Others are more usual for the species with an inflated last whorl, a wide aperture and relatively well-developed labial denticles (Pl. 18, fig. 3). For further discussion and comparison with congeners, see Van Dingenen *et al*. (2017, p. 28).

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1952a). Upper Miocene: Atlantic (Tortonian), NW France (this paper); Proto-Mediterranean, Italy (Glibert, 1952a). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al*., 2017); Guadalquivir Basin, Spain (Landau *et al*., 2011); central Mediterranean, Tunisia (Fekih, 1975). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (BL unpublished data); central Mediterranean, Italy (Bellardi, 1848; Sacco, 1904).

***Mitrella inedita* (Bellardi *in* Sacco, 1890)**
Plate 19, figs 1-3

*1890 *Columbella* (*Tetrastomella*) *inedita* Bellardi *in* Sacco, p. 42, pl. 2, fig. 44.
1904 *Mitrella* (*Atilia*) *inedita* var. *parvuloplicata* Sacco, p. 94, pl. 19, fig. 56.
1964 *Mitrella* (*Atilia*) *inedita* Bellardi, 1890 – Brébion (*partim*), p. 403, pl. 9, figs 27, 29 [not Assemblage III records = *M. vialensis* (Sacco, 1890)].
1981 *Columbella* (*Tetrastomella*) *inedita* Bellardi, 1890 – Ferrero Mortara *et al*., p. 181, pl. 57, fig. 6.
?2013 *Mitrella* aff. *inedita* (Bellardi *in* Sacco, 1890) – Landau *et al*., p. 190, pl. 29, figs 1-3, pl. 67, fig. 4.

Material and dimensions – Maximum height 12.3 mm, width 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0877-0879 (3), NHMW 2016/0103/0880 (50+), RGM.1349217 (1), RGM.1352271 (17), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0881 (50+), RGM.1349263 (1), RGM.1352249 (30), LC (15), FVD (23). **Renauleau**: NHMW 2016/0103/1803 (25), LC (25), FVD (38).

Discussion – *Mitrella inedita* (Bellardi *in* Sacco, 1890) is characterised by its regularly conical spire, angulation at the periphery of the last whorl, weakly constricted base and short siphonal canal. The protoconch is tall multispiral, composed of 3-3.5 convex whorls (Pl. 25, fig. 2c). The specimens from Assemblage I are slightly more constricted at the base than the syntype illustrated by Ferrero Mortara *et al*. (1981, pl. 57, fig. 6). Some specimens from Renauleau have colour pattern preserved consisting of vertical flammules.
In Assemblage I *M. inedita* and *Mitrella pseudoinedita* nov. sp. form a species pair with almost identical teleoconch characters, but differing in their protoconch. *Mitrella inedita* has a multispiral protoconch whereas *M. pseudoinedita* has a paucispiral protoconch. The only consistent teleoconch difference is that *M. inedita* has six denticles within the outer lip, of which D1 is twice as strong as the rest, and *M. pseudoinedita* has seven weaker denticles of which D2 is slightly strengthened (see below under *M. pseudoinedita* for further discussion).
Several closely similar *Mitrella* species were described by Bellardi (1848) and Bellardi *in* Sacco (1890) that are not easily separated, especially in their juvenile or sub-

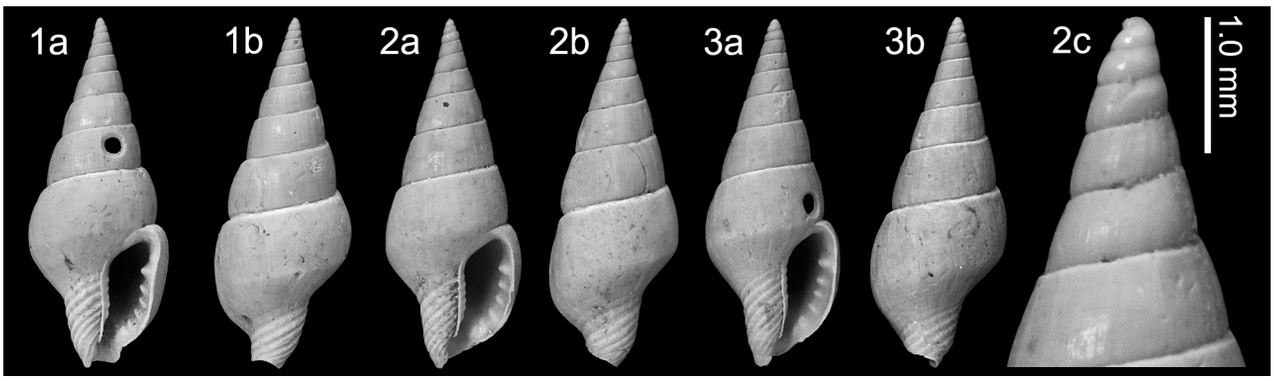


Plate 19. *Mitrella inedita* (Bellardi *in* Sacco, 1890); 1. NHMW 2016/0103/0877, height 12.0 mm, width 4.7 mm; 2. NHMW 2016/0103/0878, height 10.5 mm, width 4.0 mm, 2c. detail of protoconch; 3. NHMW 2016/0103/0879, height 9.4 mm, width 3.5 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

adult form. In the Assemblage I fauna the most closely similar species is *Mitrella borsoni* (Bellardi, 1848). Adult specimens of *M. inedita* differ from those of *M. borsoni* in having a regularly conical spire; in *M. borsoni* the spire is slightly coeloconoid and the suture is deeper, in being angular at the periphery of the last whorl and in having stronger denticulations within the outer lip. Also the ridges on the abapical portion of the columellar that correspond to cords over the siphonal fasciole are more strongly developed in *M. inedita*. The colour pattern described in *M. borsoni* (see above) we have not seen in M. *inedita*. However, as mentioned by Brébion (1964, p. 402), despite these subtle differences, there are some specimens that cannot be ascribed with certainty to one or other form.

Landau *et al*. (2013) illustrated a species as *M.* aff. *inedita* from the middle Miocene of the Karaman Basin of Turkey. It differs from typical *M. inedita* in having slightly convex spire whorls as opposed to straight-sided whorls in *M. inedita*. The base is less constricted than in the Assemblage I specimens, more like typical *M. inedita*. These small differences between populations probably do not warrant separation at species level, and the multispiral protoconch seen in this species would support a wide stratigraphic and geographic distribution.

Mitrella addita (Bellardi *in* Sacco, 1890) described from the upper Miocene Italian deposits, has similar spire whorls, but the last whorl has a more constricted base and fewer spiral cords on the siphonal fasciole. The Tortonian Italian species *Mitrella angulosolabiata* (Sacco, 1904) has a slightly broader apical angle and a more angular base (see Robba, 1968, p. 536, pl. 41, fig. 4). We have not seen this species, which may be just a form of *M. inedita*, as suggested by Sacco (1904). *Mitrella fallax* (Hoernes & Auinger, 1880) widespread in the middle Miocene Atlantic, Paratethys and eastern Proto-Mediterranean is larger, more slender, with a taller last whorl and longer aperture, and has stronger spiral cords over the siphonal fasciole.

Brébion (1964, p. 403) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and Beaulieu, to which we add St-Clément-de-la-Place and Renauleau. Brébion's records of the species in Assemblage III localities probably refer to *M. vialensis* (Sacco, 1890) (see Van Dingenen, 2017, p. 28).

Distribution – ?Middle Miocene (Serravallian): Proto-Mediterranean, Karaman Basin, Turkey (Landau *et al*., 2013); Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1890).

Mitrella inflatula **(Millet, 1865)**

Plate 20, figs 1-3

1854	*Buccinum Inflatulum* Millet, p. 165 (*nomen nudum*).
*1865	*Buccinum inflatulum* Millet, p. 596.
1964	*Pterygia* (*Alia*) *inflatula* Millet, 1854 [*sic*] – Brébion, p. 416, pl. 10, figs 11, 12.

Type material – Syntypes: Sceaux-d'Anjou, Thorigné and Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 416).

Material and dimensions – Maximum height 13.7 mm, width 5.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0861-0863 (3), NHMW 2016/0103/0864 (50+), RGM.1349190 (5), RGM.1352267 (2), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0865 (45), RGM.718099 (50+), RGM.1352247 (50+), LC (10), FVD (24).

Original description – 'Buccinum inflatulum*, Millet. Coq. de moyenne taille, allongée, aiguë au sommet, composée de 7 à 8 tours de spire renflés, le dernier présentant une espèce de bourrelet sur le bord droit. Tous les tours sont lisses et la suture qui est assez profonde laisse voir un petit filet bien distinct. L'ouverture qui est ovale, aiguë au sommet, est terminée inférieurement par un canal très-court, légèrement recourbé. Longueur: 15-16 millimètres; diamètre: 6 millimètres. Th., Sc, Ren.*' (Millet, 1865, p. 596).

Discussion – *Mitrella globosa* (Millet, 1865) is quite a

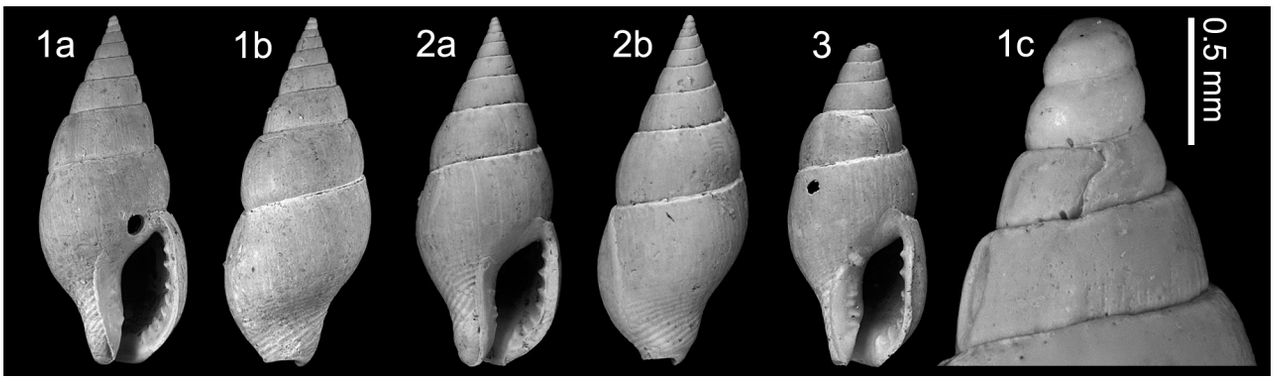


Plate 20. *Mitrella inflatula* (Millet, 1865); 1. NHMW 2016/0103/0861, height 13.7 mm, width 5.4 mm; 2. NHMW 2016/0103/0862, height 13.7 mm, width 5.6 mm; 3. NHMW 2016/0103/0863, height 14.9 mm, width 8.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

distinctive species, distinguished from all its Assemblage I congeners by the shape of its columellar callus, which is thickened and expanded abapically over the ventral portion of the base and siphonal fasciole. In all the other *Mitrella* species in Assemblage I the columella callus is narrow, straight and hardly expanded. The most closely similar species are *M. erythrostoma* (Bellardi, 1848) from the upper Miocene-Pliocene Mediterranean and adjacent Atlantic, but also recorded by Van Dingenen *et al*. (2017) in Assemblage III of NW France, which differs in being much larger, with a longer, narrower aperture and not having the shield-like expanded abapical columellar callus, and *M. semicaudata* (Bellardi, 1848), also from the Pliocene Mediterranean and adjacent Atlantic, which is closer in shape to *M. globosa*, but again lacks the abapical columellar shield.
Brébion (1964, p. 416) noted that the protoconch was paucispiral. Very few specimens have the apex preserved like one of the specimens illustrated here (Pl. 20, fig. 1c). However, several specimens have an intact protoconch and it is multispiral consisting of about three smooth convex whorls, and not paucispiral as suggested by Brébion.

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

***Mitrella ligeriana* nov. sp.**
Plate 21, figs 1-4

Type material – Holotype MNHN.F.A66729, height 6.6 mm, width 2.9 mm; paratype 1 MNHN.F.A66730, height 7.3 mm, width 3.4 mm; paratype 2 NHMW 2016/0103/0866, height 7.5 mm, width 4.1 mm; paratype 3 NHMW 2016/0103/0867, height 8.7 mm, width 4.1 mm; paratype 4 NHMW 2016/0103/0868, height 6.9 mm, width 3.2 mm; paratype 5 NHMW 2016/0103/0869, height 6.5 mm, width 2.8 mm, paratype 6 RGM.1349195, height 6.7 mm, width 3.1 mm, paratype 7 RGM.1349196, height 6.4 mm, width 2.9 mm.

Other material – Maximum height 8.5 mm, width 4.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0870 (50+), RGM.1349197 (1), RGM.1349207 (1), RGM.1352269 (3), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0871 (50+), RGM.718100 (50+), RGM.1349248 (13), RGM.1349262 (14), RGM.1349274 (6), RGM.1352246 (50+), RGM.1352578 (2), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0908 (50+), LC (50+), FVD (50+).

Etymology – Named after the '*Golfe Ligérien*', the name of the bay in which the species lived. *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of small size, low spire, paucispiral protoconch, four moderately convex teleoconch whorls separated by impressed suture, last whorl moderately inflated, outer lip thickened internally in upper third, bearing six denticles, D1 strongest, narrow columellar callus bearing weak-moderate denticles along entire length, siphonal fasciole moderately short, bearing weak cords.

Description – Shell small, solid, squat fusiform, with low spire. Protoconch paucispiral, composed of two smooth convex whorls, with large nucleus. Teleoconch of four moderately convex whorls, separated by deeply impressed suture. Last whorl moderately inflated, 68% total height, weakly convex below suture, roundly and broadly angled at periphery, moderately constricted at base. Sculpture absent, apart from weak spiral cords over siphonal fasciole, not extending onto base. Aperture 45% total height, narrowly ovate, outer lip bearing thickened callus pad within in upper third, bearing six denticles, D1 placed on centre of thickened callus pad strongest; anal canal rounded, poorly delimited; siphonal canal relatively short, open, notched at tip. Columella weakly excavated in upper third, straight below; columellar callus

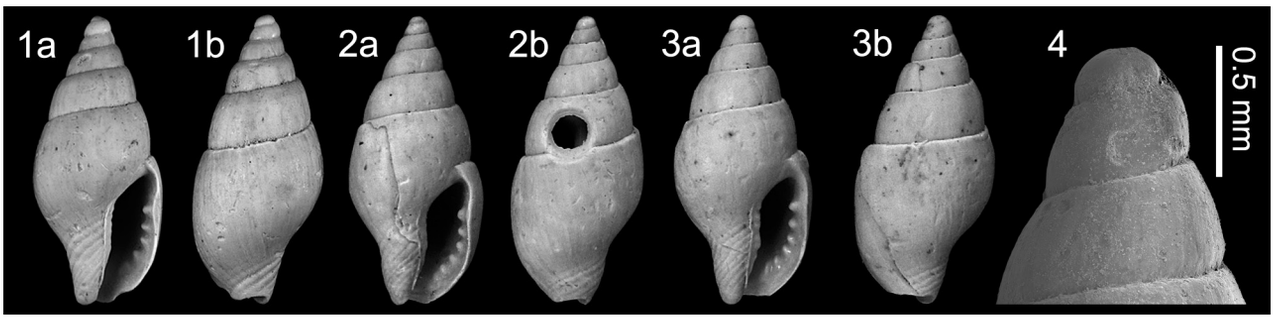


Plate 21. *Mitrella ligeriana* nov. sp.; 1. **Holotype** MNHN.F.A66729, height 6.6 mm, width 2.9 mm; 2. **Paratype 1** MNHN.F.A66730, height 7.3 mm, width 3.4 mm; 3. **Paratype 2** NHMW 2016/0103/0866, height 6.2 mm, width 3.0 mm; 4. **Paratype 5** NHMW 2016/0103/0869, height 6.5 mm, width 2.8 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

sharp, forming narrow rim, bearing weak to moderately developed denticles along inner edge; parietal callus not developed. Siphonal fasciole relatively short, broad.

Discussion – *Mitrella ligeriana* nov. sp. differs from its Assemblage I congeners in being squatter, lower spired, with a relatively inflated last whorl.
Two species from the upper Miocene Tortonian of Italy that seem superficially similar to *M. ligeriana* were published by Sacco (1890): *Columbella bellardensis* Sacco, 1890 and *C. abbreviata* Bellardi *in* Sacco, 1890. here they are both considered *Mitrella* species. The holotype of the former and a syntype of the latter were reillustrated by Ferrero Mortara *et al*. (1981, pl. 54, figs 13, 14 respectively). Both specimens illustrated are somewhat abraded and the apex is missing from both. The only difference between the two seems that the adapical portion of the last whorl is more convex in *M. abbreviata*. We have not been able to locate an intact specimen of *M. bellardensis*, but a single complete specimen of *M. abbreviata* from Rio di Bocca d'Asino (Pl. 22, fig. 1), where it is exceedingly uncommon, shows that it is not conspecific with *M. ligeriana*. Although both have a paucispiral protoconch, the spire is much taller in *M. abbreviata*, the spiral sculpture is more extensive, covering both the base and the siphonal fasciole and there are a couple of subobsolete

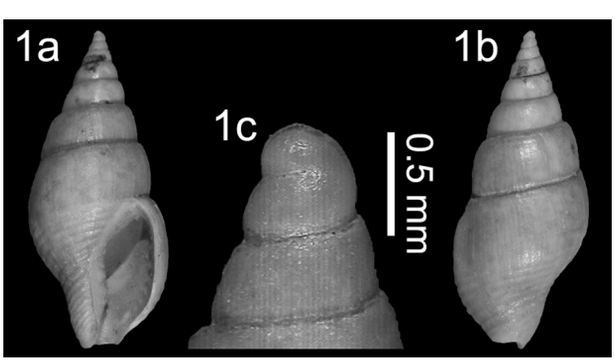


Plate 22. 1. *Mitrella abbreviata* Bellardi *in* Sacco, 1890, height 14.0 mm, Rio di Bocca d'Asino, Marne di S. Agata, Stazzano, Piedmont, Italy, Tortonian, upper Miocene, Maurizio Sosso Coll. (M. Sosso photo).

spirals below the suture in *M. abbreviata*, the outer lip does not have the thickened pad within and the labial denticles are weaker. Sacco (1890) reports Stazzano as the type locality, by which he actually meant the Rio di Bocca d'Asino locality, which is the main outrop at Stazzano (Bruno Dell'Angelo personal communication BL, 2018).

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

***Mitrella miopicta* nov. sp.**
Plate 23, figs 1-3

Type material – Holotype NHMW 2016/0103/1864, height 6.5 mm, width 3.0 mm; paratype 1 RGM.739218, height 6.9 mm, width 3.0 mm, 2c, detail of protoconch; paratype 2 RGM.1352273, height 6.7 mm, width 3.0 mm; paratype 3 RGM.1352274, height 6.8 mm, width 2.9 mm.

Other material – Known from type series only.

Etymology – Latin '*pictus,-a*', meaning coloured or decorated, with the prefix '*mio*-' referring to Miocene time in which this species lived. *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of small size, squat fusiform shape, with regularly conical spire, paucispiral protoconch, spire whorls weakly convex, last whorl inflated, moderately short siphonal canal, aperture small, outer lip moderately thickened, with callus pad within, seven small denticles, D2 strongest, columellar callus bearing tubercles at inner edge, colour pattern of alternating rows of diagonal blotches and stripes.

Description – Shell small, solid, squat fusiform. Protoconch paucispiral, small, composed of two smooth convex whorls with large nucleus. Junction with teleoconch

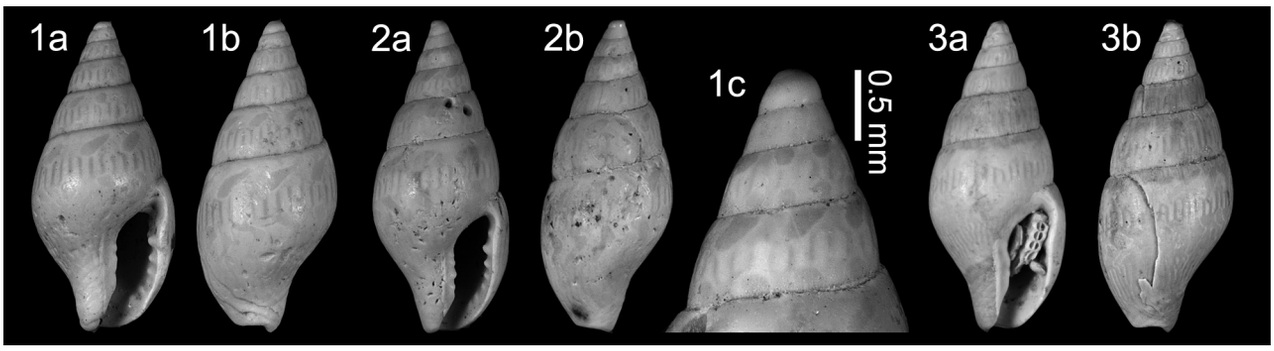


Plate 23. *Mitrella miopicta* nov. sp.; 1. **Holotype** NHMW 2016/0103/1864, height 6.5 mm, width 3.0 mm; 2. **Paratype 1** RGM.739218, height 6.9 mm, width 3.0 mm, 2c, detail of protoconch; 3. **Paratype 2** RGM.1352273, height 6.7 mm, width 3.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

marked by prosocline scar. Teleoconch of 4.5 smooth, weakly convex whorls, with periphery at abapical suture. Suture impressed. Last whorl inflated, 62-65% total height, evenly rounded at periphery placed mid-whorl, moderately constricted at base. Very weak spiral cords over siphonal fasciole, not extending onto base. Aperture 38% total height, ovately elongate, outer lip moderately thickened, U-shaped anal sinus, internally bearing slightly thickened callus pad adapically, seven short denticles within, D2 strongest; siphonal canal moderately short, open, weakly recurved, notched at tip. Columella excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing moderately developed tubercles along inner edge. Siphonal fasciole moderately short. Colour pattern preserved consisting of alternating rows of diagonal blotches starting immediately below suture and rows of short vertical stripes mid-whorls and over base.

Discussion – *Mitrella miopicta* nov. sp. is highly reminiscent of *Mitrella pygmaea* (Bellardi *in* Sacco, 1890) (see below), but is immediately separated by its paucispiral protoconch, whereas *M. pygmaea* has a multispiral protoconch. The teleoconch in both species has the same squat fusiform shape, but in *M. pygmaea* D1 is strongest, whereas in *M. miopicta* D2 is dominant. They also differ in their colour pattern see (compare Pl. 32, figs 3, 4). The Pliocene to present-day Mediterranean species with a paucispiral protoconch *M. scripta* (Linnaeus, 1758) differs in being larger, taller spired with a less inflated last whorl, D2 is not as strongly developed compared to the rest of the labial denticles and, although variable in colour pattern, does not show that seen in *M. miopicta*. *Mitrella gervillii* (Payraudeau, 1826) is again twice the size, with a taller, more pointed spire, a relatively less inflated last whorl and more numerous weaker labial denticles with none consistently more strongly developed. As with *M. scripta*, although variable in colour pattern, the pattern seen in *M. miopicta* we have not seen in any specimen of *M. gervillii*. *Mitrella svelta* Kobelt, 1889 is again larger still and, as the name would suggest, more slender. *Mitrella coccinea* (Philippi, 1836) is more similar in shape, but is again larger, with a slightly higher spire, D2 less developed and a different colour pattern. *Mitrella bruggeni* Van Aartsen, Menkhorst & Gittenberger, 1984 is also similar to *M. miopicta*, but is less squat, with higher whorls, the adapical denticles can be strengthened in some specimens, but not as strongly as in *M. miopicta*, and although very variable in colour pattern, the combination of blotches and stripes seen in the French fossil species we have not seen in *M. bruggeni*. *Mitrella broderipii* (G.B. Sowerby I, 1844) is similar in size to the French fossil species and probably the most similar in shape, but in that species D1 is strongly developed and the rest of the labial teeth are weak or subobsolete, and most specimens have a spotted colour pattern. Specimens with vertical stripes do occur, but not in the pattern seen in *M. miopicta*.

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

***Mitrella oblonga* (Millet, 1865)**
Plate 24, figs 1-3

1854	*Columbella Oblonga* Millet, p. 165 (*nomen nudum*).
*1865	*Columbella oblonga* Millet, p. 598.
?1964	*Mitrella transiens* Bellardi, 1890 – Brébion (?*partim*), p. 397, pl. 9, figs 20, 21 [*non* ***Mitrella transiens*** (Bellardi *in* Sacco, 1890)].
1964	*Mitrella turgidula* Brocchi, 1814 – Brébion (?*partim*), p. 399, pl. 9, figs 24-26 [*non Mitrella turgidula* (Brocchi, 1814)].

Type material – Syntypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 400).

Material and dimensions – Maximum height 11.7 mm, width 4.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0891-0893 (3), NHMW 2016/0103/0894 (9), LC (8), FVD (10). **Sceaux-d'Anjou**: NHMW 2016/0103/1805 (15), RGM.1352255 (17), FVD (8).

Original description – 'Columbella oblonga, *Millet. Coq.*

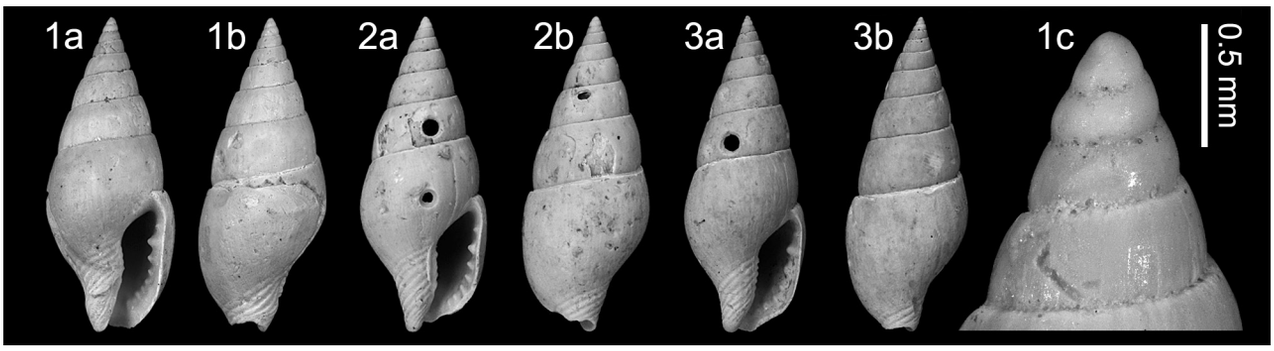


Plate 24. *Mitrella oblonga* (Millet, 1865); 1. NHMW 2016/0103/0891, height 10.9 mm, width 3.9 mm, detail of protoconch; 2. NHMW 2016/0103/0892, height 11.0 mm, width 4.4 mm; 3. NHMW 2016/0103/0893, height 11.7 mm, width 4.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

de moyenne taille, allongée et comme fusiforme, légèrement striée à sa base; composée de 8-9 tours de spire presque plans, bord droit renflé intérieurement, et couvert, en partie, de dents bien prononcées; bord gauche lamellaire, portant quelques dents peu marquées. Longueur: 19-20 millimètres; diamètre: 8 millimètres. Th., Sc, Ren.' (Millet, 1865, p. 598).

Discussion – Millet's (1865, p. 598) text describes faithfully the salient features in this species. We add that the protoconch is multispiral and typically planktrophic, there is a shallow U-shaped anal sinus adapically on the outer lip on lateral view, and that the teeth on the thickened callus pad within the outer lip are more strongly developed; D2 strongest. There is a little variability in the inflation of the last whorl, but otherwise shell characters are fairly constant.

Brébion (1964, p. 399) synonymised this species with the Italian Pliocene *Mitrella turgidula* (Brocchi, 1814). The two are indeed similar, but not conspecific. The holotype illustrated by Rossi Ronchetti (1955, p. 196, fig. 103), and specimens at hand from the Pliocene of Italy and the Estepona Basin, southern Spain (NHMW coll.), show that species to be larger, with a wider apical angle, the spire is more regularly conical composed of even flatter sided whorls, separated by a more superficial suture, the last whorl is even more globose and the base is far more weakly sculptured, subobsolete in some specimens. It is possible that some of Brébion's specimens correspond to other species described herein as *M. pseudoturgidula* nov. sp. or *M. pseudoblonga* nov. sp. (see below).

Mitrella oblonga and *M. pseudoblonga* nov. sp. is one of four mitrellid species pairs in Assemblage I that cannot be reliably separated without their protoconch. *Mitrella oblonga* has a multispiral protoconch whereas *M. pseudoblonga* has a paucispiral protoconch. The teleoconch of *M. oblonga* is less variable than that of *M. pseudoblonga*, the spire tends to be higher and the labial denticle D2 is consistently much stronger than the rest in *M. oblonga*, whereas the labial dentition in *M. pseudoblonga* is rather variable (see below under *M. pseudoblonga* for further discussion).

Millet (1865, p. 598) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d'Anjou and Renauleau, to which Brébion (1964, p. 400 added Contigné and St-Clément-de-la-Place. Brébion also recorded it from the Assemblage III locality of Le Girondor, but this lower Pliocene record was not confirmed by Van Dingenen *et al*. (2017) and is provisionally excluded.

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

***Mitrella pseudoinedita* nov. sp.**
Plate 25, figs 1-3

Type material – Holotype MNHN.F.A66731, height 13.7 mm, width 5.8 mm; paratype 1 MNHN.F.A66732, height 13.2 mm, width 5.2 mm; paratype 2 NHMW 2016/0103/0882, height 14.4 mm, width 5.3 mm; paratype 3 NHMW 2016/0103/0883, height 13.9 mm, width 5.7 mm; paratype 4 NHMW 2016/0103/0884, height 13.8 mm, width 5.7 mm, paratype 7 RGM.1349208, height 10.8 mm, width 4.3 mm, paratype 8 RGM.1349218, height 14.0 mm, width 5.3 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1349044, height 15.4 mm, width 6.5 mm; paratype 6 RGM.1349045, height 15.4 mm, width 6.5 mm, paratype 9 RGM.1352250, height 11.6 mm, width 4.3 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 15.4 mm, width 6.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0885 (13), RGM.1352266 (2 + 10 juveniles), FVD (3). **Sceaux-d'Anjou**: RGM.734974 (50+). **Renauleau**: NHMW 2016/0103/0909 (37), LC (22), FVD (20).

Etymology – Named reflecting close similarity to *Mitrella inedita* (Bellardi *in* Sacco, 1890). *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

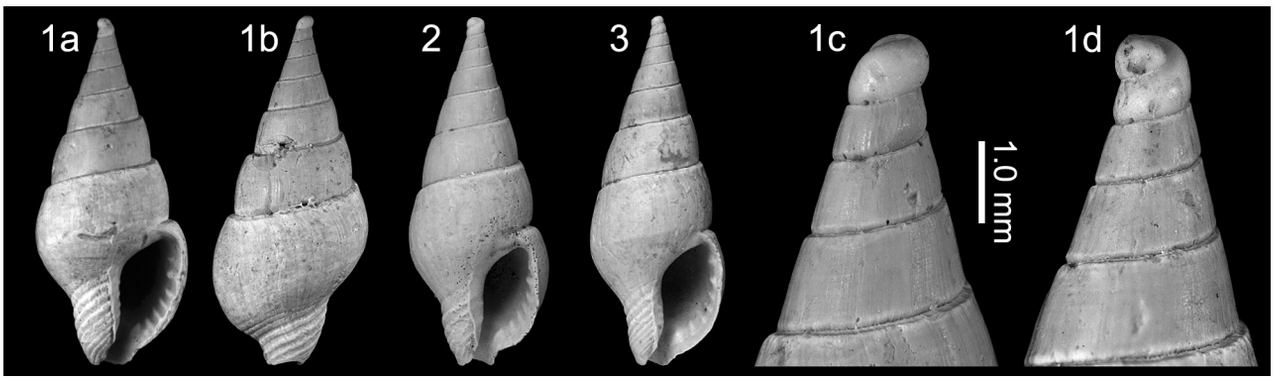


Plate 25. *Mitrella pseudoinedita* nov. sp.; 1. **Holotype** MNHN.F.A66731, height 13.7 mm, width 5.8 mm, detail of protoconch; 2. **Paratype 1** MNHN.F.A66732, height 13.2 mm, width 5.2 mm; 3. **Paratype 2** NHMW 2016/0103/0882, height 14.4 mm, width 5.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of medium size, tall conical spire, paucispiral bulbous protoconch, straight-sided early spire whorls, convex later, separated by deeply impressed suture, spiral sculpture strong, restricted to siphonal fasciole, seven moderate strength denticles within outer lip, D2 strongest.

Description – Shell medium-sized, solid, slender fusiform, with tall conical spire. Protoconch paucispiral, globular, of two smooth convex whorls with large bulbous nucleus. Junction with teleoconch marked by prosocline scar. Teleoconch of 6.5 whorls, with periphery at abapical suture. Suture deeply impressed. Early spire whorls straight sided, becoming more convex adapically. Last whorl inflated to moderately so, 55% total height, roundly to subobsoletely angled at shoulder, moderately constricted at base. Sculpture restricted to strong spiral cords over siphonal fasciole, not extending onto base. Aperture 36% total height, ovate, outer lip thickened, bearing seven moderately weak denticles within, D2 strongest; anal much reduced, poorly delimited; siphonal canal medium length for genus, open, notched at tip. Columella excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing weak to moderately developed denticles along inner edge; parietal callus hardly developed. Siphonal fasciole medium length for genus, broad.

Discussion – The teleoconchs of *Mitrella pseudoinedita* nov. sp. and *Mitrella inedita* (Bellardi *in* Sacco, 1890) in the Assemblage I deposits are almost identical. The only consistent difference is that *M. pseudoinedita* has seven weaker denticles within the outer lip, of which D2 is slightly strengthened, whereas *M. inedita* has only six of which D1 is twice as strong as the rest. However, they differ in their protoconch type; *M. pseudoinedita* has a paucispiral protoconch, with a big bulbous nucleus, consistent with a direct mode of development, whereas *M. inedita* has a multispiral protoconch, with a small nucleus, suggesting planktotrophic development.
Historically, in the older fossil literature the protoconch has seldom been described or illustrated, hindering comparison. However, based on material at hand, *Mitrella* species with a paucispiral protoconch are *M. polonica* (Pusch, 1837) from the middle Miocene Paratethys, *M. semicaudata* (Bellardi *in* Sacco, 1890) from the Mediterranean Pliocene, *M. scripta* (Linnaeus, 1758), from the Pliocene to present-day Mediterranean, *M. gervillii* (Payraudeau, 1826) and *M. svelta* Kobelt, 1889, from the present-day Mediterranean, which all differ from *M. pseudoinedita* in having a smaller, less bulbous protoconch and a more evenly fusiform teleoconch. *Mitrella souarcensis* (Degrange-Touzin, 1894), from the middle Miocene Serravallian Aquitaine Basin of France, differs in having an even more slender coeloconoid spire, with a small paucispiral protoconch, and a strongly alate outer lip that is smooth within. *Mitrella teres* (Bellardi *in* Sacco, 1890), also from the Mediterranean Pliocene has a very slender shell with strongly convex whorls, and a tall paucispiral protoconch. *Mitrella coccinea* (Philippi, 1836), *M. bruggeni* Van Aartsen, Menkhorst & Gittenberger, 1984 and *M. broderipii* (G.B. Sowerby I, 1844), from the present-day Mediterranean, all have smaller, more fusiform shells, with a lower spire.

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

***Mitrella pseudoblonga* nov. sp.**
Plate 26, figs 1-4

?1964 *Mitrella transiens* Bellardi, 1890 – Brébion (?*partim*), p. 397, pl. 9, figs 20, 21 [*non Mitrella transiens* (Bellardi *in* Sacco, 1890)].

Type material – Holotype MNHN.F.A66735, height 10.8 mm, width 5.0 mm; paratype 1 MNHN.F.A66736, height 10.2 mm, width 4.3 mm; paratype 2 NHMW 2016/0103/0886, height 10.6 mm, width 4.5 mm; paratype 3 NHMW 2016/0103/0887, height 9.7 mm, width 4.3 mm; paratype 4 NHMW 2016/0103/0888, height 10.4 mm, width 4.8 mm; paratype 5 NHMW 2016/0103/0889, height 12.0 mm, width 4.9 mm, **St-Clément-de-la-Place**.

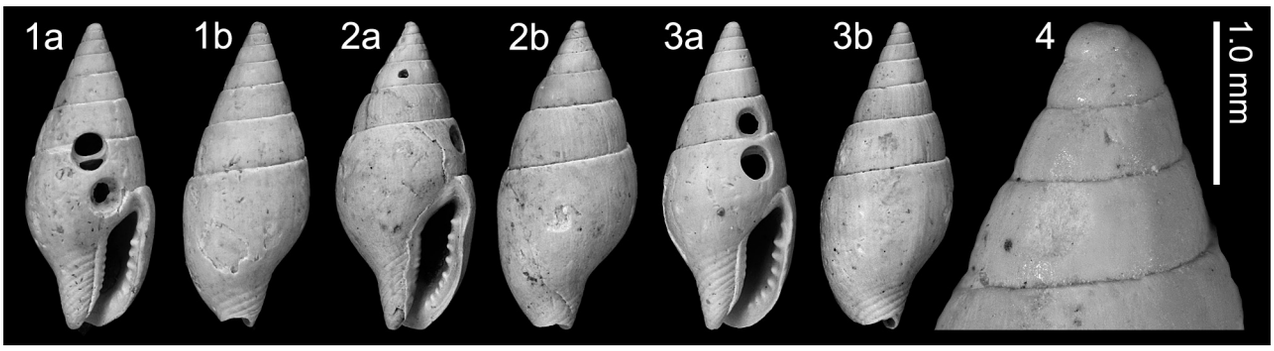


Plate 26. *Mitrella pseudoblonga* nov. sp.; 1. **Paratype 2** NHMW 2016/0103/0886, height 10.6 mm, width 4.5 mm; 2. **Holotype** MNHN.F.A66735, height 10.8 mm, width 5.0 mm; 3. **Paratype 1** MNHN.F.A66736, height 10.2 mm, width 4.3 mm; 4. **Paratype 3** NHMW 2016/0103/0887, height 9.7 mm, width 4.3 mm, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Paratype 6 RGM.1349264, height 9.6 mm, width 4.2 mm, paratype 7 RGM.1352256, height 9.6 mm, width 4.0 mm, paratype 8 RGM.1352257, height 9.6 mm, width 4.3 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 12.5 mm, width 5.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0890 (17), RGM.1349210 (2), RGM.1352272 (1), LC (20), FVD (25). **Sceaux-d'Anjou**: NHMW 2016/0103/1806 (22), RGM.1352258 (4), LC (1), FVD (11). **Renauleau**: NHMW 2016/0103/0910 (11), LC (25), FVD (24).

Etymology – Named reflecting close similarity to *Mitrella oblonga* (Millet, 1865). *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of medium size, paucispiral protoconch, squat fusiform shape, weakly convex spire whorls, moderately inflated, regularly convex last whorl, 8-9 labial denticles, those placed on labial callus pad adapically slightly stronger, siphonal canal moderately short.

Description – Shell medium-sized, solid, squat fusiform. Protoconch paucispiral, small, composed of two smooth convex whorls with large nucleus. Junction with teleoconch marked by prosocline scar. Teleoconch of 5.5 weakly convex smooth whorls, with periphery at abapical suture. Suture impressed. Last whorl inflated, 60-67% total height, evenly rounded at periphery placed mid-whorl, moderately constricted at base. Weak spiral cords over siphonal fasciole, not extending onto base. Aperture 40-42% total height, narrow elongate, outer lip hardly thickened, broad, shallow U-shaped sinus adapically on lateral view, with bevelled inner edge, bearing slightly thickened callus pad adapically, 8-9 short denticles within, those placed over thickened callus pad slightly strengthened; anal canal narrow, poorly delimited; siphonal canal moderately short, open, weakly recurved, notched at tip. Columella excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing moderately developed tubercles along inner edge; small parietal pad. Siphonal fasciole moderately short, broad.

Discussion – *Mitrella pseudoblonga* nov. sp. and *M. oblonga* (Millet, 1865) is one of four mitrellid species pairs in Assemblage I that cannot be reliably separated without their protoconch. *Mitrella pseudoblonga* has a paucispiral protoconch whereas *M. oblonga* has a multispiral protoconch, suggesting different reproductive modes. The teleoconch of *M. pseudoblonga* tends to be slightly more inflated than that of *M. oblonga*, but unlike *M. oblonga* in which the shells characters tend to be rather constant, *M. pseudoblonga* is highly variable in globosity, height of the last whorl and in the character of the labial denticles. In some specimens D2 and D3 are considerably strengthened and in the occasional specimen they fuse, whereas in others the denticles are subequal. Brébion (1964, pl. 9, figs 20, 21) illustrated a shell from Sceaux-d'Anjou as *M. transiens* (Bellardi *in* Sacco, 1890) that in our opinion is either *M. oblonga* or *M. pseudoblonga*. No description of the protoconch was given. The holotype of *M. transiens* from the upper Miocene of Italy illustrated by Ferrero Mortara *et al*. (1981, pl. 57, fig. 2) shows a shell with a taller, more regularly conical spire, flat-sided spire whorls, and a relatively shorter last whorl, which is roundly angled at the periphery. In shape it is more similar to *M. clava* nov. sp. (see under that species). Several species with paucispiral protoconchs occur today in the European faunas revised by Chiarelli *et al*. (2002). *Mitrella scripta* (Linnaeus, 1758) and *M. lanceolata* (Locard, 1886) are both higher spired and have a wider aperture. *Mitrella gervilii* (Payreaudeau, 1826) has a more pointed and often coeloconoid spire, and again the aperture is wider. Finally *M. coccinea* (Philippi, 1836) is the most similar in shape, but has a considerably wider aperture.

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

***Mitrella pseudoturgidula* nov. sp.**
Plate 27, figs 1, 2

?1964 *Mitrella turgidula* Brocchi, 1814 – Brébion (?*partim*), p. 399, pl. 9, figs 24-26 [*non Mitrella turgidula* (Brocchi, 1814)].

Type material – Holotype NHMW 2016/0103/0895, height 22.4 mm, width 9.4 mm, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/1850, height 24.5 mm, width 8.4 mm; paratype 2 RGM.1349041, height 25.2 mm, width 8.5 mm; paratype 3 RGM.1349042, height 21.8 mm, width 7.8 mm; paratype 4 RGM.1349043, height 22.6 mm, width 8.5 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 25.2 mm, width 8.5 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1983 (23), RGM.718102 (50+), RGM.739219 (1 + 4 juveniles). **Renauleau**: NHMW 2016/0103/1804 (17), LC (22), FVD (29).

Etymology – Named reflecting close similarity to *Mitrella turgidula* (Brocchi, 1814). *Mitrella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mitrella* species of medium size, tall conical spire, small paucispiral protoconch, spire whorls weakly convex, bearing two incised spiral grooves below suture, last whorl inflated, short siphonal canal, aperture narrow, outer lip hardly thickened, pinched mid-height with callus pad within on pinched portion, 12 subqual denticles, columellar callus bearing row of tubercles at inner edge, small parietal pad and tooth.

Description – Shell medium-sized, solid, fusiform, with tall conical spire. Protoconch paucispiral, small, composed of two smooth convex whorls with large nucleus. Junction with teleoconch marked by prosocline scar. Teleoconch of eight weakly convex whorls, with periphery at abapical suture. Suture impressed, linear. Surface smooth, except for two weakly incised spiral grooves below suture on spire whorls; one groove on penultimate whorl, absent on last whorl. Last whorl inflated, 62% total height, roundly angled at periphery placed mid-whorl, moderately constricted at base. Weak spiral cords over siphonal fasciole, not extending onto base. Aperture 40% total height, narrow, outer lip hardly thickened, slightly pinched mid-lip, flared abapically, with bevelled inner edge, bearing thickened callus pad within aperture coinciding with pinched portion, 12 irregular, subequal, narrow denticles placed on bevelled portion of inner lip, starting a short distance from lip edge, not extending into aperture; anal canal narrow, poorly delimited; siphonal canal short, open, recurved, notched at tip. Columella weakly excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing moderately developed tubercles along edge; small parietal pad and tooth. Siphonal fasciole short, broad.

Discussion – As discussed in the generic note above, the genus *Mitrella* Risso, 1826, as used here, is interpreted rather widely and is unlikely to be monophyletic. *Mitrella pseudoturgidula* nov. sp. is the largest mitrellid in the Assemblage I fauna. It is superficially similar in shape to *M. turgidula* (Brocchi, 1814) from the Mediterranean Pliocene, but that species has a predominant D2 and based on material at hand from the Pliocene of Pradalbino (Italy) and Estepona (Spain), *M. turgidula* has a planktotrophic-type multispiral protoconch with a small nucleus. Brébion (1964, p. 399) recorded *M. turgidula* from several NW French assemblages. He also synonymised *Columbella oblonga* Millet, 1865 (see above) with *M. turgidula*. It is possible that he combined the two species, as he described the denticles within the outer lip as small, whereas the denticles in *M. oblonga* are well developed with D2 strongly predominant, more like the dentition of *M. turgidula*. *Mitrella oblonga* also differs in having a multispiral protoconch. In apertural dentition *M. pseudoturgidula* is similar to another Mediterranean Pliocene species, *M. erythrostoma* (Bellardi, 1848) that

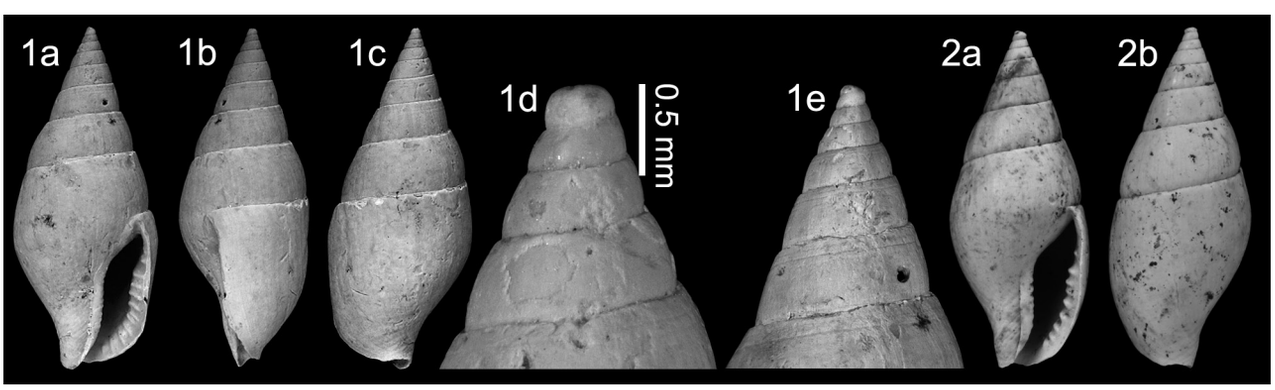


Plate 27. *Mitrella pseudoturgidula* nov. sp.; 1. **Holotype** NHMW 2016/0103/0895, height 22.4 mm, width 9.4 mm; 1d, detail of protoconch, 1e, detail of teleoconch spiral sculpture. Le Grand Chauvereau, St-Clément-de-la-Place. 2. **Paratype 1** NHMW 2016/0103/1850, height 24.5 mm, width 8.4 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

is also present in Assemblage I and was recorded in the lower Pliocene Assemblage III of NW France (Van Dingenen *et al*., 2017). Both species have a relatively broad pinched section of the outer lip, with a callus developed within the outer lip and subequal elongated rather than tubercular denticles within. However, *M. erythrostoma* is an even larger species, with more convex whorls and a wider aperture. An unusual sculptural feature in the new species are the pair of fine incised grooves placed a short distance below the suture on the spire whorls, that disappear abapically; only one groove on the penultimate whorl, none on the last whorl. Most mitrellids are predominantly smooth, with spiral sculpture restricted to the siphonal fasciole, extending onto the base in some species.

We have ascribed a number of specimens from Renauleau to *M. pseudoturgidula*, although none of them are suitable as type material, as the protoconch is not preserved. They show some variability in the convexity of the spire whorls and the strength of the labial denticles, but otherwise conform with the species description.

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

***Mitrella pygmaea* (Bellardi *in* Sacco, 1890)**
Plate 28, figs 1-4

*1890	*Columbella* (*Mitrella*) *pygmaea* Bellardi *in* Sacco, p. 38, pl. 2, fig. 35.
1964	*Mitrella pygmaea* Bellardi, 1890 – Brébion, p. 398, pl. 9, figs 22-23.
1981	*Columbella* (*Mitrella*) *pygmaea* Bellardi, 1890 – Ferrero-Mortara *et al*., p. 180, pl. 57, fig. 3.

Material and dimensions – Maximum height 5.9 mm, width 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0911-0912 (2), RGM.1349209 (1), RGM.1352268 (3). **Renauleau**: NHMW 2016/0103/0904-0905 (2), NHMW 2016/0103/0906 (50+), RGM.1348995 (50+), LC (50+), FVD (50+).

Discussion – This species is characterised by its small size, solid shell, planktotrophic-type multispiral protoconch composed of about 3.5 whorls with a small nucleus (Pl. 32, fig. 4c), its conical spire composed of weakly convex whorls separated by an impressed linear suture and its moderately inflated last whorl. The aperture is typical for the genus, with D1 most strongly developed. The siphonal canal is relatively short and sculpture restricted to weak spiral cords on the fasciole. We would agree with Brébion (1964, p. 397) that the Assemblage III specimens are probably conspecific with *Mitrella pygmaea* (Bellardi *in* Sacco, 1890), described from the upper Miocene of Italy. The syntype illustrated by Ferrero Mortara *et al*. (1981, pl. 57, fig. 3) shows the same protoconch type and shell features described above. Specimens from St-Clément-de-la-Place have a well-preserved colour pattern consisting of blotches forming irregular bands or sinuous flammules (Pl. 28, figs 3, 4), a similar pattern can be seen faintly in one of the specimens from Renauleau (Pl. 28, fig. 1).

Mitrella pygmaea is similar to *Mitrella miopicta* nov. sp. from Assemblage I, but that species has a paucispiral protoconch (for further comparison see above). *Mitrella bruggeni* Van Aartsen, Menkhorst & Gittenberger, 1984 from the present-day Alboran Sea, and recorded by Van Dingenen *et al*. (2017) in Assemblage III of NW France, is similar in shape to *M. pygmaea* and some specimens show a similar colour pattern, but differs in being about double the size, in having a paucispiral protoconch, and within the outer lip D1 is not as strongly dominant as it is in *M. pygmaea*.

Distribution – Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964); Proto-Mediterranean, Italy (Sacco, 1890).

Genus *Nassarina* Dall, 1889

Type species (by original designation) – *Nassarina bushii* Dall, 1889 [= *Nassarina bushiae* (Dall, 1889)], present-day, Caribbean.

1889 *Nassarina* Dall, p. 15, 181.

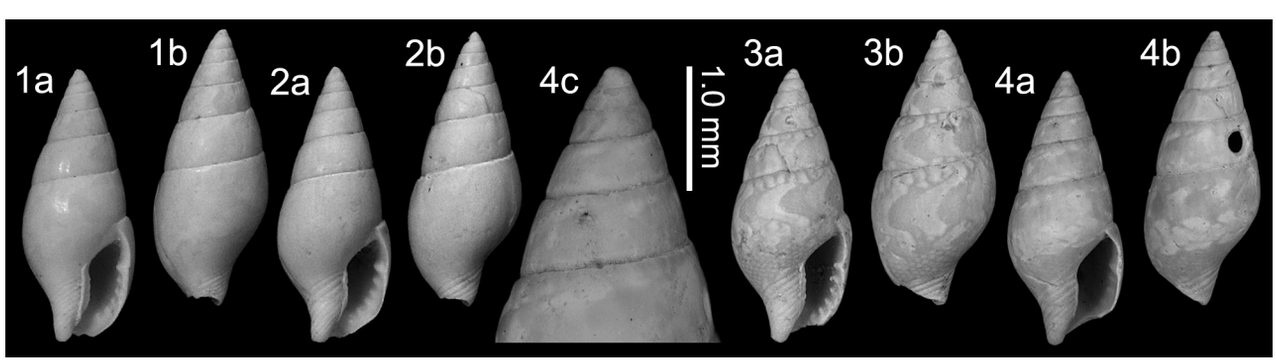


Plate 28. *Mitrella pygmaea* (Bellardi *in* Sacco, 1890); 1. NHMW 2016/0103/0901, height 5.7 mm, width 2.3 mm; 2. NHMW 2016/0103/0902, height 5.8 mm, width 2.5 mm. Renauleau. 3. NHMW 2016/0103/0911, height 5.6 mm, width 2.5 mm; 4. NHMW 2016/0103/0912, height 5.9 mm, width 2.5 mm, 2c, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1928 *Cigclirina* Woodring, 1928, p. 281. Type species (by original designation): *Cigclirina sigma* Woodring, 1928, Pliocene, Jamaica.

Note – Van Dingenen *et al*. (2017, p. 29) commented on the taxonomic placement of this European Neogene group of tall-spired, slender columbellids with cancellate sculpture that have been placed by all authors in the genus *Anachis* H. Adams & A. Adams, 1853. The Panamic Pacific type species, *Columbella scalarina* G.B. Sowerby I, 1832 is quite different with predominatly axial sculpture and a solid, inflated last whorl that is large in relation to the spire. They are probably closest to the Caribbean genus *Nassarina* Dall, 1889, especially the subgenus *Cigclirina* Woodring, 1928, which we consider a synonym, characterised by shells that possess both strong axial and spiral sculpture of almost equal strength, like the present-day Panamic Pacific *N. perata* Keen, 1971 and *N. vespera* Keen, 1971. *Nassarina* has been recorded in the extant faunas of West Africa (Pelorce & Boyer, 2005) and the Canary Islands (Segers & Swinnen, 2004). Other European fossil species that should be transferred to this group are *Anachis degrangei* Dollfus *in* Degrange-Touzin, 1894 from the middle Miocene Aquitaine and Loire basins, and possibly *Fusus clathratus* Dujardin, 1837 and *Columbella haueri* Hoernes & Auinger, 1880 from the middle Miocene of the Loire Basin.

***Nassarina collyrata* (Millet, 1865)**
Plate 29, figs 1-3

1854 *Buccinum Collyratum* Millet, p. 165 (*nomen nudum*).
*1865 *Buccinum collyratum* Millet, p. 597.
1964 *Anachis collyrata* Millet, 1854 [*sic*] – Brébion, p. 409, pl. 10, figs 2-4.

Type material – Syntypes: Sceaux-d'Anjou and Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 410).

Material and dimensions – Maximum height 11.7 mm, width 4.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0067 (1), NHMW 2016/0103/0068 (1), NHMW 2016/0103/0069 (1 juvenile protoconch), NHMW 2016/0103/0070 (50+), RGM.1349155 (50+), RGM.1349224 (50+), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0071 (50+), RGM.1348801 (14), RGM.1348918 (40), RGM.718104 (50+), RGM.1349163 (26), RGM.1349254 (12), RGM.1349283 (33), RGM.1352191 (13), RGM.1352212 (15), RGM.1352242 (50+), RGM.1352377 (20), RGM.1352419 (19), RGM.1352553 (3), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1481 (2), LC (1?), FVD (2).

Original description – 'Buccinum collyratum*, Millet. Coq. petite, comme fusiforme, aiguë au sommet, composée de 8-9 tours de spire bombés et non séparés par la suture; mais tous clathratés par la position de côtes minces, verticales, qui se croisent avec des stries transversales de même épaisseur, d'où résulte un travail gaufré et granulé des plus agréables; le bord droit, en outre, présente extérieurement un petit renflement ou bourrelet très-prononcé, et intérieurement un rang de denticules marquées; le canal est droit et légèrement retourné. Longueur: 12 millimètres; diamètre: 5 millimètres. Sc., Th.*' (Millet, 1865, p. 597).

Discussion – *Nassarina collyrata* (Millet, 1865) is the largest of this species group in Assemblage I, with the most openly reticulate surface sculpture. The protoconch is multispiral (Pl. 29, fig. 3). The first teleoconch whorl bears two spiral cords placed close to the suture, a third primary cord develops on the second whorl mid-height (Pl. 29, fig. 2c), the last whorl has four primary spiral cords above the aperture. Further weaker cords cover the base and relatively long siphonal fasciole. The spirals overrun 14-15 prosocline axial ribs, roughly equal in strength to the spirals, forming an evenly reticulate sur-

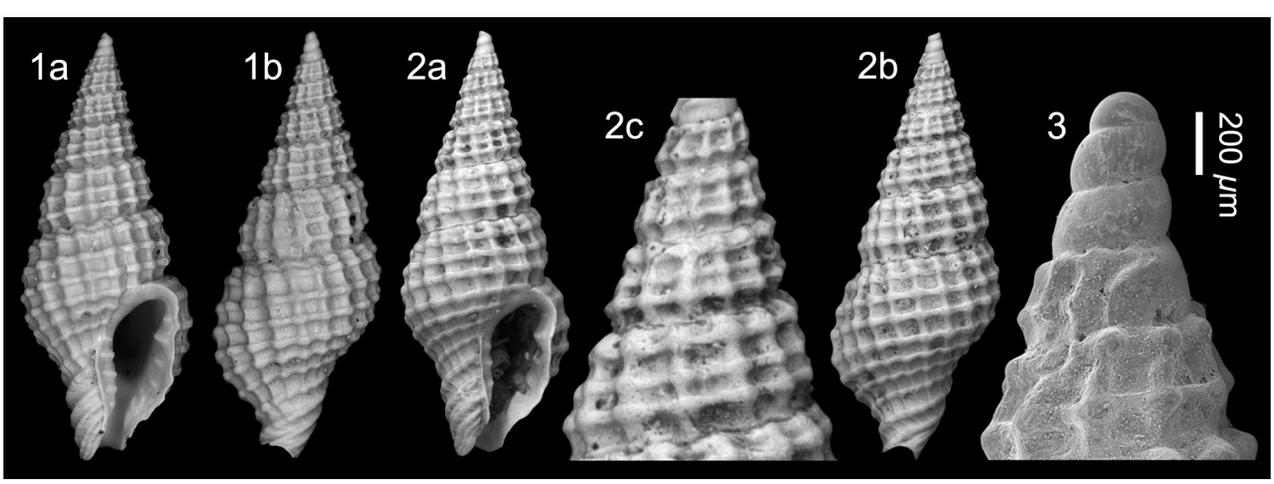


Plate 29. *Nassarina collyrata* (Millet, 1865); 1. NHMW 2016/0103/0067, height 9.0 mm; 2. NHMW 2016/0103/0068, height 11.7 mm, 2c, detail of spire sculpture; 3. NHMW NHMW 2016/0103/0069, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

face pattern. The aperture is relatively small, with a large rounded anal canal. The outer lip bears 5-6 denticles a short distance within the lip edge, of which D2 is strongly predominant. The columellar callus is sharp edged and bears 3-5 horizontally elongated denticles within, the parietal area is slightly thickened. For comparison with congeners, see below.
Brébion (1964, p. 410) recorded this species from the Assemblage I localities of Sceaux d'Anjou, Thorigné and St-Michel, to which we add St-Clément-de-la-Place and Renauleau.

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

***Nassarina hordacea* (Millet, 1865)**
Plate 30, figs 1-3

1854	*Buccinum Hordaceum* Millet, p. 165 (*nomen nudum*).
*1865	*Buccinum hordaceum* Millet, p. 597.
1964	*Anachis hordacea* Millet, 1854 [*sic*] – Brébion, p. 411, pl. 10, fig. 7.
1964	*Anachis hordacea* var. *kiliani* (Dollfus mss.) in Brébion, p. 413, pl. 10, figs 8, 9 (*nomen nudum*).

Type material – Syntypes: Sceaux-d'Anjou and Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 412).

Material and dimensions – Maximum height 9.0 mm, width 3.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0072 (1), NHMW 2016/0103/0073 (1), NHMW 2016/0103/0074 (1 juvenile protoconch), NHMW 2016/0103/0075 (50+), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0076 (50+), RGM.1348802 (15), RGM.1348919 (36), RGM.718106 (50), RGM.718107 (50+), RGM.1349145 (21), RGM.1349255 (15), RGM.1349284 (9), RGM.1352192 (34), RGM.1352201 (13), RGM.1352213 (7), RGM.1352243 (50+), RGM.1352378 (6), RGM.1352420 (10), RGM.1352554 (45), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1479 (40), RGM.1348987 (10), LC (50+), FVD (50+).

Original description – 'Buccinum hordeaceum*, Millet. Coq. fusiforme, composée de 7 tours de spire, légèrement renflés, tous marqués de côtes verticales ou obliques, coupées par des stries transversales. Ouverture étroite, allongée, marquée sur le bord droit de quatre dents arrondies et terminée par un canal étroit, légèrement arqué en dessus. Longueur: 9-10 millimètres; diamètre: 4 millimètres. Sc., Th*.' (Millet, 1865, p. 597).

Discussion – *Nassarina hordacea* (Millet, 1865) is the stockiest of this species group in Assemblage I, with a horizontally elongated reticulate surface sculpture. The protoconch is multispiral (Pl. 30, fig. 3). The first teleoconch whorl bears two spiral cords, the adapical one placed close to the suture, the abapical one placed just below mid-whorl. A third primary cord develops on the second whorl mid-whorl just above the abapical cord, which migrates abapically (Pl. 30, fig. 2c). A fourth cord develops below the adapical cord on the penultimate whorl. The last whorl has five primary spiral cords above the aperture. Further cords cover the base and medium-length siphonal fasciole. The spirals overrun 8-10 prosocline axial ribs, slightly wider than the spirals. The aperture is relatively small, with a large rounded anal canal. The outer lip bears four denticles just within the lip edge, of which D1 is strongly predominant. The columellar callus is sharp edged and bears 3-4 horizontally elongated denticles within. Brébion (1964, p. 413, pl. 10, figs 8, 9) recognised a smaller variety with a greater number of axial ribs (although in the species description he does not specify the number) as *A. hordacea* var. *kiliani* (*nomen nudum*). We consider them extreme forms of a single species.
Nassarina hordacea (Millet, 1865) differs from *N. collyrata* (Millet, 1865) in being smaller, squatter, with horizontally elongated rather than evenly reticulated surface sculpture, and having fewer denticles within the outer lip. For comparison with *N. milleti* Van Dingenen, Ceulemans & Landau, 2017, see below.
Brébion (1964, p. 412, 413) recorded this species from the

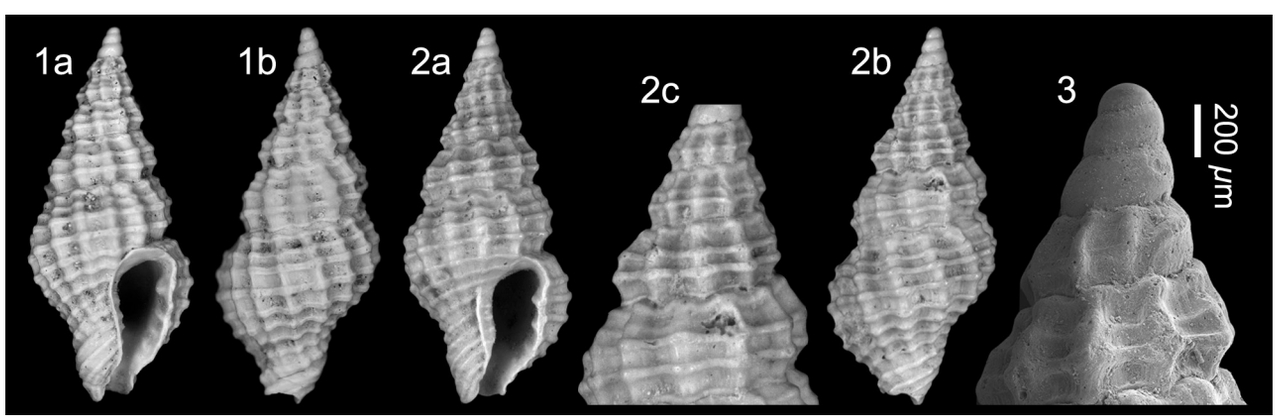


Plate 30. *Nassarina hordacea* (Millet, 1865); 1. NHMW 2016/0103/0072, height 6.9 mm; 2. NHMW 2016/0103/0073, height 6.0 mm, 2c, detail of spire sculpture; 3. NHMW 2016/0103/0074, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Assemblage I localities of Sceaux d'Anjou, Thorigné and St-Clément-de-la-Place, to which we add Renauleau.

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

Nassarina milleti (Van Dingenen, Ceulemans & Landau, 2017)

Plate 31, figs 1, 2

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

*2017 *Anachis milleti* Van Dingenen, Ceulemans & Landau, p. 29, text-fig 1/1-4, pl. 2, fig. 3.

Type material – Holotype MNHN.F.A57685, paratype 2 MNHN.F.A57686, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/0063, paratype 3 NHMW 2016/0103/0064, **St-Clément-de-la-Place**.

Other material – Maximum height 7.2 mm, width 2.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0063-0064 (2), NHMW 2016/0103/0065 (40), LC (50+), FVD (50+). **Sceaux d'Anjou**: NHMW 2016/0103/0066 (50+), RGM.1349117 (3), RGM.1349241 (12), RGM.1349256 (6), RGM.1349293 (21), RGM.1352379 (6), RGM.1352421 (5), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1808 (1), NHMW 2016/0103/1480 (50+), RGM.1348986 (20), RGM.718105 (50+), RGM.1352244 (18), RGM.1352555 (9), LC (50+), FVD (50+). **Beugnon**: RGM.1348487 (2), RGM.1349083 (1), RGM.1352351 (3).

Discussion – *Nassarina milleti* Van Dingenen, Ceulemans & Landau, 2017 is the most slender of this species group in Assemblage I, with the least convex whorls, the least impressed suture, and finest reticulated surface sculpture. The protoconch is multispiral (Pl. 31, fig. 1c). The first teleoconch whorl bears two spiral cords placed close to the suture, a third primary cord develops mid-whorl on the second whorl (Pl. 31, fig. 2c). On the penultimate whorl a fourth cord develops below the adapical cord. The last whorl has six primary spiral cords above the aperture. Further cords cover the base and medium-length siphonal fasciole. The spirals overrun 14-15 prosocline axial ribs, roughly equal in strength to the spirals, forming a finely reticulated surface pattern. The aperture is relatively small, with a large rounded anal canal. The outer lip bears 4-5 relatively weak denticles a short distance within the lip edge, of which D1 is predominant. The columellar callus is sharp-edged and bears four horizontally elongated denticles within.

This species was also recorded by Van Dingenen *et al*. (2017, p. 29) from the lower Pliocene Assemblage III of Le Pigeon Blanc, where it is far less common than it is in the Assemblage I localities. However, the few specimens available are all about half as large again as the largest from Assemblage I. The small size of the Assemblage I species is a theme we will visit repeatedly during this series of papers.

This group of *Nassarina* species with tall spires and reticulated sculpture is well represented in the French Atlantic Miocene. *Nassarina degrangei* (Dollfus *in* Degrange-Touzin, 1894) from the middle Miocene of the Aquitaine and Loire basins of France is the most similar to *N. milleti* in its tall slender shape and relatively weakly inflated last whorl, but *N. degrangei* has fewer ribs and cords and the two subsutural cords are more strongly developed, forming a subsutural collar, resulting in a somewhat scalate appearance to the spire. This subsutural collar is even more strongly developed in *N. clathrata* (Dujardin, 1837), which is lower spired than the preceding species and has predominantly axial sculpture.

In Assemblage I *N. milleti* differs from *N. collyrata* (Millet, 1865) and *N. hordacea* (Millet, 1865) in being more slender, with less convex whorls, in having a finer reticulated surface sculpture and weaker labial denticles.

Brébion (1964, p. 411) recorded *N. milleti* (as *Anachis fannyae*) from the middle Miocene Loire Basin (Manthelan), Assemblage I localities (Sceaux d'Anjou, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné, Le Temple

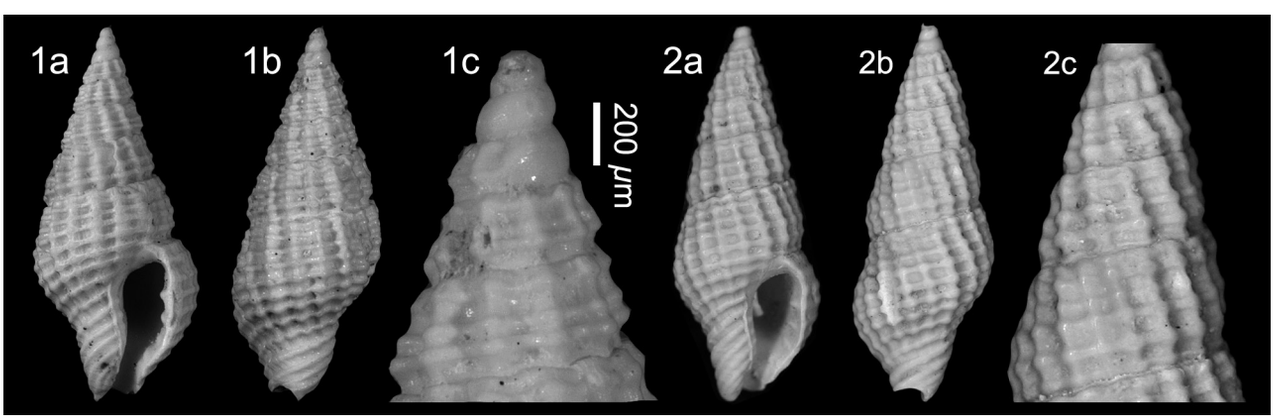


Plate 31. *Nassarina milleti* (Van Dingenen, Ceulemans & Landau, 2017); 1. NHMW 2016/0103/0064, height 7.2 mm, width 2.7 mm, 1c, detail of protoconch; 2. Holotype, MNHN.F.A57685, height 6.8 mm, 2 c, detail of teleoconch sculpture. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

du Cerisier), Assemblage III (Le Pigeon Blanc, Palluau, La Gauvinière).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al*., 2017).

Genus *Sulcomitrella* Kuroda, Habe & Oyama, 1971

Type species (by original designation) – *Mitrella monodonta* Habe, 1958, present-day, Japan.

1958 *Sulcomitrella* Habe, p. 34 [Japanese text], p. 41 [English text]. Not available, no type species, nor diagnosis given.
1971 *Sulcomitrella* Kuroda, Habe & Oyama, p. 159 [English text], p. 244 [Japanese text].

***Sulcomitrella sceauxensis* nov. sp.**
Plate 32, figs 1-3

Type material – Holotype NHMW 2016/0103/1856, height 9.5 mm, width 5.0 mm; paratype 5 NHMW 2016/0103/1865, height 10.6 mm, width 5.2 mm; paratype 1 RGM.739220, height 9.2 mm, width 5.1 mm; paratype 2. RGM.1349090, height 10.0 mm, width 5.1 mm; paratype 3. RGM.1349091, height 9.5 mm (incomplete), width 5.3 mm; paratype 4 RGM.1352252, height 10.9 mm, width 5.5 mm.

Other material – NHMW 2016/0103/2025 (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Sulcomitrella* species of small size, medium-height spire, paucispiral protoconch, five moderately convex teleoconch whorls separated by impressed suture, spire whorls with 2-3 infrasutural cords, last whorl moderately inflated, base and siphonal canal covered in cords, outer lip thickened internally in mid-third, bearing eight denticles, D2 and D3 strongest, narrow columellar callus bearing weak denticles along entire length, siphonal fasciole moderately short.

Description – Shell small, solid, fusiform, with medium-height spire. Protoconch abraded, but paucispiral, composed of just under two whorls. Teleoconch of five moderately convex whorls, separated by deeply impressed suture. Spire whorls sculptured by 2-3 narrow infrasutural cords separated by narrow grooves. Last whorl moderately inflated, 63% total height, weakly convex below suture, rounded at periphery, moderately constricted at base. Base and siphonal fasciole sculptured by narrow cords separated by deep grooves. Aperture 42% total height, elongate, outer lip bearing thickened callus pad within placed at mid-third, bearing about eight denticles, D2 and D3 placed on thickened callus pad strongest; anal canal narrow, rounded; siphonal canal relatively short, open, notched at tip. Columella excavated in upper third, straight below; columellar callus sharp, forming narrow rim, bearing weak denticles along inner edge; parietal callus not developed. Siphonal fasciole relatively short, broad.

Discussion – *Sulcomitrella sceauxensis* nov. sp. is separated from all other Assemblage I *Columbella* and *Mitrella* species in having stronger spiral sculpture consisting of 2-3 infrasutural cords and on the last whorl cords that cover not only the siphonal fasciole, but also extend over the base. The cords are also better defined and separated by deeper and wider grooves. The subsutural grooves seen in this species, combined with the *Mitrella*-like shape, are characteristic of the genus *Sulcomitrella* Kuroda, Habe & Oyama, 1971. Today the genus is Pacific. We are not aware of the use of this genus in the European fossil literature before, but two species in the middle Miocene Paratethys may also be included: *Columbella austriaca* Hoernes & Auinger, 1880 has similar spiral sculpture, but differs in having a smaller aperture, strongly constricted base and a longer sipho-

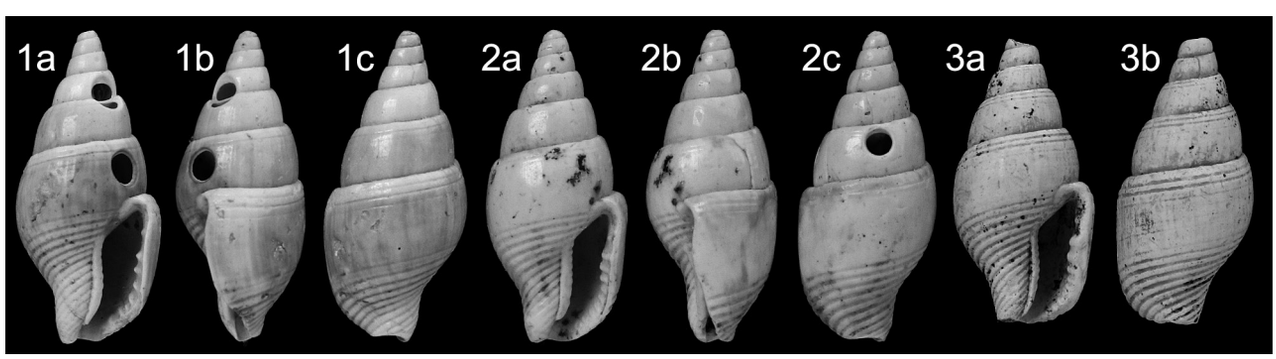


Plate 32. *Sulcomitrella sceauxensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1856, height 9.5 mm, width 5.0 mm; 2. **Paratype 1** RGM.739220, height 9.2 mm, width 5.1 mm; 3. **Paratype 2** RGM.1349090, height 10.0 mm, width 5.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

nal fasciole and *Columbella bellardii* Hörnes, 1852 that differs in having spiral sculpture on the entire surface. *Sulcomitrella sceauxensis* is extremely uncommon in the Assemblage I deposits and has so far only been found at Sceaux-d'Anjou.

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

Family Fasciolariidae Gray, 1853
Subfamily Fasciolariinae Gray, 1853
Genus *Polygona* Schumacher, 1817

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

1817 *Polygona* Schumacher, p. 241.

Note – *Polygona* Schumacher, 1817 is transferred from the Peristerniinae Tryon, 1880 to the Fasciolariinae Gray, 1853 following the molecular phylogeny by Couto *et al*. (2016).

***Polygona substrigosa* nov. nom.**
Plate 33, figs 1-3

1854 *Fusus Strigosus* Millet, p. 162 (*nomen nudum*).
1865 *Fusus strigosus* Millet, p. 590 (*non* Lamarck, 1822).
1964 *Fusinus* (*Aptyxis*) (?) *strigosus* Millet 1854 [*sic*] – Brébion, p. 481, pl. 12, figs 9, 10.

Type material – Syntypes: Thorigné or Sceaux-d'Anjou; Musée d'Angers (*fide* Brébion, 1964, p. 481).

Material and dimensions – Maximum height 29.9 mm, width 10.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1316 (2), FVD (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1828 (3), NHMW 2016/0103/1859-1860 (2), RGM.718115 (32), RGM.734969 (1), RGM.1349168 (10), RGM.1349269 (2), RGM.1352208 (6), RGM.1352230 (16 subadults and juveniles), LC (26).

Etymology – Name including the original specific epithet proposed by Millet, which is a secondary homonym. *Polygona* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Original description – 'Fusus strigosus. *Millet. Coq. fusiforme, de neuf tours de spire et de moitié moins grand que le precedent* [Fusus lepidus], *auquel il ressemble beaucoup, s'en distinguant surtout par sa taille et sa forme plus effilée. On le rencontre ordinairement dans un mauvais état de conservation. Longueur: 15-16 millimètres; diamètre: 6 millimètres. Th., Sc.*' (Millet, 1865, p. 590).

Revised description – Shell small for genus, slender fusiform. Protoconch paucispiral, consisting of 1.5 smooth convex whorls with large nucleus. Teleoconch of seven convex whorls, with periphery just above suture. Suture weakly impressed, broadly undulating. Axial sculpture of seven non-aligned, broad, rounded ribs, slightly narrower than their interspaces. Spiral sculpture of three narrow primary cords, with further secondary cords on subsutural ramp and intercalated between primaries. Close-set axial growth lines most evident on subsutural ramp give surface slightly lamellar appearance. Last whorl strongly inflated mid-whorl and strongly constricted at base, sculpture of narrow alternating cords continues over base. Aperture ovate, small; outer lip thin, deeply lirate within; siphonal canal relatively long, narrow, open, bent abaxially. Columella weakly concave, weakly callused, bearing two narrow folds abapically and a few small tubercles in parietal portion. Siphonal fasciole rounded, forming small umbilical chink.

Discussion – Unfortunately, *Fusus strigosus* Millet, 1865 is a junior homonym of *F. strigosus* Lamarck, 1822 [= *Gracilipurpura rostrata* (Olivi, 1792)]. We introduce the replacement name *Polygona substrigosa* nov. nom. This species is uncommon in Assemblage I, and as rightly commented by Millet (1865, p. 590), the shells are of-

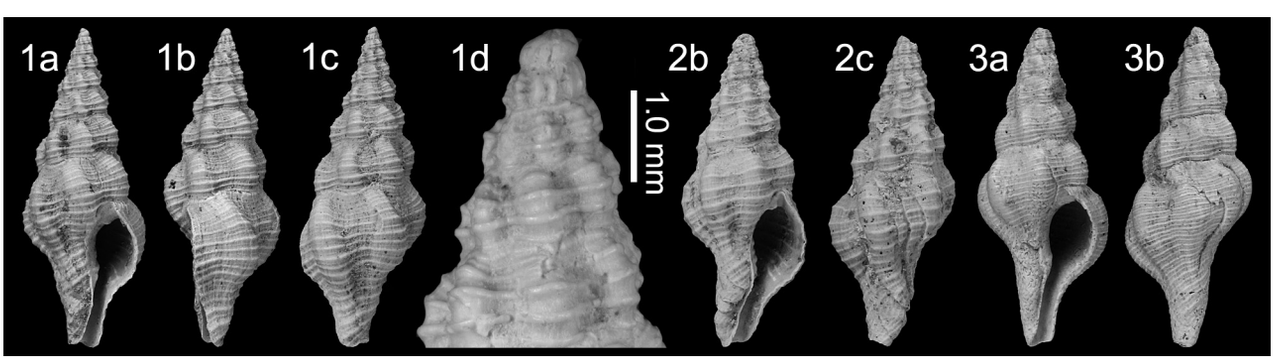


Plate 33. *Polygona substrigosa* nom. nov.; 1. NHMW 2016/0103/1859, height 25.0 mm, width 7.9 mm, 1d, detail of protoconch; 2. NHMW 2016/0103/1860, height 17.2 mm, width 7.0 mm; 3. RGM.734969, height 25.0 mm, width 9.9 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ten poorly preserved. Placement in the genus *Polygona* Schumacher, 1817 follows Vermeij & Snyder (2006), and it is probably closer to the *P. angulata* (Röding, 1798) group that includes some small tropical American species, although the shoulder is less angular than is usual for the group. This is a good example of the presence of dwarf species in Assemblage I belonging to genera that usually have considerably larger shells. Several similar species were described from the Italian Neogene. *Polygona transitans* (Bellardi, 1884) from the lower Pliocene is larger, has eight axial ribs, and the last whorl is not as strongly inflated mid-whorl. Bellardi (1884, p. 22) did not describe the columellar folds, and they are not clearly visible in the syntype figured by Ferrero-Mortara *et al*. (1981, pl. 39, fig. 5), but they are clearly visible in the syntype of the previous species described in Bellardi's '*VIII sezione*', *P. patruelis* (Bellardi, 1884) (Ferrero-Mortara *et al*., 1981, pl. 39, fig. 6), from the lower Miocene, which also has seven axial ribs, but these are aligned vertically and again the last whorl is less inflated mid-whorl. In the lower Miocene of the Aquitaine Basin of France *P. peyreirensis* (Peyrot, 1928) is another similar small species, although larger than *P. substrigosa*. It differs in having eight axial ribs as opposed to seven in *P. substrigosa*, and seven strong folds on the columella, as opposed to two weak ones in *P. substrigosa*.
Brébion (1964, p. 481) recorded this species from the Assemblage I localities of Thorigné, St-Clément-de-la-Place and Sceaux-d'Anjou.

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

Subfamily Fusininae Wrigley, 1927
Genus *Aptyxis* Troschel, 1868

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

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

For generic synonymy see Van Dingenen *et al*. (2017, p. 31).

Note – *Aptyxis* Troschel, 1868 is a small-shelled genus, and therefore not included in the generic revision proposed by Vermeij & Snyder (2018). It was reviewed by Russo (2015), who included two species; the type *Murex syracusanus* Linnaeus, 1758 in the Mediterranean and eastern Atlantic from Portugal to the Canary Islands, and *Fusus luteopictus* Dall, 1877 from the Gulf of California. This disjunct distribution was rectified by Snyder & Vermeij (2016) who considered them not to be congeneric and erected the genus *Hesperaptyxis* for the western American species. Therefore *Aptyxis* is a southern European and tropical/subtropical eastern Atlantic genus since at least the middle Miocene (Landau *et al*., 2013).

***Aptyxis lepidus* (Millet, 1865)**
Plate 34, figs 1-4

1854 *Fusus Lepidus* Millet, p. 162 (*nomen nudum*).
*1865 *Fusus lepidus* Millet, p. 590.
1964 *Fusinus* (*Aptyxis*) *lepidus* Millet, 1854 [*sic*] – Brébion, p. 479, pl. 12, fig. 8.

Type material – Syntypes: Thorigné, Sceaux-d'Anjou and Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 480).

Material and dimensions – Maximum height 19.1 mm, width 8.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1314 (1), NHMW 2016/0103/1325 (2), FVD (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1861 (1), NHMW 2016/0103/1833 (1), NHMW 2016/0103/1326 (2), RGM.1349088 (1), RGM.1349089 (1), RGM.718114 (6 juveniles), LC (4), FVD (1).

Original description – 'Fusus lepidus*, Millet. Coq. allongée, fusiforme, composée de neuf à dix tours de spire, marqués de côtes verticales, croisées par deux ou trois filets tranchants sur les premiers tours et d'un plus grand nombre sur le dernier, mais faisant bosse aiguë sur tous au-dessus des côtes. Ouverture ovale, lisse, terminée par un canal de moyenne longueur. Longueur 35-36 millimètres; diamètre: 15 millimètres. Th., Sc., Ren.*' (Millet, 1865, p. 590).

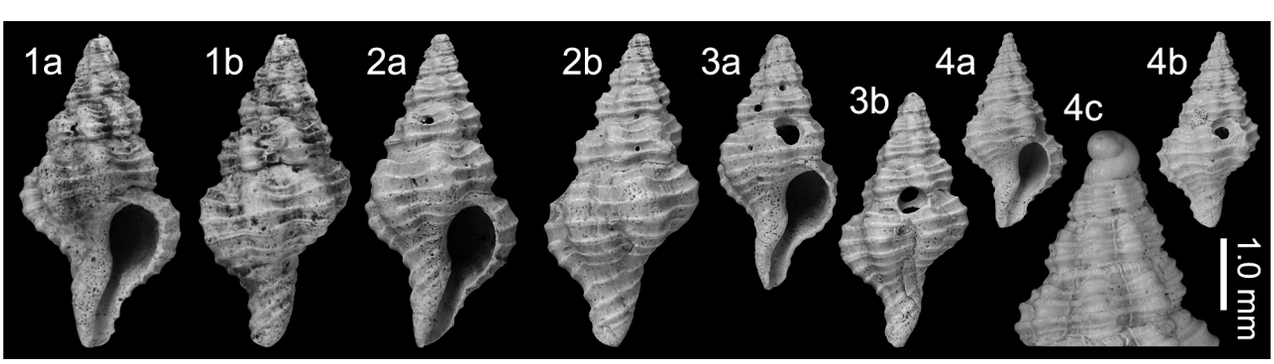


Plate 34. *Aptyxis lepidus* (Millet, 1865); 1. RGM.1349088, height 21.4 mm, width 9.8 mm; 2. NHMW 2016/0103/1861, height 16.1 mm, width 8.0 mm; 3. RGM.1349089, height 14.3 mm, width 6.9 mm; 4. NHMW 2016/0103/1833, height 12.4 mm, width 6.7 mm, 4c, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – We have not found the Assemblage I *Aptyxis* species easy to separate. Most of the material is damaged and/or juvenile, all specimens have a paucispiral protoconch, and the the most common species, *Aptyxis omphale* (Millet, 1864) is extremely variable in shape and sculpture (see below). We have, nevertheless, separated a small number of specimens as *Aptyxis lepidus* (Millet, 1865). We interpret this species as being small, rather broadly fusiform, with strongly convex whorls. The axial ribs are very broad and strongly raised at the periphery and, most importantly, crossed by three narrow elevated spiral cords without secondaries in the interspaces. In all specimens of *A. omphale* cords of secondary and often tertiary strength appear in the interspaces.

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

Aptyxis omphale (Millet, 1864)

Plate 35, figs 1-8

1854 *Fusus Rostratus* Sismonda [*sic*] – Millet, p. 162 (*non Fusus rostratus* Olivi, 1792; *non* Solander, 1766 = *Fusinus sanctaluciae* (von Salis-Marschlins, 1793).
1854 *Fusus Omphale* Millet, p. 162 (*nomen nudum*).
1854 *Fusus Vicinus* Millet, p. 162 (*nomen nudum*).
1854 *Fusus Ventricosus* Millet, p. 162 (*nomen nudum*).
*1864 *Fusus omphale* Millet, p. 674.
1865 *Fusus vicinus* Millet, p. 590.
1865 *Fusus ventricosus* Millet, p. 590 (*non* Lesson, 1842; Menke, 1843 and others).
1938 *Fusus* (*Aptixis* [*sic*]) *rostratus* var. *ligeriana* Peyrot, p. 233, pl. 4, figs 13, 14.
1938 *Fusus* (*Aptixis* [*sic*]) *rostratus* var. *simplicior* Peyrot, p. 234.
1938 *Fusus* (*Aptixis* [*sic*]) *turonensis* Peyrot, p. 235, pl. 4, figs 28, 34 (not fig. 16 as stated in text; *lapsus*).
1952a *Fusus* (*Aptyxis*) *rostratus ligerianus* Peyrot, 1938 – Glibert, p. 349, pl. 11, fig. 3.
1964 *Fusinus* (*Aptyxis*) *ligerianus* Peyrot, 1938 – Brébion, p. 478.
2017 *Aptyxis omphale* (Millet, 1864) – Van Dingenen *et al*., p. 31, pl. 2, figs 5, 6.

Material and dimensions – Maximum height 27.7 mm, width 11.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1317-1320 (4), NHMW 2016/0103/1314 (1), NHMW 2016/0103/1321 (11), NHMW 2016/0103/1325 (2), RGM.1349123 (1), RGM.1349147 (6), RGM.1349157 (7), RGM.1349166 (1), LC (2), FVD (14). **Sceaux-d'Anjou**: NHMW 2016/0103/1322 (1), NHMW 2016/0103/1862 (1), RGM.7349100 (1), RGM.7349101 (50+ subadults and juveniles), RGM.1352229 (12 subadults and juveniles), LC (50+). **Renauleau**: NHMW 2016/0103/1829-1832 (4), NHMW 2016/0103/1834 (40 juveniles).

Discussion – *Aptyxis omphale* (Millet, 1864) is closely similar to the extant type species *A. syracusanus* (Linnaeus, 1758), and exhibits the separation of the last whorl into three sections (subsutural ramp, shoulder to

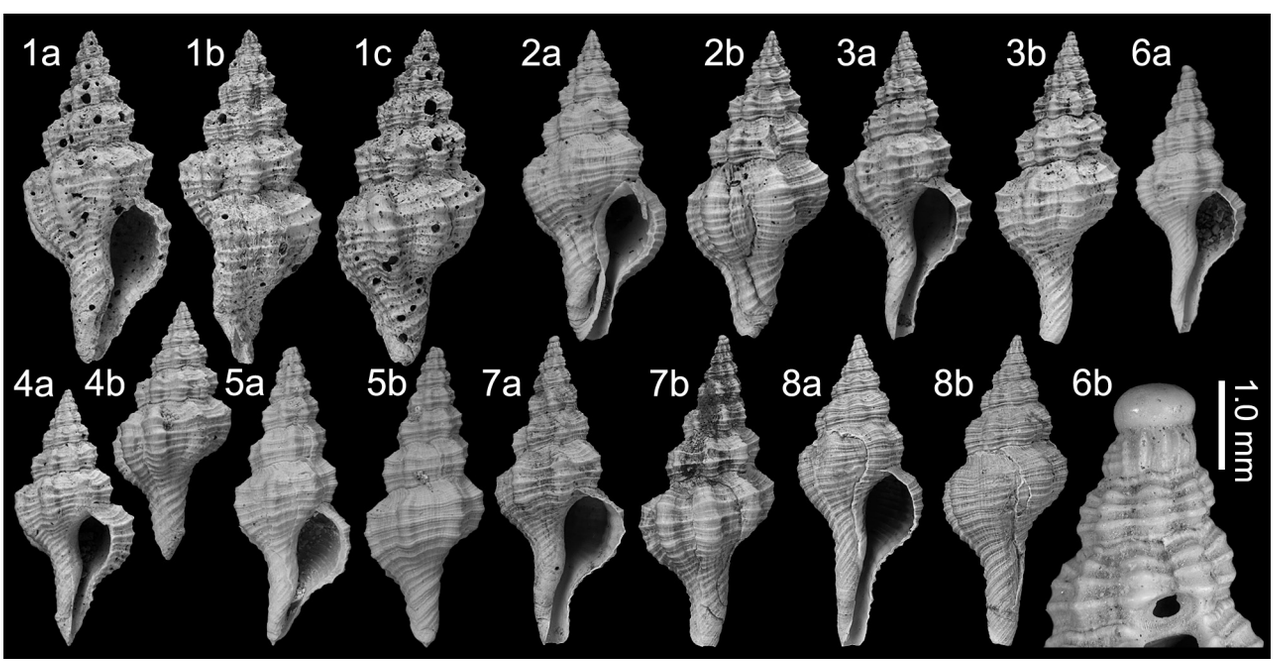


Plate 35. *Aptyxis omphale* (Millet, 1864); 1. NHMW 2016/0103/1829, height 41.7 mm, width 18.5 mm; 2. NHMW 2016/0103/1830, height 24.5 mm, width 10.53 mm; 3. NHMW 2016/0103/1831, height 24.7 mm, width 10.1 mm; 4. NHMW 2016/0103/1832, height 21.9 mm, width 9.9 mm. Renauleau. 5. NHMW 2016/0103/1314, height 24.9 mm, width 9.6 mm; 6. NHMW 2016/0103/1319, height 18.5 mm, width 7.5 mm, 6b; detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 7. NHMW 2016/0103/1862, height 27.5, width 12.0 mm; 8. RGM.1349100, height 29.8, width 12.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

base, base), considered by Russo (2015, fig. 4a) to be typical for the genus. Both have a small paucispiral protoconch composed of about 1.5 whorls, with a large bulbous nucleus, with axial riblets on the last half to one-third protoconch whorl (Pl. 35, fig. 6b). However, *A. omphale* is slightly lower spired than *A. syracusanus*, the subsutural ramp is convex, whereas in *A. syracusanus* it is weakly concave, and there are fewer axial ribs (8-9 vs 11-12). *Fusus lamellosus* Borson, 1821 from the Mediterranean upper Miocene and Pliocene has been placed in the genus/subgenus *Aptyxis* by some authors (*i.e*. Sacco, 1904; Montanaro, 1935; Pelosio, 1967; Pavia, 1976, *inter alii*.). However, that species does not have a tripartite last whorl and it does not have an erect detached abapical portion to the columellar callus, considered by Snyder & Vermeij (2016, p. 124) to be a generic character. *Fusus lamellosus* differs from both species discussed above in having a multispiral protoconch. *Murex affinis* (Bronn, 1831) from the Pliocene of Italy may belong within *Aptyxis*; it has a straight siphonal canal, not upturned at the tip and the columellar callus is weakly erect abapically. It differs from *A. omphale* in being higher spired and having a broader siphonal fasciole. The smaller European Neogene fusinids are still in need of generic revision.

The enormous variability found in this species was discussed at length by Glibert (1952a), who synonymised the various forms described by Peyrot (1938). As illustrated above (Pl. 35, figs 1-8) the specimens from Assemblage I are enormously variable in almost every character. For further discussion see Van Dingenen *et al*. (2017, p. 31).

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

Distribution – Middle Miocene: Atlantic (Langhian) Loire Basin, France (Glibert, 1952a). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Van Dingenen *et al*., 2017).

Subfamily Peristerniinae Tryon, 1880
Genus *Tarantinaea* Monterosato, 1917

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

1917 *Tarantinaea* Monterosato, p. 21.

***Tarantinaea acutangula* (Millet, 1865)**
Plate 36, figs 1-5

1854 *Fusus Acutangulus* Millet, p. 62 (*nomen nudum*).
*1865 *Fusus acutangulus* Millet, p. 590.
1964 *Latirus subspinosus* Bellardi, 1884 – Brébion, 472, pl. 12, figs 1, 2.

Type material – Syntypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 412).

Material and dimensions – Maximum height 29.5 mm, width 10.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1308-1310 (2), NHMW 2016/0103/1311 (1), RGM.1349165 (1), LC (4). **Sceaux-d'Anjou**: NHMW 2016/0103/1312 (1), NHMW 2016/0103/1857 (1), NHMW 2016/0103/1313 (12), RGM.718117 (25), RGM.1349071 (4), RGM.1349102 (2 + 2 fragments + 2 juveniles), RGM. 1349247 (1), RGM.1352209 (4), RGM.1352236 (2 + 4 juveniles), LC (21), FVD (1).

Original description – 'Fusus acutangulus. *Millet. Coq. allongée, effilée, fusiforme, composée de dix tours de spire, marqués de côtes verticales très-espacées, surtout sur le dernier, qui présente trois stries plus fortes que les autres, et dont la supérieure, bornant la rampe en question, se trouve distancée des deux antres qui sont rapprochées entre elles par un espace double de celui qu'occupent ces dernières. Ouverture ovale, terminée par un canal ouvert, et dont la longueur égale celle de l'ouverture. Longueur: 27-28 millimètres; diamètre: 9-10 millimètres*' (Millet, 1865, p. 590).

Discussion – *Fusus acutangulus* Millet, 1865 is similar

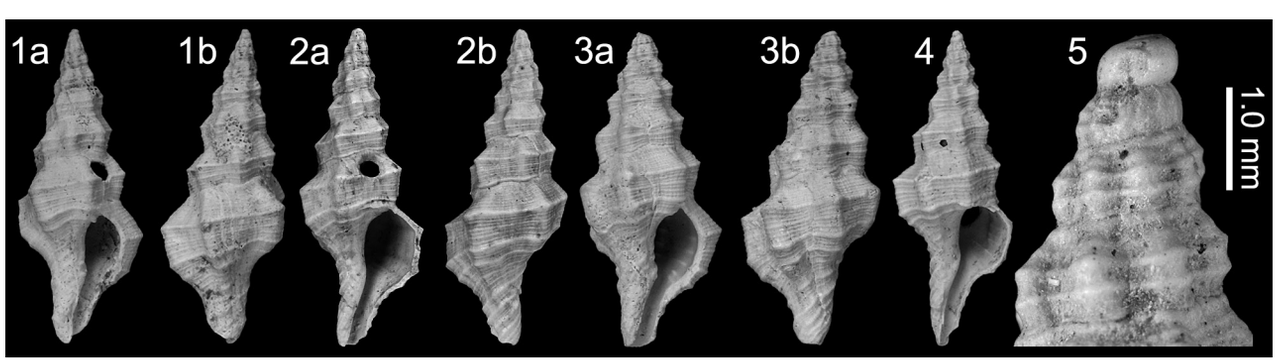


Plate 36. *Tarantinaea acutangula* (Millet, 1865); 1. NHMW 2016/0103/1312, height 17.1 mm, width 6.7 mm; 2. NHMW 2016/0103/1857, height 24.0 mm, 9.1 mm. La Presselière, Sceaux-d'Anjou. 3. NHMW 2016/0103/1308, height 16.2 mm, width 7.2 mm; 4. NHMW 2016/0103/1309, height 16.1 mm, width 5.6 mm; 5. NHMW 2016/0103/1310, height 10.4 mm (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

to *Murex fimbriatus* Brocchi, 1814 from the Pliocene of the Mediterranean, and we follow Snyder *et al*. (2012, p. 55) in placing these species within the Peristerniinae Tryon, 1880, genus *Tarantinaea* Monterosato, 1917. As with *Polygona substrigosa* nom. nov. (see above), this is another example of a usually large-shelled genus being represented by small-shelled species in Assemblage I.

The original description characterises the elongated slender shape of the shell that has strongly angular whorls, and the sculpture composed of nine rounded ribs and three primary spiral cords on the last whorl, the adapical cord delimiting the broad subsutural ramp and two closer-set cords delimiting the base. Between these run numerous fine cords of secondary and tertiary strength. The siphonal canal is moderately long and bears cords equal in strength to the primaries. The aperture is small, the outer lip weakly lirate within, and the columella bears several folds, variably developed. We note that the protoconch is paucispiral, with a large nucleus, suggestive of non-planktotrophic development.

Brébion (1964, p. 472) synonymised Millet's taxon with *Latirus subspinosus* Bellardi, 1884 from the Mediterranean lower Pliocene of Italy, which we also place in *Tarantinaea*. However, *T. acutangula* is only half the maximum height, more slender, the whorls more sharply angular, and the siphonal fasciole is slightly longer. *Tarantinaea subspinosa* is more closely similar to *T. fimbriata*, from which it differs in being smaller, higher spired, less sharply angular at the shoulder and base, and having a shorter siphonal canal. As mentioned above, *T. acutangula* is closely similar to *T. fimbriata*, especially in the strength and position of the primary spiral cords, but smaller and more slender. None of the numerous specimens at hand of *T. fimbriata* have their protoconch preserved, but according to Muñiz Solís (1998, p. 8) it is also paucispiral. Landau *et al*. (2013, p. 198) considered the Miocene references to *T. fimbriata* to represent *T. hoernesii* (Seguenza, 1875), which differs in having a wider apical angle, in having a lower spire with the whorls less stepped, in having sharper sculpture with more strongly developed secondary cords and in having better developed columellar folds. Moreover, it has a multispiral protoconch (Landau *et al*., 2013, pl. 67, fig. 7) as opposed to a paucispiral protoconch in *T. acutangula* and *T. fimbriata*. *Tarantinaea hoernesii* is much larger and broader than *T. acutangula*. Brébion (1964, p. 472) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné, St-Michel and St-Clément-de-la-Place.

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

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

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

1826 *Tritia* Risso, p. 172.

For generic synonymy see Van Dingenen *et al*. (2017, p. 33).

Note – Nassariids became enormously diversified in the European Neogene and are usually abundant in both numbers and species in most assemblages. In the European Pliocene assemblages along the eastern Atlantic frontage revised by our group, NW France Assemblage III yielded 13 species (Van Dingenen *et al*., 2017), the Mondego Basin 24 species, the Guadalquivir Basin 22 species and in the adjacent Mediterranean Estepona Basin 46 species (Landau *et al*., 2009). In the middle Miocene assemblages of the Loire Basin there are at least 13 species (Glibert, 1952a) and in the upper Miocene Tortonian of the Algarve Basin at least 14 (BL unpublished data). Therefore, it is surprising that we were only able to identify six species in the species-rich Assemblage I fauna. However, Brébion (1964) identified 12 species from Assemblage I localities, the ones not verified herein are listed in the discussion at the end of this paper.

Tritia clathrata species group (see Landau *et al*., 2009, p. 5).

***Tritia brugnonis* (Bellardi, 1882)**
Plate 37, figs 1, 2

1866 *Buccinum prismaticum* [*sic*] Brocc. – Pereira da Costa, p. 99, pl. 14, fig. 16 [*non Tritia prysmatica* (Brocchi, 1814)].
*1882 *Nassa Brugnonis* Bellardi, p. 73, pl. 5, fig. 2.
1927 *Nassa* (*Uzita*) *Brugnonis* Bellardi – Peyrot, p. 57, pl. 2, figs 37, 39.
1964 *Niotha emiliana* Mayer, 1872 – Brébion, p. 470, pl. 11, fig. 38 [*non Tritia emiliana* (Mayer, 1872)].
1976 *Nassarius brugnonis* (Bellardi, 1882) – Adam & Glibert, p. 15, pl. 1, fig. 4, pl. 4, figs 1, 2.

Material and dimensions – Maximum height 22.0 mm, width 10.1 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1858 (1), LC (1).

Discussion – We ascribe two specimens from Sceaux-d'Anjou to *Tritia brugnonis* (Bellardi, 1882). The protoconch and sculpture agree with that described by Adam & Glibert (1976) for the species in their revision of the *T. clathrata* species group. Compared to specimens at hand from Cacela Velha, included by those authors in *T. brugnonis*, the shells from Sceaux-d'Anjou are more solid and the apertural armature is stronger. However, we consider these differences to fall within the intraspecific variability for the species, especially as we only have two specimens from Assemblage I to compare. The specimen from Sceaux d'Anjou identified by Brébion as *Niotha emiliana* Mayer, 1872 (1964, p. 470, pl. 11, fig. 38) is probably also *T. brugnonis*. It is not *T. emiliana*, which has finer sculpture, predominantly spiral on the last whorl,

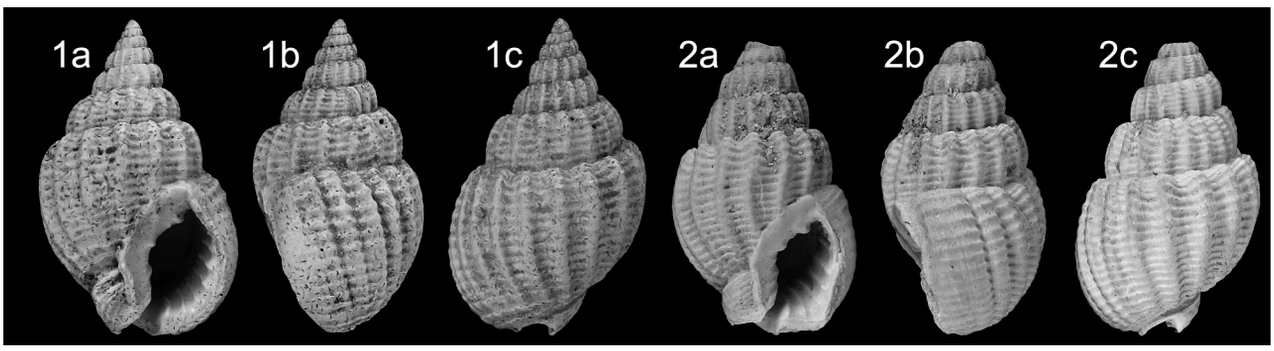


Plate 37. *Tritia brugnonis* (Bellardi, 1882); 1. NHMW 2016/0103/1858, height 22.0 mm, width 10.1 mm; 2. LC coll., height 17.3 mm, width 10.2 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

a weaker labial varix and a very narrow, hardly thickened columellar callus rim (see Adam & Glibert, 1976, pl. 4, figs 8, 9). *Tritia brugnonis* is also closely similar to *T. contorta* (Dujardin, 1837) (see Glibert, 1952a, pl. 10, fig. 8), which has an identical multispiral protoconch of three smooth whorls, but in that species the last whorl is larger in comparison to the total height, the whorls are less convex, the flattened cords are separated by narrower grooves and according to the original figure (Dujardin, 1837, pl. 20, fig. 1) and the description given by Glibert (1952a, p. 343) the labial varix is narrow and the apertural armature weak.

Distribution – Middle Miocene: Atlantic (Langhian), Aquitaine Basin (Peyrot, 1927). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964), Algarve Basin, Portugal (Pereira da Costa, 1866; Adam & Glibert, 1976), Morocco (Adam & Glibert, 1976); central Proto-Mediterranean (Bellardi, 1882).

***Tritia spectabilis* (Nyst, 1845)**
Plate 38, figs 1-3

1837 *Buccinum elegans* Dujardin, p. 298 (*non* J. Sowerby, 1825; *nec* O.G. Costa, 1830; *nec* Kiener, 1834).
*1845 *Buccinum spectabilis* Nyst, p. 577.
1852 *Buccinum prismaticum* [*sic*] Brocc. – Hörnes, p. 146, pl. 12, figs 13, 14 [*non Tritia prysmatica* (Brocchi, 1814)].
1854 *Nassa Isolita* Millet, p. 164 (*nomen nudum*).
1865 *Nassa insolita* Millet – Millet, p. 596.
1882 *Nassa* (*Caesia*) *limata* Chemn. – Hoernes & Auinger, p. 130, pl. 13, figs 2-7 [*non* Chemnitz, 1786, work invalidated ICZN, Direction 1, 1954; = *Tritia limata* (Deshayes *in* Lamarck, 1844)].
1906 *Nassa* (*Caesia*) *limata* Chemn. – Boettger, p. 26 [*non* Chemnitz, 1786, see above].
1911 *Nassa limata* Chemnitz – Friedberg, p. 88, pl. 5, figs 7, 8 (*non* Chemnitz, 1786, see above).
1938 *Nassa* (*Uzita*) *spectabilis* Nyst – Peyrot, p. 217, pl. 4, figs 41, 50.
1951 *Nassa limata* Chemn. – Friedberg, p. 86, pl. 5, figs 7, 8 [*non* Chemnitz, 1786, see above].
1952a *Nassa* (*Uzita*) *spectabilis* Nyst, 1843 – Glibert, p. 346, pl. 10, fig. 11.
1958 *Hinia* (*Uzita*) *limata* (Chemnitz) – Beer-Bistrický, p. 60, pl. 2, fig. 13 [*non* Chemnitz, 1786, see above].
1958 *Nassa* (*Hima*) cf. *incrassata* (Müller) – Erünal-Erentöz, p. 68, pl. 11, fig. 1 [*non Tritia incrassata* (Müller, 1776)].
1960 *Nassa* (*Hinia*) *limata* (Chemnitz 1786) – Kojumdgieva & Strachimirov, p. 177, pl. 44, fig. 11 [*non* Chemnitz, 1786, see above].
?1964 *Hinia* (*Uzita*) *caroli* Dollfus & Dautzenberg, 1886 – Brébion, p. 450 [*non Tritia caroli* (Dollfus & Datzenberg, 1886)].
1964 *Hinia* (*Uzita*) *spectabilis* Nyst, 1843 – Brébion, p. 452.
1966 *Nassa* (*Tritia*) *limata* Chemnitz 1786 – Strausz, p. 312, pl. 37, figs 22, 23 [*non* Chemnitz, 1786, see above].
1968 *Nassa limata* Chemnitz, 1782 [*sic*] – Zelinskaya *et al*., p. 194, pl. 46, figs 3, 4 (*non* Chemnitz, 1786, see above).
1973 *Hinia* (*Uzita*) *limata* Chemnitz – Steininger, p. 424, pl. 6, fig. 11 [*non* Chemnitz, 1786, see above].
1976 *Nassarius spectabilis spectabilis* (Nyst, 1843) – Adam & Glibert, p. 41, pl. 2, fig. 4, pl. 5, fig. 10.
1985 *Hinia* (*Uzita*) *limata* Chemnitz – Atanacković, p. 157, pl. 35, figs 9, 10) [*non* Chemnitz, 1786, see above].
1993 *Nassarius* (*Hinia*) *limatus* (Chemnitz, 1786) – Iljina, p. 91, pl. 11, fig. 29 (*non* Chemnitz, 1786, see above).
1997 *Hinia* (*Uzita*) *limata* (Chemnitz, 1786) – Bałuk, p. 15, pl. 2, figs 1, 2 [*non* Chemnitz, 1786, see above].
1998 *Hinia* (*Uzita*) *clathrata* (Born, 1778) – Schultz, p. 66, pl. 26, fig. 18 [*non Tritia clathrata* (Born, 1778)].
2003 *Nassarius limatus* (Chemnitz, 1786) – Złotnik, p. 363, fig. 3 K-L [*non* Chemnitz, 1786, see above].
2004 *Nassarius spectabilis* (Nyst, 1843) – Harzhauser & Kowalke, p. 21, pl. 2, fig. 20, pl. 3, fig. 1.
2009 *Hinia* (*Uzita*) *limata* (Chemnitz, 1786) – Mikuž,

p. 22, pl. 6, figs 77, 78 [*non* Chemnitz, 1786, see above].

2013 *Nassarius spectabilis* (Nyst, 1845) – Landau *et al*., p. 172, pl. 21, fig. 17; pl. 64, fig. 9.

Material and dimensions – Maximum height 18.0 mm, width 9.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0843-0845 (3), NHMW 2016/0103/0846 (50+), RGM.1348858 (8), RGM.1349052 (5), RGM.1349054 (50+), RGM.1349072 (50+), RGM.1349073 (50+ juveniles), RGM.1349153 (27), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0847 (16), RGM. 1348798 (3), RGM.718110 (50+), RGM.1349049 (50+), RGM.1349050 (16), RGM.1349051 (50+ juveniles), RGM.1349053 (5 + 40 juveniles), RGM.1349069 (50+), RGM.1349139 (15), RGM.1349250 (20 fragments and juveniles), RGM.1352231 (27 fragments), LC (2), FVD (5). **Renauleau**: NHMW 2016/0103/0848 (26), LC (50+), FVD (30). **Beugnon**: RGM.1349055 (3 fragments), RGM.1349056 (1), RGM.1349081 (1 + 6 juveniles), RGM. 1349121 (1 + 6 fragments).

Dicussion – Although the title page of Nyst's work is dated 1843, it was not published until 1845 (for additional data, see Anderson, 1964, p. 121). *Tritia spectabilis* (Nyst, 1845) is a small member of the *Tritia clathrata* species group (see Landau *et al*., 2009, p. 5), characterised by its dome-shaped multispiral protoconch composed of 3-3.25 smooth whorls, with a small nucleus. The spire is conical, composed of relatively strongly convex whorls. The sculpture is relatively weak, consisting of 13-20 narrow axial ribs, occasionally one or two ribs become varicose, overrun by 9-11 fine spiral cords separated by even narrow interspaces, the adapical three cords stronger in most specimens. The last whorl is moderately globose, the aperture ovate, the outer lip somewhat thickened by a modest labial varix, bearing 12-15 short lirations within. Within these parameters, the spire angle, globosity of the last whorl, number and strength of varices if present, strength of the labial denticles and formation of a well-defined columellar callus are all rather variable.

As discussed by Adam & Glibert (1976), this species has often been recorded in the Miocene fossil literature as *Nassa* or *Hinia limata* (Chemnitz, 1786) [work invalidated ICZN, Direction 1, 1954; = *Tritia limata* (Deshayes *in* Lamarck, 1844)], but that Pliocene to present-day Mediterranean species is larger and has a paucispiral protoconch of less than two whorls. *Tritia spectabilis* is found exclusively in the Miocene along the Atlantic frontage of France and the Paratethys, and was recently recorded in the eastern Proto-Mediterranean (Landau *et al*., 2013). *Tritia spectabilis* is also similar to *T. prysmatica* (Brocchi, 1814), which also has a multispiral protoconch, but more slender than that of *T. spectabilis*. *Tritia caroli* (Dollfus & Dautzenberg, 1886) is another closely similar species from the middle Miocene of the Loire Basin that differs from *T. spectabilis* in having a more slender shell, with more numerous, narrower, more elevated ribs and more regular spiral cords, separated by deeper interspaces, a stronger labial varix thickening the outer lip, and the adapical four denticles are stronger than the abapical ones, whereas in *T. spectabilis* the denticles are more numerous and equal in strength (Peyrot, 1938, p. 221). Brébion (1964, p. 450) recorded, but did not figure, *T. caroli* from various Assemblage I localities including a large number from Sceaux-d'Anjou. The degree of slenderness is highly variable in *T. spectabilis*, but considering the apertural characters alone, all the Assemblage I specimens are attributable to that species and none to *T. caroli*.
Adam & Glibert (1976) recognised a North Sea Basin Pliocene chrono-subspecies, *T. spectabilis vandewouweri* (Glibert, 1959), which differs from the type in having a more elongated shell with even finer sculpture. We prefer to keep them separate at full species rank.
Tritia spectabilis has been recorded from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and St-Michel (Millet, 1854, 1865; Brébion, 1964, p. 452; Adam & Glibert, 1976, p. 41), to which we add St-Clément-de-la-Place and Renauleau, and the Assemblage II locality of Apigné (Adam & Glibert, 1976, p. 42).

Distribution – Lower Miocene: Paratethys, Austria (Stei-

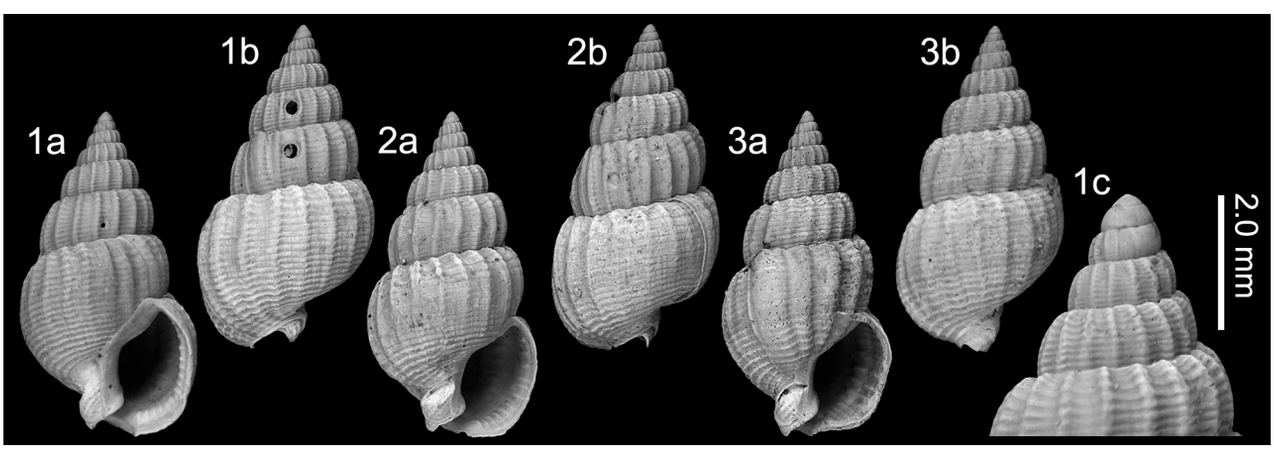


Plate 38. *Tritia spectabilis* (Nyst, 1845); 1. NHMW 2016/0103/0843, height 16.1 mm, width 8.4 mm, 1c. detail of protoconch; 2. NHMW 2016/0103/0844 height 16.0 mm, width 8.2 mm; 3. NHMW 2016/0103/845 height 18.0 mm, width 9.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ninger, 1973). Middle Miocene: Atlantic (Langhian), Aquitaine Basin (Adam & Glibert, 1976), Loire Basin, France (Peyrot, 1938; Glibert, 1952a; Adam & Glibert, 1976); Paratethys, Austria (Hörnes, 1852; Hoernes & Auinger, 1882; Beer-Bistrický, 1958; Schultz, 1998; Harzhauser & Kowalke, 2004), Bosnia (Atanacković, 1985), Bulgaria (Kojumdgieva & Strachimirov, 1960), Hungary (Strausz, 1966), Poland (Friedberg, 1951; Bałuk, 1997; Adam & Glibert, 1976), Romania (Boettger, 1906), Slovenia (Mikuž, 2009), Ukraine (Zelinskaya *et al*., 1968), eastern Paratethys (Tarkhanian and Chokrakian) (Iljina, 1993); Proto-Mediterranean (Serravallian), Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1865; Brébion, 1964; Adam & Glibert, 1976).

***Tritia turtaudierei* nov. sp.**
Plate 39, figs 1-4

1964 *Niotha milleti* Brébion, p. 469, pl. 11, fig. 37 (*nomen nudum*).

Type material – Holotype MNHN.F.A66737, height 15.4, width 9.2 mm; paratype 1 MNHN.F.A66738, height 15.7 mm, width 10.5 mm; paratype 2 NHMW 2016/0103/1679, height 15.6 mm, width 10.3 mm; paratype 3 NHMW 2016/0103/1680, height 15.4 mm, width 9.3 mm; paratype 4 NHMW 2016/0103/1681, height 13.6 mm, width 9.6 mm; paratype 5 RGM.1349038, height 14.2 mm, width 9.0 mm; paratype 6 RGM.1349039, height 16.8 mm, width 11.5 mm; paratype 7 RGM.1349040, height 8.7 mm, width 9.3 mm; paratype 8 NHMW 2016/0103/1848, height 15.2 mm, width 10.2 mm; paratype 9 NHMW 2016/0103/1849, height 15.1 mm, width 10.1 mm.

Other material – Maximum height 16.8 mm, width 11.5 mm. **St-Clément-de-la-Place**: LC (1 fragment). **Sceaux-d'Anjou**: NHMW 2016/0103/1809 (10), RGM.718113 (50+), RGM.1349057 (5 + 20 juveniles and fragments), RGM.1349058 (14), RGM.1349064 (7 juveniles), RGM. 1349082 (21 juveniles), RGM.1349178 (2 + 3 juveniles), RGM.1349238 (1 fragment), RGM.1349252 (2 juveniles), RGM.1352219 (4 juveniles), RGM.1352224 (10 + 2 juveniles), RGM.1352232 (2 juveniles), LC (3), FVD (14).

Etymology – Respecting Brébion's wishes, named after Pierre-Aimé Millet de la Turtaudière (1783-1873), French naturalist and Secrétaire Général de la Société d'Agriculture d'Angers in recognition of his pioneering work on the upper Miocene assemblages of northwestern France. *Tritia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Tritia* species of medium-size, solid, with low conical spire, globose last whorl, paucispiral protoconch of two whorls, with medium sized nucleus, low spire whorls sculptured by 7-9 weak narrow cords, axial sculpture appears on penultimate whorl, about 30 low, narrow, prosocline ribs, outer lip bearing about ten interrupted lirae within, columella and parietal callus forming

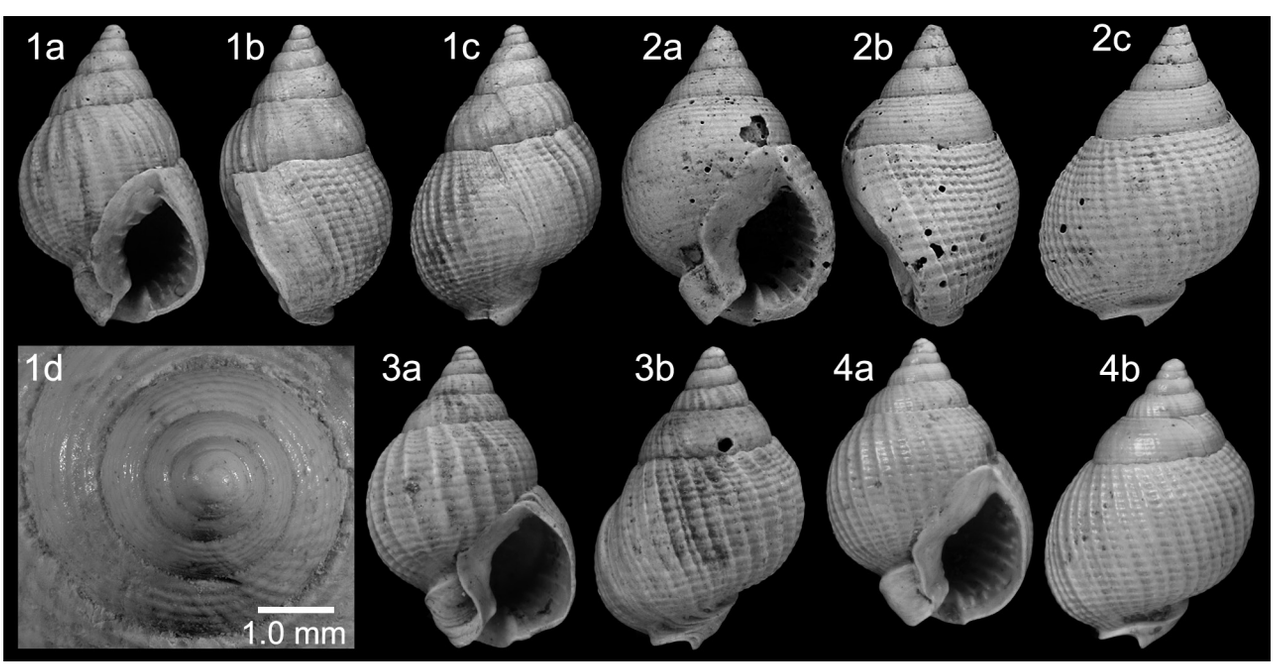


Plate 39. *Tritia turtaudierei* nov. sp.; 1. **Holotype** MNHN.F.A66737, height 15.4, width 9.2 mm, 1d, detail of protoconch; 2. **Paratype 1** MNHN.F.A66738, height 15.7 mm, width 10.5 mm; 3. **Paratype 8** NHMW 2016/0103/1848, height 15.2 mm, width 10.2 mm; 4. **Paratype 9** NHMW 2016/0103/1849, height 15.1 mm, width 10.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

wide callus rim, erect abapically, with about five strong tubercles or ridges at inner edge.

Description – Shell medium-sized, solid, low conical spire, globose last whorl. Protoconch paucispiral, composed of two smooth whorls, with medium sized nucleus. Teleoconch of five convex whorls, with periphery at abapical suture. Suture impressed, linear. Spire whorls depressed, sculptured by low, narrow spiral cords separated by weak grooves, 7-9 on penultimate whorl. Axial sculpture starts on penultimate whorl, 30-50 low, narrow, prosocline ribs that tend to weaken further on dorsum of last whorl and strengthen again over outer lip. Last whorl strongly inflated, globose 74-78% total height, evenly convex, strongly constricted at base. Aperture 41-47% total height, ovate, outer lip hardly thickened by varix, flared abapically, strongly prosocline on lateral view, bearing about ten strong, irregular, interrupted lirae that extend a short distance within the aperture; the abapical denticles, delimiting the lateral border of the siphonal canal, strongest. Columella concave, excavated in mid-portion. Columellar and parietal callus continuous, thickened, sharply delimited, forming a broad callus rim, erect over siphonal fasciole and base, apressed in parietal region, bearing about five strong tubercles or ridges at inner edge. Siphonal fasciole short, flattened, separated from base by rounded groove.

Discussion – *Tritia turtaudierei* nov. sp., with its short spire, globose last whorl and fine sculpture in which the axial ribs only start on the penultimate whorl, cannot be confused with any of its Assemblage I congeners. As pointed out by Brébion (1964, p. 469) it is a little variable in spire height, in number of axial ribs and apertural armature. That author recorded a maximum height for the species of 24.0 mm, but we have not encountered any specimens that large. *Tritia crossei* (Mayer, 1862) from the middle Miocene Langhian of the Loire Basin, is very similar in shape and size, but differs in having fewer ribs (20 vs 30-50) and cords (5 vs 7-9). *Tritia crossei* must be uncommon in the Loire assemblages, as Glibert (1952a, p. 335) could not attribute any specimens to this species with certainty. *Tritia contorta* (Dujardin, 1837), also from the Loire Basin, bears a superficial resemblance to *T. turtaudierei*, but has a higher spire, far fewer axial ribs and weak apertural armature.
Brébion (1964, p. 470) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and St-Clément-de-la-Place.

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

Tritia incrassata species group (see Landau *et al*., 2009, p. 33).

***Tritia blesensis* (Mayer, 1862)**
Plate 40, figs 1-3

1854	*Nassa Modesta* Millet, p. 164 (*nomen nudum*).
*1862	*Buccinum Blesense* Mayer, p. 268, pl. 12, fig. 7.
1865	*Nassa modesta* Millet, p. 595.
1952a	*Nassa* (*Hima*) *blesensis* Mayer, 1862 – Glibert, p. 341, pl. 10, fig. 6.
1964	*Hinia* (*Tritonella*) *blesensis* Mayer, 1862, p. 462.

Material and dimensions – Maximum height 8.5 mm, width 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0825-0826 (2), NHMW 2016/0103/0827 (6), RGM.1349213 (4), LC (1), FVD (2). **Sceaux-d'Anjou**: NHMW 2016/0103/0828 (1), NHMW 2016/0103/0829 (39), RGM.718111 (50+), RGM.1349140 (24), RGM.1349154 (15), RGM.1349237 (1), RGM.1349244 (18), RGM.1352233 (9), LC (3), FVD (21). **Beugnon**: RGM.1349122 (5).

Discussion – *Tritia blesensis* (Mayer, 1862) is a member of the *Tritia incrassata* species group (see Landau *et al*., 2009, p. 33; originally described as *Nassarius incrassatus* species group), characterised by their small, relatively robust shells, with a more or less elevated spire, convex whorls, reticulate sculpture, outer lip strongly thickened by a prominent labial varix, denticulate within. These species have traditionally been placed within the genus or subgenus *Hima* Leach *in* Gray, 1847, which is now considered a synonym of *Tritia*. All members of this group have a multispiral dome-shaped protoconch

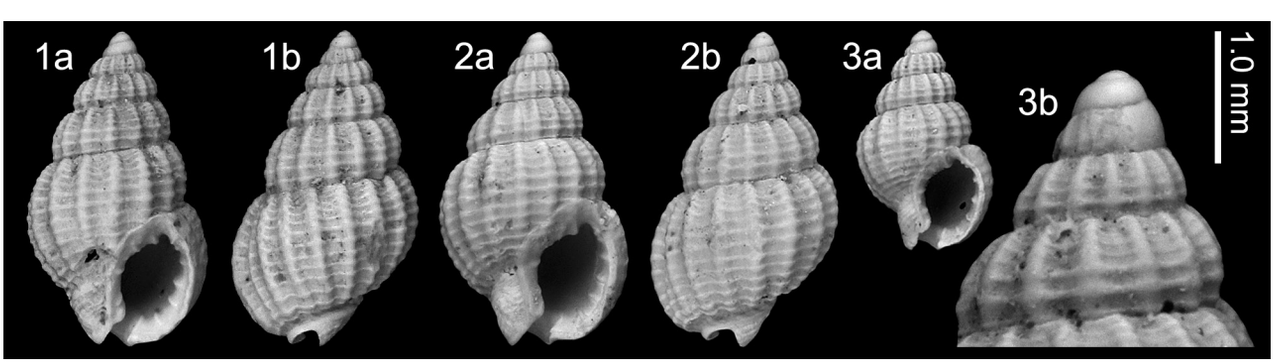


Plate 40. *Tritia blesensis* (Mayer, 1862); 1. NHMW 2016/0103/0828, height 8.5 mm, width 4.7 mm. La Presselière, Sceaux-d'Anjou. 2. NHMW 2016/0103/0825, height 7.7 mm, width 4.3 mm; 3. NHMW 2016/0103/0826 height 6.5 mm (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

of about 3-3.5 whorls. *Tritia blesensis* has a rather low spired squat shell with a moderately globose last whorl. The aperture is small with well developed apertural armature. It differs from the Pliocene to present-day European Atlantic and Mediterranean *T. incrassata* (Ström, 1768) in being smaller, with a less inflated last whorl, and having a smaller aperture surrounded by stronger apertural armature. *Tritia angulata* (Brocchi, 1814), from the upper Miocene to Pleistocene Mediterranean and adjacent Atlantic is similar in size to *T. blesensis*, but has less convex whorls, a more inflated last whorl, and a larger aperture with weaker denticles within the outer lip. *Tritia asperula* (Brocchi, 1814) from the Pliocene of the Mediterranean and adjacent Atlantic is taller spired than *T. blesensis*, with more convex whorls. *Tritia turgens* (Bellardi, 1882) from the upper Miocene and Pliocene of the Mediterranean is extremely similar to *T. blesensis* in almost every character. The syntype illustrated by Ferrero Mortara *et al*. (1981, pl. 27, fig. 4) has a rib less per whorl and slightly less convex whorls, but it is difficult to highlight a constant feature that separates the two. We have not seen *T. turgens* from the Pliocene type locality of Villalvernia, Italy and therefore hesitate to synonymise the two. If they are found to be synonymous, Mayer's (1862) senior name takes priority.
Brébion (1964, p. 462) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and St-Clément-de-la-Place, to which we add Beugnon.

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

***Tritia turonensis* (Deshayes, 1844)**
Plate 41, figs 1-5

1837	*Buccinum graniferum* Dujardin, p. 299, pl. 20, figs 10, 11 [*non Nassarius graniferus* (Kiener, 1834), now accepted as *N. granifer* (Kiener, 1834)].
*1844	*Buccinum Turonense* Deshayes, p. 223 (*nom. nov. pro Buccinum graniferum* Dujardin, 1837).
1872	*Nassa granifera* Dujardin – S.V. Wood, p. 11, pl. 6, fig. 11 [*non Nassarius graniferus* (Kiener, 1834)].
1914	*Nassa turonica* (Deshayes) – Harmer, p. 85, pl. 5, figs 14, 15.
1918	*Nassa* (*Hima*) *turonica* (Deshayes) – Harmer, p. 328, pl. 34, figs 11-14.
1925	*Nassa* (*Hima*) *turonensis* (Deshayes) – Peyrot, p. 144, pl. 3, figs 34-36.
1952a	*Nassa* (*Hima*) *verrucosa* Brocchi, 1814 – Glibert, p. 340, pl. 10, fig. 5 (*non* Brocchi).
1964	*Hinia* (*Tritonella*) *verrucosa* Brocchi, 1814 – Brébion, p. 463 (*non* Brocchi).
2015	*Nassarius turonensis* (Deshayes, 1844) – Van Dingenen *et al*., p. 87, pl. 4, figs 5-8, pl. 9, fig. 3.
2017	*Tritia turonensis* (Deshayes, 1844) – Van Dingenen *et al*., p. 34.

Material and dimensions – Maximum height 8.6 mm, width 4.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0818-0822 (5), NHMW 2016/0103/0823 (50+), RGM.1349087 (50+), RGM.1349214 (50+), RGM.1352221 (8), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0824 (35), RGM.718112 (50+), RGM.1349085 (2), RGM.1349141 (26), RGM.1349267 (6), RGM.1352234

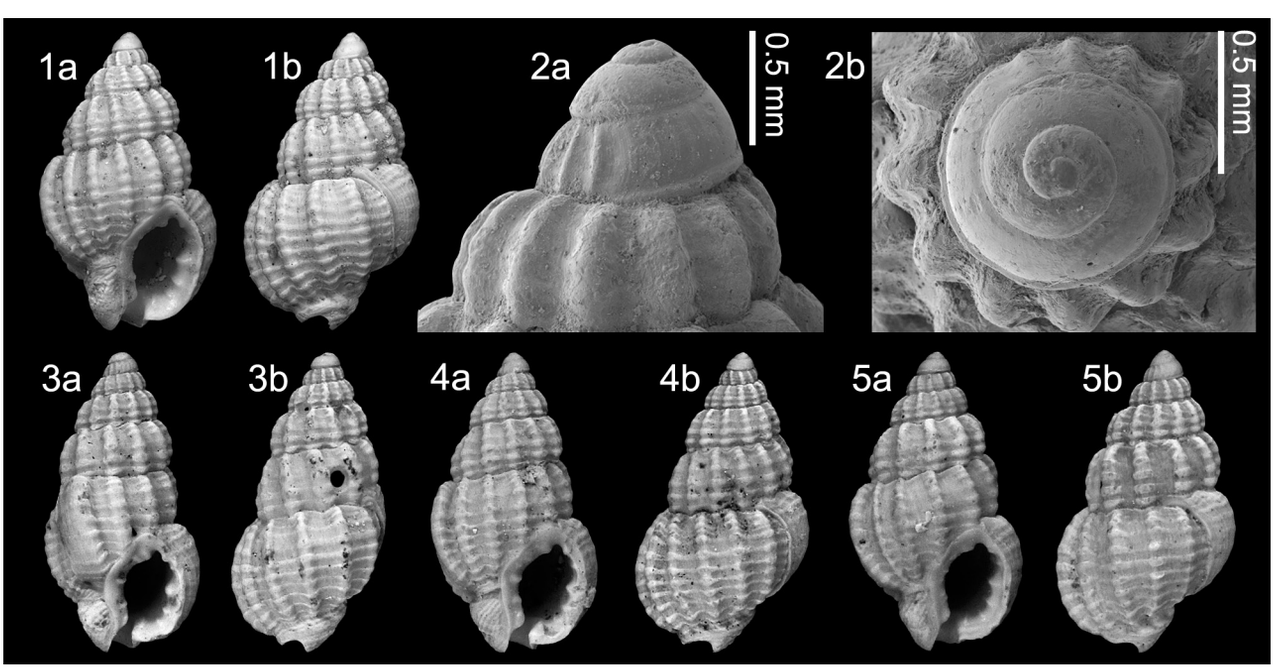


Plate 41. *Tritia turonensis* (Deshayes, 1844); 1. NHMW 2016/0103/0818, height 7.1 mm, width 4.1 mm; 2. NHMW 2016/0103/0819 (juvenile), detail of protoconch (SEM image); 3. NHMW 2016/0103/0820 height 8.1 mm, width 4.2 mm; 4. NHMW 2016/0103/821 height 8.1 mm, width 4.4 mm; 5. NHMW 2016/0103/0822 height 7.2 mm, width 4.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(19), LC (4), FVD (18). **Renauleau**: NHMW 2016/0103/1471 (35), LC (50+), FVD (50+).

Discussion – Like *Tritia blesensis* (Mayer, 1862) (see above), *T. turonensis* (Deshayes, 1844) is a member of the *Tritia incrassata* species group (see Landau *et al*., 2009, p. 33). For discussion on the species name, see Van Dingenen *et al*. (2015, p. 87). As in the lower Pliocene Assemblage III locality of Le Pigeon Blanc, it is the most abundant nassariid and the shells are highly variable in spire height. In adult shells a large varix is formed on the venter of the last whorl, about 60º from the aperture. In some specimens a varix is also present on the penultimate whorl. The axial sculpture consists of 9-13 ribs and six or seven narrow cords separated by wider interspaces on the penultimate whorl. The last whorl is strongly convex, with a groove separating the base from the siphonal fasciole. The inner lip bears four or five irregular denticles a short distance within, D2 is more strongly developed. The medial side of the aperture is bordered by a thickened callus rim, which is not expanded onto the venter, and bears two or three strong abapical and one or two parietal tubercles. The protoconch is multispiral, dome-shaped, consisting of 3.5 smooth whorls with a small nucleus, similar to that illustrated by Van Dingenen *et al.* (2015, pl. 9, fig. 3) for the Le Pigeon Blanc specimens. In the Assemblage I specimens an abapical cord, placed just above the suture, delimits the periphery of the last two protoconch whorls (Pl. 41, fig. 2a). This feature was not commented on by Van Dingenen *et al*., as the material from Assemblage III is not as well preserved, but can just be see in the Le Pigeon Blanc specimen illustrated as well (Van Dingenen *et al*., 2015, pl. 9, fig. 3a).
Tritia turonensis differs from *T. blesensis* in having fewer axial ribs, a less inflated last whorl that carries at least one strong varix, and a smaller aperture with stronger labial dentition. *Tritia asperula* (Brocchi, 1814) from the Pliocene of the Mediterranean and adjacent Atlantic usually also has varices on the last two whorls, but that species is taller spired, with a larger aperture and weaker apertural dentition.
Brébion (1964, p. 464) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné, St-Michel), to which we add St-Clément-de-la-Place and Renauleau, Assemblage II (Apigné), Assemblage III (Le Pigeon Blanc, Palluau, Le Girondor, La Dixmérie, Le Temple du Cerisier) and Assemblage IV (Le Bosq d'Aubigny, Gourbesville).

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Dujardin, 1837; Peyrot, 1925; Glibert, 1952a; Harmer, 1914, 1918). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964). Lower Pliocene: Atlantic NW France (Brébion, 1964; Van Dingenen *et al*., 2015, 2017); NSB, Coralline Crag Formation, England (S.V. Wood, 1872; Harmer, 1914). Upper Pliocene: NSB, Red Crag Formation, England (S.V. Wood, 1872; Harmer, 1914). Upper Pliocene-lower Pleistocene: Atlantic, upper Piacenzian-lower Gelasian, NW France (Brébion, 1964). Lower Pleistocene: Atlantic (Gelasian), St. Erth Formation, England (Harmer, 1914, 1918).

Tritia pyrenaica species group (see Landau *et al*., 2009, p. 25).

***Tritia pyrenaica* (Fontannes, 1879)**
Plate 42, figs 1-8

*1879	*Nassa pyrenaica* Fontannes, p. 72, pl. 5, figs 17, 18.
1925	*Nassa* (*Amycla*) *Lambertiei* Peyrot, p. 169, pl. 3, figs 84, 86.
1964	*Amyclina* cf. *lambertiei* Peyrot, 1927 [*sic*] – Brébion, p. 435, pl. 10, figs 34-39.
2009	*Nassarius pyrenaicus* (Fontannes, 1879) – Landau *et al*., p. 27, pl. 5, figs 8-12, pl. 17, fig. 3 (*cum syn*.).

Material and dimensions – Maximum height 20.8 mm, width 8.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0849-0853 (5), NHMW 2016/0103/0854 (20), RGM.1349079 (11), RGM.1349086 (5), RGM.1349191 (1), LC (22), FVD (8). **Sceaux-d'Anjou**: NHMW 2016/0103/0855 (38), NHMW 2016/0103/1835-1837 (3), RGM.718109 (50+), RGM.1349060 (24), RGM.1349063 (27), RGM.1349084 (5 fragments), RGM.1349231 (3), RGM.1349243 (8), RGM.1349271 (13), RGM.1349273 (15), RGM.1352198 (13), RGM.1352202 (50+), RGM.1352245 (18), RGM.1352575 (3), LC (21), FVD (17). **Renauleau**: NHMW 2016/0103/1413 (2), LC (10), FVD (3).

Discussion – *Tritia pyrenaica* (Fontannes, 1879) belongs to the *Tritia pyrenaica* species group (see Landau *et al*., 2009, p. 25), characterised by having small ovate, glossy shells, of medium thickness, relatively weakly sculptured; sculpture usually restricted to the early teleoconch whorls, the outer lip is simple, or weakly thickened by labral varix, the parietal callus is usually greatly expanded, closely adherent, but poorly delimited, blending in with the glossy surface. Species of the *N. pyrenaicus* group have sometimes been placed within the genera or subgenera *Gussonea* Monterosato, 1912 or *Amyclina* Iredale, 1918.
Tritia pyrenaica (Fontannes, 1879) is characterised by its low dome-shaped multispiral protoconch, although the size of the protoconch is somewhat variable, its subobsolete spiral teleoconch sculpture, partly obscured by the glossy surface, and its ovate aperture with a relatively deep and narrow anal groove. The outer lip is strongly flared abapically, extending further than the tip of the short, open, notched siphonal canal. The outer lip bears a row of 14-23 short, relatively weak, subequal lirae within. The columella callus is thickened, but poorly delimited, apressed and expanded over the venter. Parietal callus only develops in the most gerontic specimens that may develop a small parietal tooth.

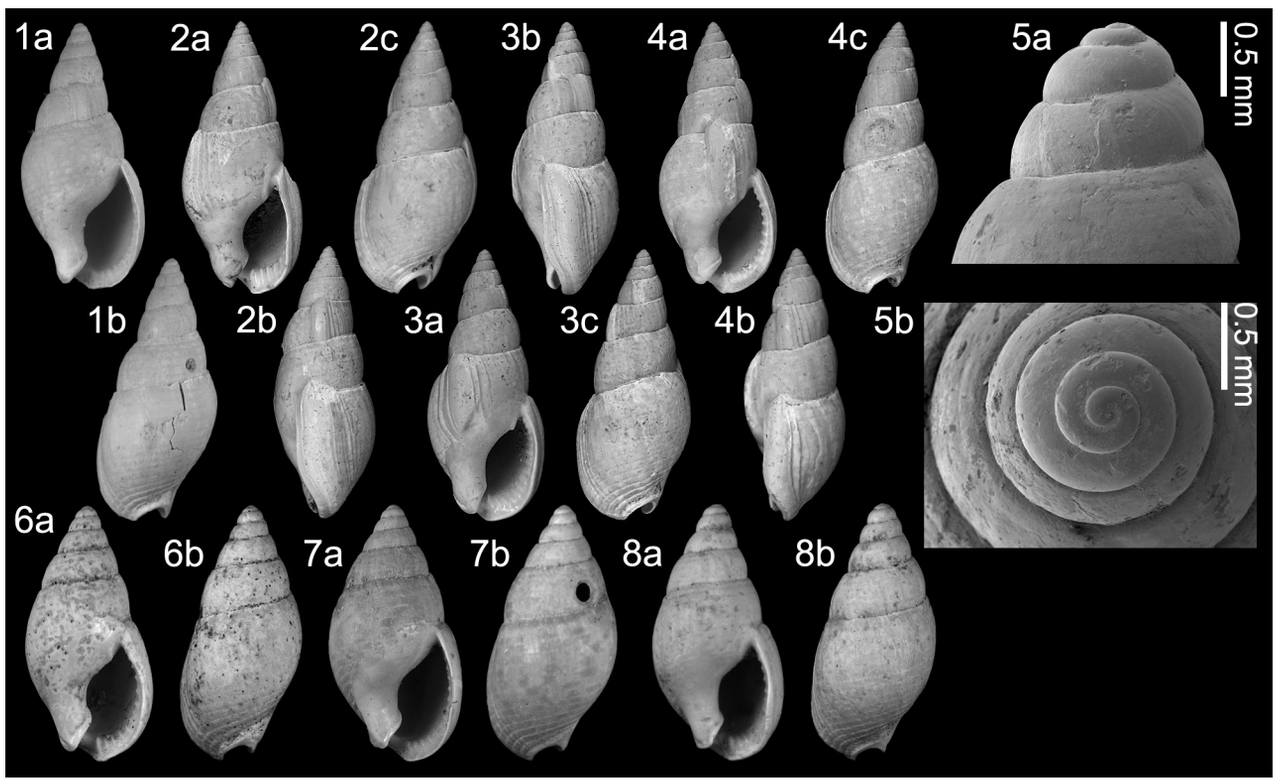


Plate 42. *Tritia pyrenaica* (Fontannes, 1879); 1. NHMW 2016/0103/0849, height 17.3 mm, width 7.7 mm; 2. NHMW 2016/0103/0850 height 20.9 mm, width 8.6 mm; 3. NHMW 2016/0103/0851 height 19.8 mm, width 8.3 mm; 4. NHMW 2016/0103/0852 height 20.8 mm, width 8.6 mm; 5. NHMW 2016/0103/0853 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place. 6. NHMW 2016/0103/1835, height 11.1 mm, width 5.3 mm; 7. NHMW 2016/0103/1836 height 11.2 mm, width 6.0 mm; 8. NHMW 2016/0103/1837 height 9.0 mm, width 4.5 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Based on material available at the time, Landau *et al*. (2009, p. 28) recognised small differences in the teleoconch morphology between the Atlantic and Mediterranean specimens. The adult size for Mediterranean specimens was reported as greater (maximum height; France 18.1 mm, north-east Spain 13.5 mm, Estepona Basin 16.8 mm) than in the Atlantic (Mondego Basin10.3 mm). The plentiful material from Assemblage I shows that most specimens are relatively small and typical for the species (Pl. 42, figs 6-8). However, at all localities, especially St-Clément-de-la-Place, large gerontic specimens occur, attaining the greatest maximum size we have seen for this species (20.8 mm). In these specimens (Pl. 42, figs 1-4) the spire becomes more elongated, a prominent varix develops on the later adult whorls, and the columellar callus thickens further. There are numerous intermediates between the gerontic form and the more plentiful smaller adults.

Gili (1991) synonymised *Nassa tersa* Bellardi, 1882 and *Nassa tersa* var. *abbreviatula* Sacco, 1904 with *T. pyrenaica*. Landau *et al*. (2009, p. 28) considered the present-day West African *Nassa heynemanni* von Maltzan, 1884 also to fit within the species variability. Brébion (1964, p. 435) identified this species as *Amyclina* cf. *lambertiei* (Peyrot, 1925), described from the middle Miocene Serravallian of the Aquitaine Basin. The description given by that author, including the low dome-shaped multispiral protoconch, is indistinguishable from that of *T. pyrenaica*. We therefore herein include *Nassa* (*Amycla*) *lambertiei* Peyrot, 1925 in the synonymy of *T. pyrenaica*.

Brébion (1964, p. 437) recorded this species from the middle Miocene of the Loire Basin (La Beurelière), where it also occurs at Ferrière Larçon (NHMW coll.), and several Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel), to which we add St-Clément-de-la-Place.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin (Brébion, 1964), (Serravallian) Aquitaine Basin, France (Peyrot, 1925). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964). Lower Pliocene: western Mediterranean, Morocco, Tetuan (Lecointre, 1952); central Mediterranean, Italy (Bellardi, 1882). Upper Pliocene: Atlantic, Mondego Basin, Portugal, (Gili *et al*., 1995; Silva, 2001; Landau *et al*., 2009); western Mediterranean, Estepona Basin, S. Spain (Landau *et al*., 2009), S. France (Fontannes, 1879; Gili, 1991); central Mediterranean, Italy (Bellardi, 1882; Sacco, 1904; Mauro & Vecchi, 2005; Cavallo & Repetto, 1992). Present-day: Atlantic, West African Coasts, rarely in the western Mediterranean (Gubbioli & Nofroni, 1985; Giannuzzi-Savelli *et al*., 2003).

Family Pisaniidae Gray, 1857
Genus *Aplus* de Gregorio, 1885

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

1885 *Aplus* de Gregorio, p. 279.

For generic synonymy and discussion see Van Dingenen *et al*. (2017, p. 23).

***Aplus dispar* (Millet, 1865)**
Plate 43, figs 1-3

1854 *Nassa Dispar* Millet, p. 164 (*nomen nudum*).
*1865 *Nassa dispar* Millet, p. 595.
1964 *Cantharus* (*Pollia*) *dispar* Millet, 1854 – Brébion, p. 430, pl. 10, figs 28, 29.

Type material – Syntypes: Thorigné and Sceaux-d'Anjou, Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 431).

Material and dimensions – Maximum height 10.5 mm, width 5.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0801 (9), LC (5), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0797-0799 (3), NHMW 2016/0103/0800 (28), RGM.718093 (50+), RGM.1349152 (12), RGM.1349257 (1), RGM.1349277 (1), RGM.1349287 (4), RGM.1349294 (9), RGM.1352200 (32), RGM.1352227 (6), LC (3), FVD (17).

Discussion – Aplus dispar (Millet, 1865) has a relatively slender biconic shell shape. The protoconch is paucispiral, composed of two whorls, with a medium-sized nucleus. Sculpture consists of 12 orthocline axial ribs overrun by narrow spirals; three on the first teleoconch whorl; secondary cords develop in the interspaces, rapidly strengthening abapically, so that the penultimate whorl bears five spiral cords; cords 1 and 4 slightly strengthened, cord 4 forming a weakly angled shoulder. The last whorl is modestly inflated, roundly shouldered, the axial ribs weaken and the cords become predominant, of alternate strength. The outer lip, moderately thickened by varix, bears six denticles within, the adapical one strongest; the anal canal is well-developed, U-shaped; the siphonal canal is relatively long, open, and deviated adaxially. The columella is thickened by callus, but not greatly expanded, bearing a well developed parietal tooth and several irregular broad folds placed mid-columella. The series illustrated (Pl. 43, figs 1-3) shows some variability in shell shape, in the angulation of the shoulder, and the strength of the denticles within the outer lip and columellar sculpture. However, this degree of variability is usual within the genus.
Aplus dispar lacks tertiary spiral threads, which immediately separates it from several of its congeners such as *A. scaber* (Millet, 1865), with which it co-occurs, *A. ansus* (De Gregorio, 1884), *A. nilus* (De Gregorio, 1884), *A plioparvus* (Sacco, 1904) and *A. pliorecens* Brunetti & Della Bella, 2014, all from the Pliocene of the Mediterranean, and *A. dorbignyi* (Payraudeau, 1826) from the present-day Atlantic and Mediterranean.
Millet (1854, p. 164; 1865, p. 596) recorded this species from the Assemblage I localities of Thorigné and Sceaux-d'Anjou, to which we add St-Clément-de-la-Place.

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

***Aplus scaber* (Millet, 1865)**
Plate 44, figs 1-4

1854 *Fusus Scaber* Millet, p. 162 (*nomen nudum*).
*1865 *Fusus scaber* Millet, p. 591.
1964 *Cantharus* (*Pollia*) *exculpta* Dujardin, 1837 – Brébion (*partim*), p. 428 (*non Aplus exculptus* (Dujardin, 1837)].
1964 *Cantharus* (*Pollia*) *aequicostata* Bellardi, 1872 [*sic*] – Brébion, p. 429, pl. 10, figs 24, 25.
2017 *Aplus scaber* (Millet, 1865) – Van Dingenen *et al*., p. 24, pl. 1, figs 1-3 (*cum syn*).

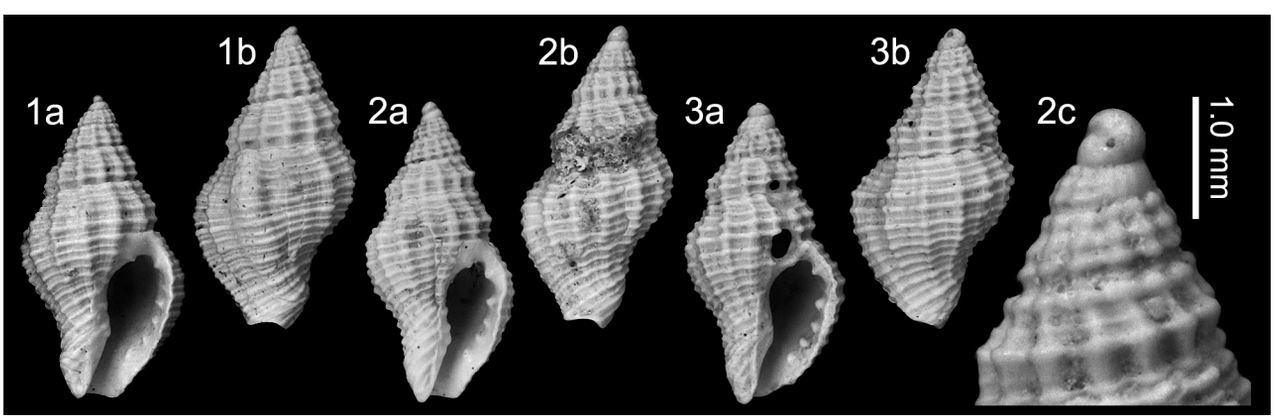


Plate 43. *Aplus dispar* (Millet, 1865); 1. NHMW 2016/0103/0797, height 8.3 mm, width 4.3 mm; 2. NHMW 2016/0103/0798, height 8.0 mm, width 4.0 mm, 2c detail of protoconch; 3. NHMW 2016/0103/0799, height 7.1 mm, width 3.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

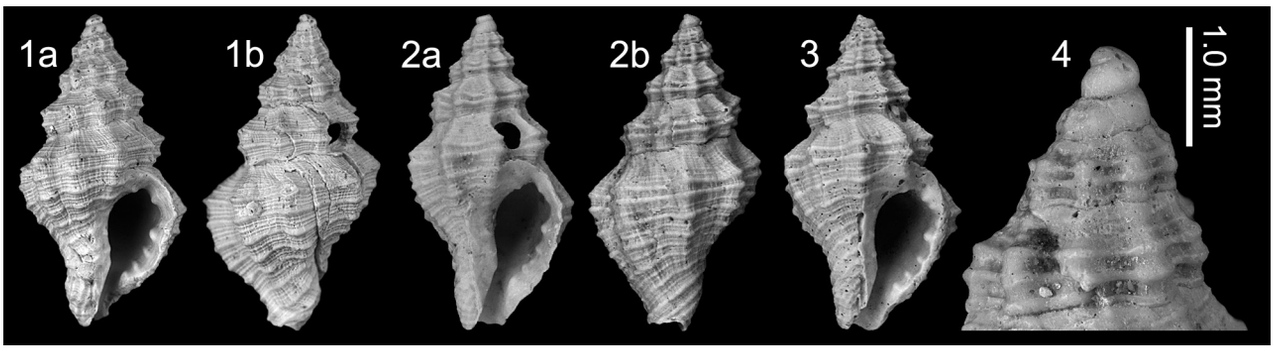


Plate 44. *Aplus scaber* (Millet, 1865); 1. NHMW 2016/0103/0785, height 10.0 mm, width 5.2 mm; 2. NHMW 2016/0103/0786, height 9.4 mm, width 4.7 mm; 3. NHMW 2016/0103/0787, height 10.5 mm, width 4.9 mm; 4. NHMW 2016/0103/0788 (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Type material – Syntype: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 429).

Material and dimensions – Maximum height 11.3 mm, width 5.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0785-0788 (4), NHMW 2016/0103/0789 (2), LC (1), FVD (3). **Sceaux-d'Anjou**: NHMW 2016/0103/0790 (28), RGM.1348296 (1), RGM.718092 (50+), RGM.1352228 (26), LC (5), FVD (18).

Discussion – *Aplus scaber* (Millet, 1865) differs from *A. dispar* (Millet, 1865), with which it co-occurs in the Assemblage I deposits, in having angular whorls with a sharp shoulder, formed by a strengthened spiral cord placed mid-whorl and a further equally strong cord just below, and by the presence of tertiary spiral sculpture, absent in *A. dispar*. Both species have a protoconch of about 2-2.5 whorls. The apertural characters of the two species are similar and show some variability; the adapical labial tooth is bifid in some specimens (Pl. 44, fig. 3).
Van Dingenen *et al*. (2017, p. 24) considered *Aplus aequicostatus* (Bellardi, 1873) a junior subjective synonym of *Aplus scaber* (Millet, 1865).
We note that the present-day European species of *Aplus* recently revised by Aissaoui *et al*. (2016) recognised *Aplus scaber* (Locard, 1891) as valid. Unfortunately it is a secondary homonym of Millet's (1865) species. Two further names may be available for the extant species that are presently recorded as dubious synonyms by WoRMS (MolluscaBase, 2019b): *Mitrella marminea* Risso, 1826 and *Cantharus scaber unicolor* Norsieck, 1972.
Brébion (1964, p. 428) recorded *A. scaber* from the Assemblage I localities of Thorigné, Sceaux d'Anjou and St-Michel, to which we add St-Clément-de-la-Place. Van Dingenen *et al*. (2017, p. 24) recorded the species from Assemblage III (Le Pigeon Blanc).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Van Dingenen *et al*., 2017). Upper Pliocene: Italy (Brunetti & Della Bella, 2014).

Genus *Engina* Gray, 1839

Type species (by subsequent designation; Gray, 1847) – *Engina zonata* Gray, 1839 (= *Purpura turbinella* Kiener, 1836), present-day, Caribbean.

1839 *Engina* Gray, p. 112.
1840 *Pusiostoma* Swainson, p. 151, 313. Type species (by subsequent designation, Herrmannsen, 1848): *Voluta mendicaria* Linnaeus, 1758, present-day, Indo-Pacific.

***Engina brunettii* nov. sp.**
Plate 45, figs 1-3

1964 *Cantharus* (*Pollia*) *pusilla* Bellardi, 1872 [*sic*] – Brébion, p. 430, pl. 10, figs 26, 27 [*non Engina pusilla* (Bellardi, 1873)].

Type material – Holotype MNHN.F.A66727, height 8.1 mm, width 4.3 mm; paratype 1 MNHN.F.A66728, height 8.1 mm, width 4.2 mm; paratype 2 NHMW 2016/0103/0793, height 7.5 mm, width 4.1 mm; paratype 3 NHMW 2016/0103/0791, height 9.1 mm, width 5.2 mm; paratype 4 NHMW 2016/0103/0792, height 8.3 mm, width 4.8 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1349046, height 10.3 mm, width 5.4 mm; paratype 6 RGM.1349047, height 9.8 mm, width 5.8 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 10.5 mm, width 5.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0794 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0795 (43), RGM.718086 (50+), RGM.1349288 (11), RGM.1352226 (50+), LC (15), FVD (50+). **Renauleau**: NHMW 2016/0103/0802 (10), LC (12), FVD (10).

Etymology – Named after the Italian palaeomalacologist Mauro Brunetti in recognition of his contribution to Italian Neogene buccinid systematics. *Engina* gender feminine.

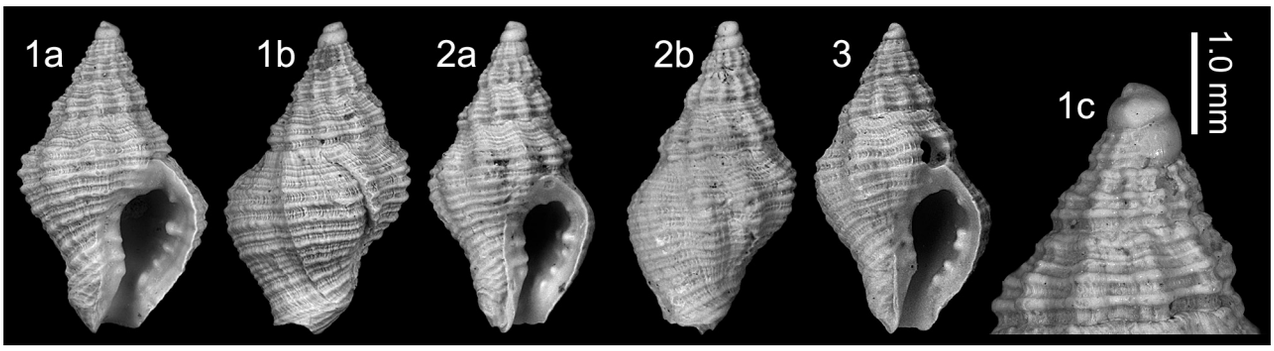


Plate 45:.*Engina brunettii* nov. sp.; 1. **Holotype** NHMW 2016/0103/0791, height 8.1 mm, width 4.3 mm, 1c detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/0792, height 8.1 mm, width 4.2 mm; 3. **Paratype 2** NHMW 2016/0103/0793, height 7.5 mm, width 4.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Engina* species of small size, squat biconic shell shape, protoconch of two whorls, teleoconch of four weakly shouldered whorls, sculptured by 9-10 low rounded ribs and narrow cords, outer lip bearing five denticles within; anal denticle weak, D2 most strongly developed, weak parietal tooth, four strong columellar folds.

Description – Shell small, squat, solid, biconic. Protoconch of two smooth whorls. Teleoconch of four whorls separated by impressed suture. Sculpture composed of 9-10 orthocline, rounded axial ribs, broadening abapically, overrun by three primary spiral cords, the adapical cord placed at shoulder, delimiting subsutural ramp. On last two whorls weaker secondary cords develop on shoulder and below single secondary between primaries. Tertiary cords develop in interspaces in some specimens. Last whorl inflated, roundly angled at shoulder, moderately constricted at base. Aperture small; outer lip strongly thickened by callus, strongly denticulate within; D1 (anal denticle) weak, D2 strongest, knob-like, fused with D3 in some specimens, D4-D5 moderately strongly developed; anal canal shallow U-shaped; siphonal canal moderately long and wide, open. Columella strongly and roundly excavated adapically; columellar callus thin in parietal area, bearing weak parietal tooth, thickened abapically, bearing 3-4 broad horizontal folds.

Discussion – We have placed this species in the genus *Engina* Gray, 1839 rather than *Aplus* de Gregorio, 1885 based on the squat, solid, biconic shell shape, predominant axial sculpture, small aperture, and the character of the apertural armature. The anal denticle (D1) is relatively weak in *Engina brunettii* nov. sp. compared to some of its congeners, but shows the gap typical for the genus between D1 and the rest of the outer lip denticles (see Landau & Vermeij, 2012, p. 122).
Brébion (1964, p. 430) misidentified the species as *Cantharus* (*Pollia*) *pusilla* (Bellardi, 1873), from the Mediterranean upper Miocene and Pliocene of Italy, recently also placed in the genus *Engina* (Brunetti & Della Bella, 2014). However, that species differs in having a multispiral protoconch of just over three whorls (not 2.5 as stated in the description; see Brunetti & Della Bella, 2014, fig. 11E), the spire is more scalate, composed of more convex, distinctly shouldered teleoconch whorls, separated by a deeper suture, and the outer lip denticles are more numerous (7 vs 5). The extant Mediterranean *Enginella leucozona* (Philippi, 1844) is similar in shape to *E. pusilla*, with a scalate spire that is somewhat more slender than in *E. pusilla*, and was indeed placed in the genus *Engina* by Brunetti & Della Bella, 2014, but it differs in having a paucispiral protoconch of only 1.5 whorls (Brunetti & Della Bella, 2014, p. 28). Moreover, it does not have the horizontal folds on the columella typical for the genus. This lack of columellar folds distinguishes the genus *Enginella* Monterosato, 1917 from *Engina* (Cernohorsky, 1975).

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

Genus *Pisania* Bivona-Bernardi, 1832

Type species (by subsequent designation; ICZN Opinion 740, 1965) – *Pisania striatula* Bivona-Bernardi, 1832, present-day, Mediterranean.

1832 *Pisania* Bivona-Bernardi, p. 8.
1884 *Hilda* Hoernes & Auinger, p. 172. Type species (by monotypy): *Triton transylvanicus* R. Hoernes & Auinger, 1884, Miocene, Romania.
1912 *Jeannea* Iredale, p. 220. Type species (by original designation): *Jeannea hedleyi* Iredale, 1912, present-day, Kermadec Islands.
1929 *Appisania* Thiele, p. 314. Type species (by monotypy): *Pisania montrouzieri* Crosse, 1862, present-day, New Caledonia.
1966 *Sukunaia* Cernohorsky, p. 229. Type species (by original designation): *Sukunaia jenningsi* Cernohorsky, 1966, present-day, Fiji.

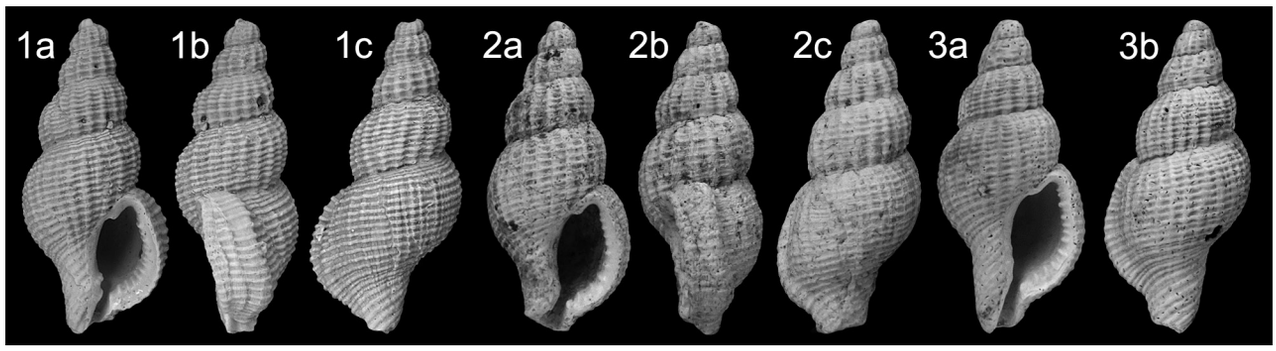


Plate 46. *Pisania redoniensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/0796, height 13.1 mm, width 5.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. **Paratype 1** NHMW 2016/0103/1854, height 13.0 mm, width 5.5 mm; 3. **Paratype 2** RGM.734967, height 13.1 mm, width 6.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Pisania redoniensis* nov. sp.**
Plate 46, figs 1-3

Type material – Holotype NHMW 2016/0103/0796, height 13.1 mm, width 5.8 mm, **St-Clément-de-la-Place**. Paratype 1 NHMW 2016/0103/1854, height 13.0 mm, width 5.5 mm; paratype 2 RGM.734967, height 13.1 mm, width 6.0 mm, **Sceaux-d'Anjou**.

Other material – **St-Clément-de-la-Place**. LC (3). **Sceaux-d'Anjou**: RGM.1349092 (10 juveniles), RGM.1352197 (2 fragments), RGM.1352253 (1 juvenile).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pisania* species of small size, slender bucciniform shape with moderately high spire, convex whorls, sculpture of narrow ribs overrun by regular narrow crowded cords, predominantly axial on early whorls, spiral on last two whorls, small aperture, denticulate within, deep anal sinus, moderate length, narrow siphonal canal, columella callus forming narrow rim with stout parietal tooth and several tubercles abapically.

Description – Shell small, slender bucciniform, with moderately high spire. Protoconch not preserved. Teleoconch of four evenly convex whorls, with periphery below mid-whorl, separated by impressed suture. Sculpture of narrow, rounded, orthocline axial ribs, 16 on penultimate whorl, that weaken on last whorl, overrun by narrow regular spiral cords, five on first teleoconch whorl, secondary cords develop in interspaces on penultimate whorl, rapidly strengthening so that all cords of roughly equal strength on last whorl. Sculpture predominantly axial on early whorls, spiral on last two whorls. Last whorl evenly convex, moderately constricted at base, bearing 24 spiral cords, slightly narrower just below suture and thicker over siphonal fasciole. Aperture small to medium sized, ovate; outer lip strongly thickened by varix, bearing row of 14 elongated denticles on inner side of bevelled edge that extend short distance into aperture; anal sinus narrow U-shaped, deep; siphonal canal moderate length, twisted slightly adaxially, narrow, open. Columella shallowly excavated. Columellar callus thickened, poorly expanded forming narrow callus rim, bearing stout parietal tooth and several tubercles abapically just above and at edge of siphonal canal.

Discussion –*Pisania redoniensis* nov sp. is extremely uncommon in Assemblage I. There is a little variability in regards to the inflation of the last whorl, the size of the aperture and the length of the siphonal canal, as seen in the series illustrated (Pl. 46, figs 1-3).
We are not aware of any Neogene to present-day European species with which to compare this new species. The most similar is possibly *P. sacyi* (Cossmann & Peyrot, 1924) from the lower Miocene Burdigalian Aquitaine Basin of France, but that species is immediately separated by its more slender shell shape, with less convex whorls, broader axial ribs on the spire whorls and spiral sculpture composed of cords of primary to tertiary strength.
The new species is most like the non-European pisanine *Prodotia shepstonensis* (Tomlin, 1926) from South Africa, which is closely similar in shape and far less fusiform than other *Prodotia* Dall, 1924 species. We note that Vermeij (2006, p. 86) did not include it in his list of species within the genus *Prodotia*. The assignation to that genus was suggested by Fraussen *in* Kilburn *et al*. (2010). *Prodotia shepstonensis* differs mainly in having slightly broader axial ribs, that are more regular and do not fade on the last whorl, as they do in *P. redoniensis*, and in having the entire columellar callus covered in tubercles and folds. It is possible that the South African species should be placed in *Pisania* rather than *Prodotia*.

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

Superfamily Muricoidea Rafinesque, 1815

Published separately; see Landau *et al*. (2019).

Superfamily Turbinelloidea Rafinesque, 1815

Note – Since the publication of Van Dingenen *et al*. (2017), two important papers have been published on molecular phylogenetics in the family Costellariidae (Fedosov *et al*., 2017) and Mitridae (Fedosov *et al*., 2018). In this paper we adopt the taxonomic changes suggested by these authors.

Family Costellariidae MacDonald, 1860
Genus *Pusia* Swainson, 1840

Type species (by monotypy) – *Mitra microzonias* Lamarck, 1811, present-day, Indo-Pacific.

1840 *Pusia* Swainson, p. 320.

Subgenus *Ebenomitra* Monterosato, 1917

Type species (by subsequent designation, Coan, 1966) – *Mitra ebenus* Lamarck, 1811, present-day, Mediterranean.

1912 *Pusiola* Monterosato *in* Pallary, p. 190. Type species (by subsequent designation, Lamy, 1920): *Voluta tricolor* Gmelin, 1791, present-day, Mediterranean. Junior homonym of *Pusiola* Wallengren, 1863 [Lepidoptera].
1917 *Ebenomitra* Monterosato, p. 26.
1921 *Pusiolina* Cossmann, p. 79. *Nom. nov. pro Pusiola* Monterosato, 1912, *non* Wallengren, 1863 [Lepidoptera].

Note – The molecular phylogeny of Fedorov *et al.* (2017) has important implications for the taxonomy of European costellariids. They concluded that all present-day Mediterranean species formed a single monophyletic group, for which they used *Ebenomitra* Monterosato, 1917 as a subgenus of *Pusia* Swainson, 1840. This group was characterised by having a paucispiral protoconch, indicative of non-planktotrophic larval development, a character they considered unique among species of *Pusia* (Fedorov *et al*., 2017, p. 601). In their diagnosis of the genus *Vexillum* Röding, 1798, the protoconch is described as '*tall, conical, whitish or brown, translucent, with three or more evenly convex glossy whorls*' (Fedorov *et al*., 2017, p. 617). We must therefore conclude that the species below with a paucispiral protoconch are *Pusia* (*Ebenomitra*) species. Today *Ebenomitra* does not occur further north than the Mediterranean, but in the warmer Miocene its range extended along the European Atlantic frontage at least to NW France.

***Pusia* (*Ebenomitra*) *brebioni* nov. sp.**
Plate 47, figs 1-9

1964 *Vexillum* (*Uromitra*) *similatum* var. *mauryi* Brébion, p. 494, pl. 12, figs 20, 21 (*nomen nudum*).
1964 *Vexillum* (*Uromitra*) *similatum* var. *transiens* Brébion, p. 495, pl. 12, figs 22,23 (*nomen nudum*).

Type material – Holotype MNHN.F.A66739, height 9.6 mm, width 3.6 mm; paratype 1 MNHN.F.A66740 (juvenile), height 7.6 mm, width 3.2 mm; paratype 2 MNHN.F.A66741, height 11.5 mm, width 4.5 mm; paratype 3 NHMW 2016/0103/1149, height 12.5 mm, width 4.5 mm; paratype 4 NHMW 2016/0103/1150, height 10.6 mm, width 3.7 mm; paratype 5 NHMW 2016/0103/1151, height 10.6 mm, width 3.7 mm; paratype 6 NHMW 2016/0103/1152, height 10.3 mm (juvenile); paratype 7 NHMW 2016/0103/1842, height 12.0 mm, width 4.9 mm; paratype 8 NHMW 2016/0103/1843, height 10.2 mm, width 4.2 mm, **St-Clément-de-la-Place**: paratype 9 RGM.1349104, height 10.5 mm, width 4.0 mm; paratype 10 RGM.1349105, height 10.0 mm, width 3.6 mm, paratype 11 RGM.1349106, height 12.1 mm, width 4.1 mm; paratype 12 RGM.1349107, height 11.0 mm, width 3.9 mm **Sceaux-d'Anjou**.

Other material – Maximum height 12.5 mm, width 4.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1148 (50+), RGM.1349146 (1), RGM.1349211 (5), LC (32), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1810 (50+), NHMW 2016/0103/1844 (1), RGM.718121 (50+), RGM.718122 (50+), RGM.1349181 (11), RGM.1349259 (8), RGM.1349275 (5), RGM.1349281 (19), RGM.1352204 (6), RGM.1352259 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1349143 (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pusia* (*Ebenomitra*) species of small-medium size, paucispiral protoconch, fusiform shape, sculpture of 18-24 narrow axials predominant, crossed by 6-7 weak cords, sculpture tending to weaken over last whorl, aperture lirate within, four strong columellar folds.

Description – Shell small-medium sized, solid, fusiform, spire weakly scalate. Protoconch paucispiral, composed of 1.5 smooth whorls, with a large nucleus. Teleoconch boundary marked by beginning of axial sculpture. Teleoconch of five weakly convex whorls, with periphery just above abapical suture. Suture impressed. Axial sculpture of 18-24 weakly prosocline, narrow, rounded ribs, about one-third width of their interspaces. Spiral sculpture of

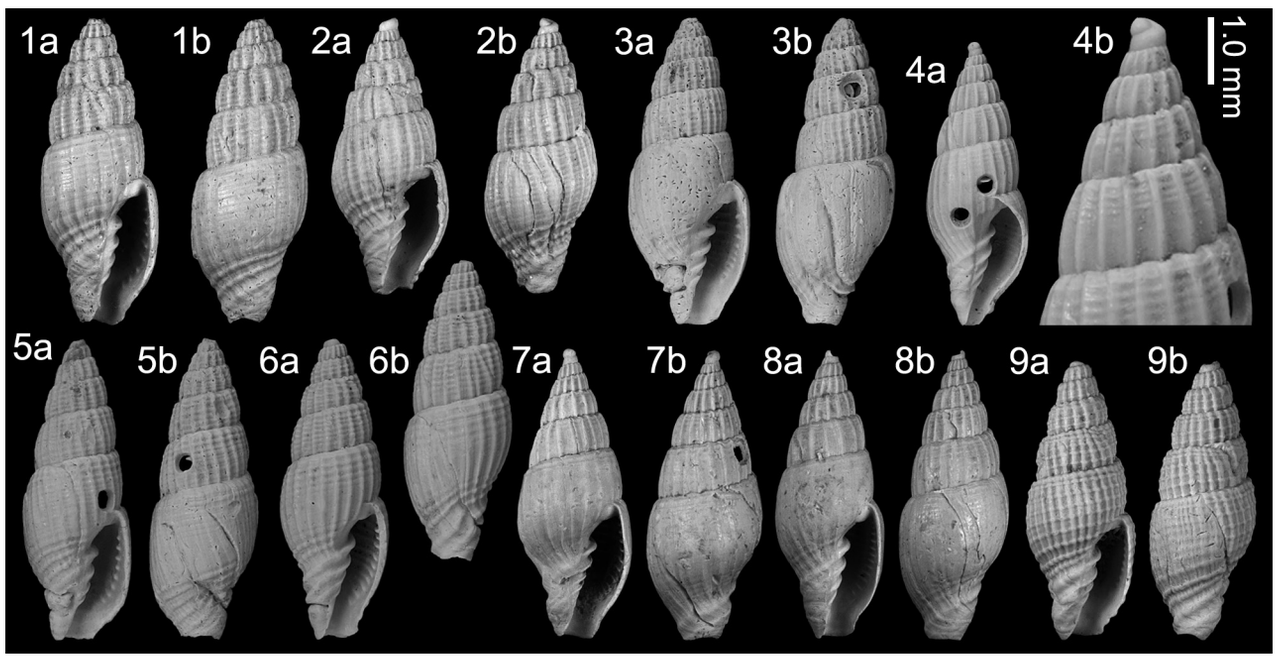


Plate 47. *Pusia* (*Ebenomitra*) *brebioni* nov. sp.; 1. **Holotype** MNHN.F.A66739, height 9.6 mm, width 3.6 mm; 2. **Paratype 1** MNHN.F.A66740 (juvenile), height 7.6 mm, width 3.2 mm; 3. **Paratype 2** MNHN.F.A66741, height 11.5 mm, width 4.5 mm; 4. **Paratype 3** NHMW 2016/0103/1149, height 12.5 mm, width 4.5 mm, 4b. detail of protoconch; 5. **Paratype 4** NHMW 2016/0103/1150, height 10.6 mm, width 3.7 mm; 6. **Paratype 5** NHMW 2016/0103/1151, height 10.6 mm, width 3.7 mm; 7. **Paratype 7** NHMW 2016/0103/1842, height 12.0 mm, width 4.9 mm; 8. **Paratype 8** NHMW 2016/0103/1843, height 10.2 mm, width 4.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 9. NHMW 2016/0103/1844, height 9.1 mm, width 4.0 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

irregular, narrow cords overrun axial ribs, separated by narrow interspaces; 6-7 on penultimate whorl. Last whorl about 60% total height, weakly convex, constricted at base, sculpture weakens over last whorl, especially mid-whorl, becoming obsolete in some gerontic specimens; spirals strengthen over base. Aperture elongate, narrow, about 38% total height; anal canal marked by small notch; siphonal canal medium length, wide, open, bent to left. Outer lip not thickened, bearing ten irregular, interrupted lirae within of variable strength, extending far within aperture. Columella straight, not callused, forming depression on venter, bearing four strong, stout, oblique folds at inner edge, adapical fold strongest. Siphonal fasciole moderate length, bearing strong spiral cords continuous from columellar folds.

Discussion – *Pusia* (*Ebenomitra*) *brebioni* nov. sp. was described by Brébion as a subspecies of *Mitra similata* Millet, 1865 (see below). They do indeed both represent a species group we have not seen elsewhere in the Neogene-extant European faunas, but the two are consistently different. They are best separated by the character of their early teleoconch whorls. In *P.* (*E.*) *brebioni* they are weakly convex the axials are relatively close-spaced and although weakly developed, spiral sculpture is present from the first whorl. In *P.* (*E.*) *similata* the first two whorls are straight sided and coronate in profile and devoid of spiral sculpture, which only appears from the third teleoconch whorl. Moreover, *P.* (*E.*) *brebioni* attains a larger maximum size, the last whorl is constricted at the base, the siphonal canal is longer and there are four strong columellar folds as opposed to three in most specimens of *P.* (*E.*) *similata*, although a weak fourth abapical fold is present in some specimens. Despite these constant differences, *P.* (*E.*) *brebioni* is highly variable as seen in the series illustrated. The number of ribs is variable and in large gerontic specimens the sculpture is lost on the last whorl (Pl. 47, figs 1, 3, 5). At St-Clément-de-la-Place some specimens are present that hardly have any spiral sculpture (Pl. 47, figs 7, 8), whilst at Sceaux-d'Anjou there are specimens that have fewer spiral cords that form small tubercles at the intersections with the ribs (Pl. 47, fig. 9), and there are numerous intermediate forms.
Uromitra crebricostata Bellardi, 1887 from the upper Miocene of Italy is similar in shape and sculpture, but has a less scalate spire and only three columellar folds. We have not seen this species and do not have a description of its protoconch.

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

***Pusia* (*Ebenomitra*) *pseudoplicatula* nov. sp.**
Plate 48, figs 1-4

1854 *Mitra Plicatula* Br. – Millet, p. 159 (*non* Brocchi, 1814).

1964 *Vexillum* (*Uromitra*) *pseudoebenus* Brébion, p. 489, pl. 12, fig. 13 (*nomen nudum*).
1964 *Vexillum* (*Uromitra*) *pseudoebenus* var. *totocostatum* Brébion, p. 490, pl. 12, fig. 14 (*nomen nudum*).
1964 *Vexillum* (*Uromitra*) *similatum* var. *laevispira* Brébion, p. 496, pl. 12, fig. 24 (*nomen nudum*).

Type material – Holotype MNHN.F.A70507, height 15.2 mm, width 5.3 mm; paratype 1 MNHN.F.A70508, height 13.9 mm, width 4.9 mm; paratype 2 MNHN.F.A70509 (juvenile), height 6.0 mm; paratype 3 NHMW 2016/0103/1141, height 12.5 mm, width 4.5 mm; paratype 4 NHMW 2016/0103/1142, height 15.3 mm, width 5.0 mm; paratype 5 NHMW 2016/0103/1143, height 15.5 mm, width 5.5 mm; paratype 6 NHMW 2016/0103/1144, height 16.5 mm, width 5.6 mm.

Other material – Maximum height 17.2 mm, width 6.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1145 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1146 (50+), RGM.718123 (50+), RGM.734979 (3), RGM.1349182 (50+), RGM.1349201 (5), RGM. 1349212 (9), RGM.1349278 (35), RGM.1352207 (46), RGM.1352260 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1147 (50+), RGM.1348992 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1349138 (2).

Etymology –Philippe Brébion stressed the similarity of this species to the present-day *Pusia* (*Ebenomitra*) *ebena* (Lamarck, 1811) in using the *nomen nudum* '*pseudoebena*'. We respect and agree with this position by naming it '*pseudoplicatula*', *Mitra plicatula* Brocchi, 1814 is a junior subjective synonym of *P.* (*E.*) *ebena*. *Pusia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pusia* (*Ebenomitra*) species of medium size, paucispiral protoconch, fusiform shape, sculpture of 16-18 narrow axials, weakening abapically, last whorl smooth in most adult specimens, spiral sculpture absent or almost so, last whorl strongly constricted at base, aperture narrow, weakly lirate within, four strong columellar folds, moderately long siphonal canal.

Description – Shell medium-sized, fusiform. Protoconch paucispiral, composed of 1.5 smooth whorls, with a large nucleus. Teleoconch boundary marked by beginning of axial sculpture. Teleoconch of six weakly convex whorls, with periphery at abapical suture. Suture impressed, linear. Axial sculpture of 16-18 narrow, weakly opisthocline, rounded ribs, about one-third width of their interspaces, weakening abapically, obsolete, or almost so, on last whorl in most specimens. Spiral sculpture absent, although suggestion of 1-2 faint cords on early spire whorls in some specimens. Last whorl 58-62% total height, convex, moderately strongly constricted at base. Aperture elongate, narrow, 38-40% total height; anal canal marked by small notch; siphonal canal moderately long, open, bent to left. Outer lip not thickened, bearing 7-10 weak lirae within, extending far within aperture. Columella straight, not callused, forming weak depression on venter, bearing four stout, oblique folds at inner edge, adapical fold strongest, that continue as cords over siphonal fasciole. Siphonal fasciole moderately long, delimited from base by strong spiral cord originating from adapical columellar fold.

Discussion – *Pusia* (*Ebenomitra*) *pseudoplicatula* nov. sp. is closely similar to the Pliocene to present-day Mediterranean *P.* (*E.*) *ebena* (Lamarck, 1811), which is extremely variable in shape and sculpture (see Giannuzzi Savelli *et al*., 2003, figs 652-667), but we agree with Brébion (1964, p. 490) that the two are not conspecific. *Pusia* (*Ebenomitra*) *pseudoplicatula* has a narrower shell, the base is more strongly constricted so that the siphonal canal is more strongly delimited from the base, and the aperture is narrower. The specimen of *P.* (*E.*) *ebena* from the lower Pliocene Coralline Crag of England illustrated by Harmer (1918, pl. 33, fig. 4) is slender,

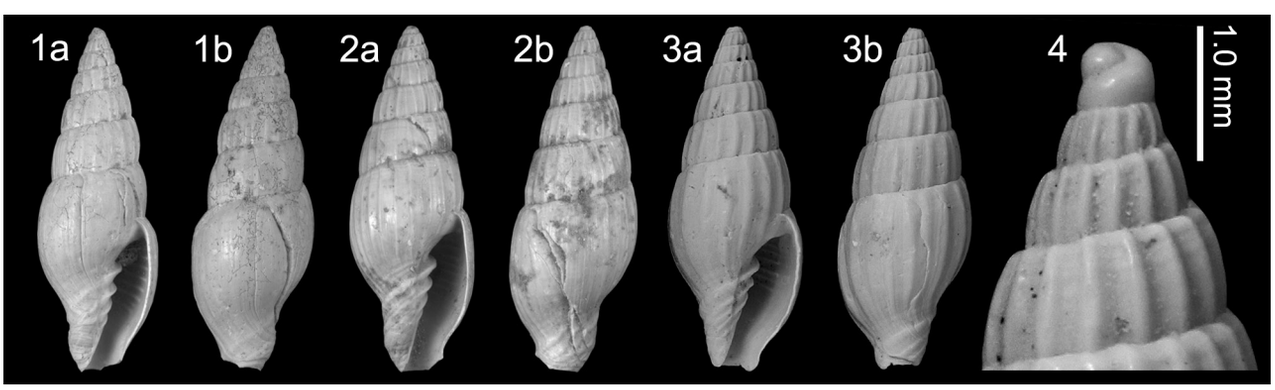


Plate 48. *Pusia* (*Ebenomitra*) *pseudoplicatula* nov. sp.; 1. **Holotype** MNHN.F.A70507, height 15.2 mm, width 5.3 mm; 2. **Paratype 1** MNHN.F.A70508, height 13.9 mm, width 4.9 mm; 3. **Paratype 3** NHMW 2016/0103/1141, height 12.5 mm, width 4.5 mm; 4. **Paratype 2** MNHN.F.A70509 (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

like the Assemblage I species, but has a less constricted base. The aperture of the English shell appears narrow, but this is misleading, as the outer lip is incomplete. *Pusia* (*Ebenomitra*) *pseudoplicatula* differs from its Assemblage I consubgeners in lacking spiral sculpture, although in some specimens there is a trace of subobsolete spiral cords on the early spire whorls. Like its consubgeners, *P.* (*E.*) *pseudoplicatula* is highly variable, especially in sculpture. Brébion (1964, p. 490) separated specimens in which the axial sculpture persisted on the last whorl as var. *totocostata* (*nomen nudum*), and also noted the very faint spiral sculpture, but intermediates occur.
Brébion (1964, p. 490) recorded this species from numerous Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, St-Michel, Beaulieu), to which we add Renauleau.

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

***Pusia* (*Ebenomitra*) *renauleauensis* nov. sp.**
Plate 49, figs 1-3

Type material – Holotype MNHN.F.A70510, height 6.6 mm, width 2.9 mm; paratype 1 MNHN.F.A70511, height 6.4 mm, width 2.3 mm; paratype 2 NHMW 2016/0103/1812, height 6.6 mm, width 2.5 mm; paratype 3 NHMW 2016/0103/1813, height 6.5 mm, width 2.9 mm; paratype 4 NHMW 2016/0103/1814, height 6.9 mm, width 3.2 mm.

Other material – Maximum height 12.5 mm, width 4.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1817 (2). **Renauleau**: NHMW 2016/0103/1815 (15), LC (26), FVD (31).

Etymology – Named after the type locality of Renauleau. *Pusia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pusia* (*Ebenomitra*) species of small size, paucispiral protoconch, low fusiform shape, sculpture of 19-28 narrow axials, spiral sculpture absent, aperture weakly or subobsoletely lirate within, three strong columellar folds.

Description – Shell small, solid, stout fusiform, conical spire. Protoconch paucispiral, composed of 1.5 smooth whorls, with a large nucleus. Teleoconch boundary marked by beginning of axial sculpture. Teleoconch of 4.5 low convex whorls, with periphery at abapical suture. Suture impressed, linear. Axial sculpture of 19-28 narrow, orthocline, rounded ribs, slightly narrower than their interspaces. Spiral sculpture absent. Last whorl 63% total height, weakly convex, weakly constricted at base, axials persist over outer lip and base. Aperture elongate, relatively wide, about 44% total height; anal canal marked by small notch; siphonal canal moderately short, wide, open, bent slightly to left. Outer lip not thickened, weakly to subobsoletely lirate within. Columella straight, not callused, forming depression on venter, bearing three strong, stout, oblique folds at inner edge, adapical fold strongest, that continue as cords over siphonal fasciole. Siphonal fasciole short, delimited from base by strong spiral cord originating from adapical columellar fold. Narrow colour band placed just above mid-whorl on last whorl preserved.

Discussion – *Pusia* (*Ebenomitra*) *renauleauensis* nov. sp. is characterised by its small, stout, fusiform shell, close-set axial sculpture, lack of spiral sculpture, and the presence of three columellar folds. It is somewhat variable, especially in the number of axial ribs and some specimens have a slightly scalate spire (Pl. 49, fig. 3), but the shell form is more constant than seen in most of its consubgeners. A narrow band of lighter colour placed just above mid-whorl is preserved in some specimens. Banded colour pattern seems to be common to *Pusia* (*Ebenomitra*) species.
The most similar species is *P* (*E.*) *leucozona* (Andrzejowski, 1830), from the middle Miocene Atlantic coast of France and Paratethys, which is also stout fusiform in shape and has three columellar folds, but that species is larger, with far fewer and broader axial ribs, and two broader bands of colour pattern (for further discussion see

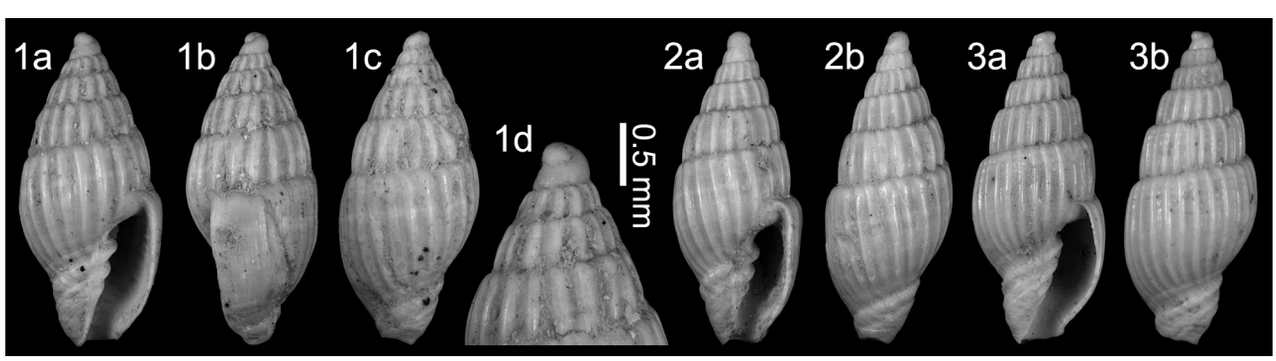


Plate 49. *Pusia* (*Ebenomitra*) *renauleauensis* nov. sp.; 1. **Holotype** MNHN.F.A70510, height 6.6 mm, width 2.9 mm, 1d, detail of protoconch; 2. **Paratype 1** MNHN.F.A70511, height 6.4 mm, width 2.3 mm; 3. **Paratype 2** NHMW 2016/0103/1812, height 6.6 mm, width 2.5 mm,. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Landau *et al*., 2013, p. 215). *Pusia* (*Ebenomitra*) *ebenus* (Lamarck, 1811) also has a single band of colour placed just above mid-whorl, but is again larger, with fewer ribs and four columellar folds.

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

Pusia* (*Ebenomitra*) cf. *renauleauensis
Plate 50, figs 1-4

Material and dimensions – Height 7.4 mm, width 3.2 mm. **Sceaux-d'Anjou**: RGM.734978 (1), RGM.1352275-1352276 (2). **Renauleau**: NHMW 2016/0103/1816 (1).

Discussion – A single specimen from Renauleau and some worn specimens from Sceaux-d'Anjou might represent an extreme form of *Pusia* (*Ebenomitra*) *renauleauensis* nov. sp., but we hesitate to synonymise them as the well-preserved specimen from Renauleau (Pl. 50, fig. 1) is slightly larger than the maximum size for that species and has far fewer axial ribs. It seems intermediate between that species and *P* (*E.*) *leucozona* (Andrzejowski, 1830), which can have a similar number of ribs, but that species is twice the size and more fusiform. We await further material to better characterise this form.

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

***Pusia* (*Ebenomitra*) *similata* (Millet, 1865)**
Plate 51, figs 1-4

1854	*Mitra Similata* Millet, p. 160 (*nomen nudum*).
*1865	*Mitra similata* Millet, p. 586.
1964	*Vexillum* (*Uromitra*) *similatum* Millet, 1854 [sic] – Brébion, p. 492, pl. 12, figs 17-19.

Type material – Syntypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 493).

Material and dimensions – Maximum height 10.1 mm, width 3.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1135-1138 (4), NHMW 2016/0103/1139 (50+), RGM.1349226 (5 juveniles), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1140 (50+), RGM.718120 (50+), RGM.1349258 (4), RGM.1349279 (24), RGM.1352205 (15), LC (12), FVD (50+). **Renauleau**: NHMW 2016/0103/1811 (10), LC (8), FVD (5).

Original description – 'Mitra similata. *Millet. Coq. petite, fusiforme, composée de 7-8 tours de spire, couverts de petites côtes verticales, croisées par des stries transversales très-rapprochées. Ouverture étroite, faisant un peu plus du tiers de la longueur totale de la coq. Bord droit strié intérieurement. 2 ou 3 plis à la columelle se prolongent en dehors jusqu'au bord droit. Longueur: 10-11 millimètres; diamètre: 5 millimètres. Sceaux. Cette espèce a quelques rapports avec* M. plicatula, *Sismonda*.' (Millet, 1865, p. 586).

Revised description – Shell small, solid, fusiform, scalate spire. Protoconch tall, paucispiral, composed of 1.5 smooth whorls, with a large nucleus. Teleoconch boundary marked by beginning of axial sculpture. Teleoconch of 4.5 almost straight-sided whorls, with periphery at abapical suture. Suture impressed, linear. Axial sculpture of 12-14 orthocline, rounded ribs, slightly narrower than their interspaces; on first two whorls ribs extend slightly above suture, making whorls coronate. Spiral sculpture from third teleoconch whorl overruns axial ribs, separated by narrow interspaces; 5-6 on penultimate whorl. Last whorl 62-65% total height, weakly convex, hardly constricted at base, axials weaken over last half whorl and interspaces between spirals widen, roughly equal to width of spirals; spirals strengthen over base. Aperture elongate, narrow, about 43% total height; anal canal marked by small notch; siphonal canal moderately short, wide, open, bent slightly to left. Outer lip not thickened, bearing 8-10 variable lirae within, short and weak to strong and extending far within aperture. Columella straight, not callused, forming depression on venter, bearing three, exceptionally four strong, sharp, oblique folds at inner edge, adapical fold strongest, that continue as cords over siphonal fasciole. Siphonal fasciole short, delimited from base by strong spiral cord originating from adapical columellar fold.

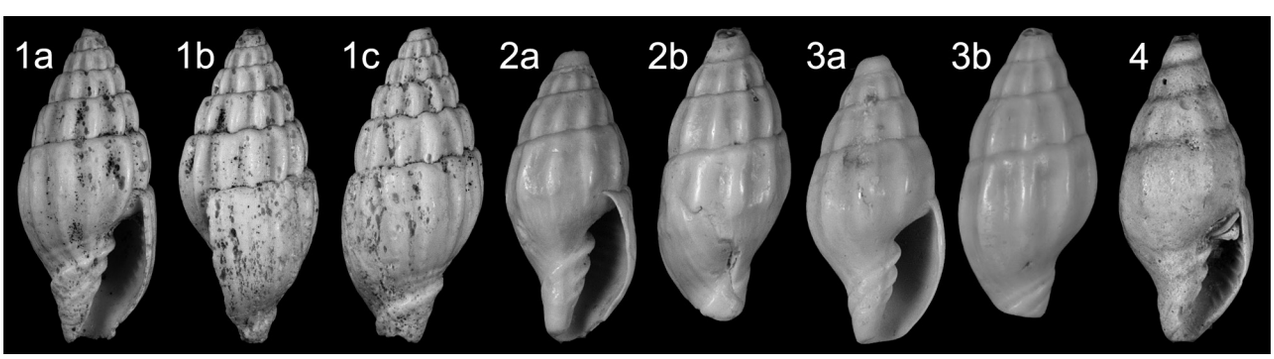


Plate 50. *Pusia* (*Ebenomitra*) cf. *renauleauensis* nov. sp.; 1. NHMW 2016/0103/1816, height 7.4 mm, width 3.2 mm. Renauleau. 2. RGM.734978, height 4.4 mm, width, 2.0 mm; 3. RGM.1352275, height 4.3, width 2.1 mm; 3. RGM.1352276, height 4.8, width 2.2 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

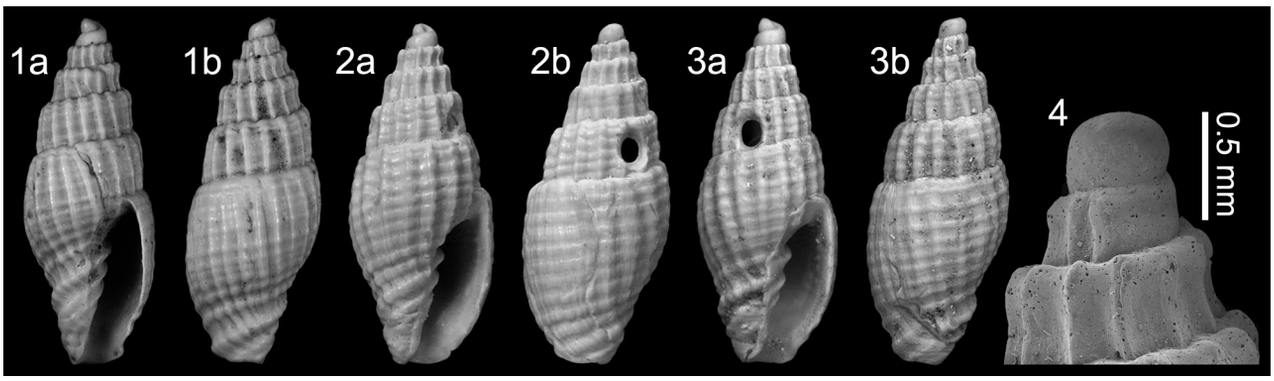


Plate 51. *Pusia* (*Ebenomitra*) *similata* (Millet, 1865); 1. NHMW 2016/0103/1135, height 6.6 mm, width 2.7 mm; 2. NHMW 2016/0103/1136, height 6.3 mm, width 2.7 mm; 3. NHMW 2016/0103/1137, height 6.8 mm, width 2.7 mm; 4. NHMW 2016/0103/1138, height 6.2 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Pusia* (*Ebenomitra*) *similata* (Millet, 1865) is a curious little species quite unlike any of its congeners. The original description does not highlight the unique characters sufficiently, and a revised description is offered. The protoconch is paucispiral with the first whorl tall and loosely coiled, which has led us to place it in *Pusia* (*Ebenomitra*) (see note under generic placement), although the sculpture has little in common with any of its extant congeners, none of which have strong spiral sculpture. Unusual characters are the coronate first two teleoconch whorls, the late appearance of spiral sculpture on the third whorl, the strong spiral cord delimiting the base from the siphonal fasciole, and the columella area that is marked by a depression on the medial wall of the aperture. It is difficult to find any species with which to compare *P.* (*E.*) *similata*. As noted by Brébion (1964, p. 493) *Uromitra mutabilis* Bellardi, 1887 from the lower Miocene of Italy is superficially similar in having cancellate sculpture, but that species is larger, with more convex whorls. The resemblance is due in part to the siphonal canal being incomplete in that species. For comparison with *P.* (*E.*) *brebioni* nov. sp., see under discussion of that species.

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

***Pusia* (*Ebenomitra*) *sublaevis* nov. sp.**
Plate 52, figs 1-4

Type material – Holotype MNHN.F.A70512, height 10.9 mm, width 4.9 mm; paratype 1 NHMW 2016/0103/1383, height 12.6 mm, width 5.2 mm; paratype 2 NHMW 2016/0103/1384, height 10.2 mm, width 4.2 mm; paratype 3 NHMW 2016/0103/1818, height 13.5 mm, width 5.3 mm.

Other material – Maximum height 13.2 mm, width 5.6 mm. **Sceaux-d'Anjou**: RGM.1349200 (9), RGM.1349242 (8). **Renauleau**: NHMW 2016/0103/1385 (6), LC (5), FVD (9).

Etymology – Latin '*laevis, -e, -oir*', adjective meaning smooth, with prefic *sub*-, denoting a subset, as it is totally smooth. *Pusia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pusia* (*Ebenomitra*) species of medium size, broad fusiform shape, sculpture of 12-14 narrow axials only present on first three whorls, spiral sculpture absent, aperture weakly lirate within, three strong columellar folds.

Description – Shell medium-sized, broad fusiform. Protoconch not preserved. Teleoconch of six weakly convex whorls, with periphery at abapical suture. Suture impressed, linear. Axial sculpture of 12-14 narrow, weakly opisthocline, rounded ribs, about one-half width of their interspaces, present on first three whorls, rapidly weakening and disappearing at beginning fourth whorl. Spiral sculpture absent. Last whorl 58-62% total height, convex, moderately constricted at base. Aperture elongate, relatively broad, 38-40% total height; anal canal marked by small notch; siphonal canal moderately short, open, wide, slightly bent to left. Outer lip not thickened, bearing 9-12 weak lirae within, extending far within aperture. Columella straight, not callused, forming weak depression on venter, bearing three stout, oblique folds at inner edge, adapical fold strongest, that continue as cords over siphonal fasciole. Weak fourth fold present adapically in the ocassional specimen. Siphonal fasciole moderately short, delimited from base by strong spiral cord originating from adapical columellar fold.

Discussion – We have placed this species in *Pusia* (*Ebenomitra*), although we note that none of the specimens has its protoconch preserved (see generic note). *Pusia* (*Ebenomitra*) *sublaevis* nov. sp. is separated from all its Assemblage I consubgeners in having sculpture

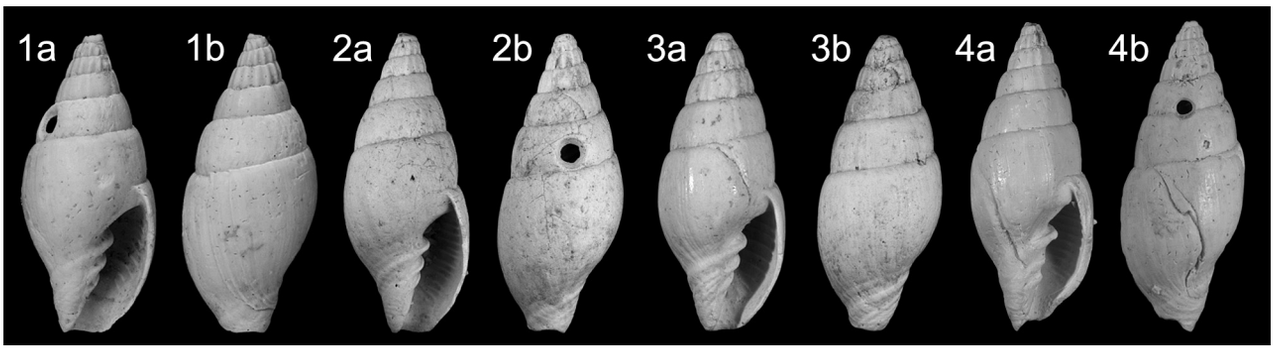


Plate 52. *Pusia* (*Ebenomitra*) *sublaevis* nov. sp.; 1. **Holotype** MNHN.F.A70512, height 10.9 mm, width 4.9 mm; 2. **Paratype 1** NHMW 2016/0103/1383, height 12.6 mm, width 5.2 mm; 3. **Paratype 2** NHMW 2016/0103/1384, height 10.2 mm, width 4.2 mm; 4. **Paratype 3** NHMW 2016/0103/1818, height 13.5 mm, width 5.3 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

only on the first three teleoconch whorls. At the beginning of the fourth whorl the axials rapidly weaken and disappear, so that the last three whorls are smooth, except for some cords over the siphonal fasciole extending from the columellar folds. Like all its consubgeners the shape and sculpture are somewhat variable, and although some specimens are slightly more slender, it is the broadest *Pusia* (*Ebenomitra*) species in Assemblage I. It can only be confused with gerontic specimens of *P.* (*E.*) *pseudoplicatula* nov. sp. (Pl. 48, fig. 1), but that species is more slender and the axials persist longer. Moreover, it has four columellar folds instead of usually three in *P.* (*E.*) *sublaevis*. Gerontic specimens of *P.* (*E.*) *brebioni* nov. sp. (Pl. 47, fig. 1), in which the sculpture also weakens on the last whorl, are immediately separated by having spiral sculpture. *Pusia* (*Ebenomitra*) *subcoronata* (Bellardi, 1877) from the upper Pliocene of Italy (holotype figured by Ferrero Mortara *et al*., 1981, pl. 51, fig. 9) is similar in size and sculpture to *P.* (*E.*) *sublaevis*, and also has three columellar folds, but the axials persist longer, so that only the last 1.5 whorls are smooth. We have not seen this uncommon Italian species, and cannot comment on the protoconch type.

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

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

Type species (by subsequent designation, Cossmann, 1899) – *Mitra mirifica* Reeve, 1845, present-day, Philippines.

1853 *Thala* H. Adams & A. Adams, p. 178.

***Thala pupa* (Dujardin, 1837)**
Plate 53, figs 1-3

*1837 *Mitra pupa* Dujardin, p. 301, pl. 20, fig. 14.
1899 *Thala pupa* Duj. – Cossmann, p. 176, pl. 8, fig. 5.
1952a *Pusia* (*Thala*) *pupa* Dujardin, 1837 – Glibert, p. 359, pl. 12, fig. 1.

Material and dimensions – Maximum height 8.0 mm, width 3.2 mm. **Renauleau**: NHMW 2016/0103/1153-1155 (3), NHMW 2016/0103/1156 (50+), RGM.1348985 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1348488 (7), RGM.1349142 (2), RGM.1352348 (5).

Discussion – *Thala pupa* (Dujardin, 1837) is characterised by its pointed spire, pupoid last two whorls, and predominantly axial sculpture, although like most *Thala*

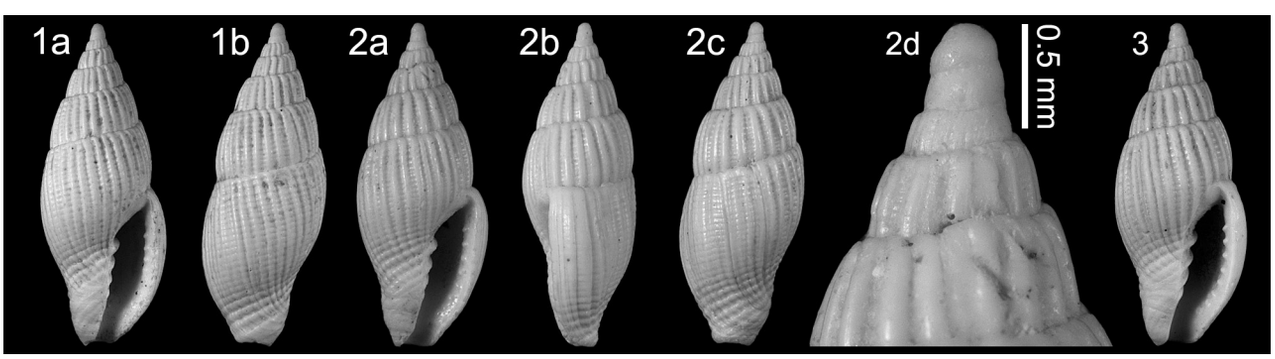


Plate 53. *Thala pupa* (Dujardin, 1837); 1. NHMW 2016/0103/1153, height 8.0 mm, width 3.2 mm; 2. NHMW 2016/0103/1154, height 7.4 mm, width 3.0 mm, 2d, detail of protoconch; 3. NHMW 2016/0103/1155, height 6.6 mm, width 2.7 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

species the sculpture is somewhat variable. Landau *et al*. (2013) stated that the protoconch of *T. pupa* was paucispiral. This is not the case. This observation was based on a juvenile *Mitromorpha* species that was inadvertently placed in a tube of *T. pupa* specimens from Thenay, Indre department. We take the opportunity of correcting this embarrassing error. As correctly commented by Glibert (1952a, p. 359) *T. pupa* has a tall cylindrical multispiral protoconch composed of three smooth whorls (Pl. 53, fig. 2d). This species is most like *T. obsoleta* (Brocchi, 1814) from the middle Miocene of the Paratethys and Mediterranean and the Pliocene of the Mediterranean, but that species is smaller, more elongated, with a less inflated last whorl, and a less pointed spire. The protoconch illustrated by Giannuzzi-Savelli & Reina (1983, p. 235, fig 2/2) is also multispiral, but pointed and not cylindrical, as in *T. pupa*. For discussion and comparison with other European *Thala* species see Landau *et al*. (2013, p. 218). It seems strange that Brébion did not record this species for the 'Redonian', as although we have only found it at Renauleau and adjacent Beugnon, it is abundant at these localities.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Dujardin, 1837; Cossmann, 1899; Peyrot, 1938; Glibert, 1952a). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (this paper).

Superfamily Mitroidea Swainson, 1831
Family Mitridae Swainson, 1831
Subfamily Mitrinae Swainson, 1831

Note – Brébion (1964) recorded 12 species of Mitrinae from Assemblage I, his identifications often based on abraded and fragmentary material. We have only been able to characterise six species satisfactorily. This has left us with a small number of poorly preserved mitrids from each locality that we cannot identify. Therefore, it is likely that the number of species present in the Assemblage I fauna will grow as better material becomes available.

Genus *Episcomitra sensu lato* Monterosato, 1917

Type species (by monotypy) – *Mitra zonata* Marryat, 1818, present-day, Mediterranean.

1917 *Episcomitra* Monterosato, p. 26.

Note – The molecular phylogenetic work of Fedosov *et al*. (2018) was not kind to palaeontologists working on eastern Atlantic European and Mediterranean assemblages. As far back as Landau *et al*. (2011, p. 29) we argued that the Mediterranean mitrids should be placed in the genus *Episcomitra* Monterosato, 1917, reiterated again in Landau *et al*. (2013, p. 209). Unfortunately, the genetic work of Fedosov *et al*. (2018) showed that the three extant Mediterranean species fell into two separate clades that were indistinguishable based on shell characters. *Mitra cornicula* (Linnaeus, 1758) and *M. zonata* Marryat, 1818 they placed in *Episcomitra*, and *M. cornea* Lamarck, 1811 in *Isara* H. Adams & A. Adams (1853) (*Fuscomitra* Pallary, 1900 is a synonym). As we have used the genus *Episcomitra* for these European mitrids in previous papers, we continue to use this genus *sensu lato*.

***Episcomitra s.l. apicina* (Millet, 1865)**
Plate 54, figs 1-3

1854 *Mitra Apicina* Millet, p. 159 (*nomen nudum*).
*1865 *Mitra apicina* Millet, p. 585.
1964 *Mitra apicina* Millet, 1854 – Brébion, p. 511, pl. 12, fig. 40.

Material and dimensions – Maximum height 33.7 mm, width 9.1 mm. **Sceaux-d'Anjou**: RGM.719017 (1), ?RGM. 1352300 (1), FVD (1).

Original description – 'Mitra apicina, *Millet. Coq. allongée, effilée et comme fusiforme; composée de 8-9 tours de spire aplatis. La longueur de l'ouverture fait le tiers de la longueur totale de la coq. Des stries fines se font*

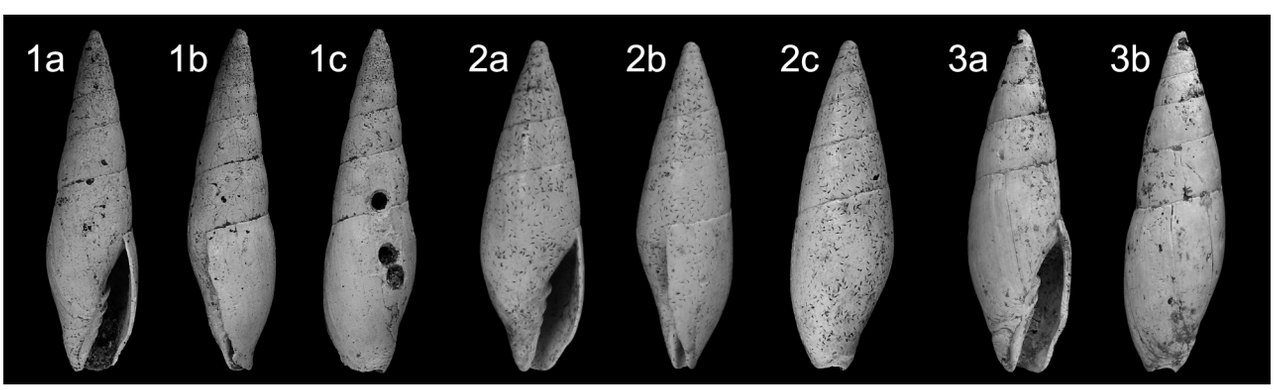


Plate 54. *Episcomitra s.l. apicina* (Millet, 1865); 1. RGM.719017, height 27.5 mm, width 8.0 mm. 2. ?*Episcomitra s.l. apicina* (Millet, 1865) RGM.1352300, height 21.2 mm, width 7.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene. 3. *Mitra* sp. 1 (of Van Dingenen *et al*., 2017, pl. 2, fig. 10) NHMW 2015/0133/0395, height 26.6 mm. Le Landreau, Le Pigeon Blanc, Loire-Atlantique department, France, Zanclean, lower Pliocene.

remarquer a chaque extrémité, ainsi que trois plis sur la columelle. Longueur: 28-30 millimètres; diamètre: 8 millimètres. Th., Sc.' (Millet, 1865, p. 585).

Discussion – *Episcomitra s.l. apicina* (Millet, 1865) is characterised by its very slender fusiform shell shape, almost straight-sided spire whorls separated by a weakly impressed strongly oblique suture. We have only ascribed one somewhat worn specimen in the RGM collection from Sceaux-d'Anjou to this species with certainty (Pl. 54, fig. 1). The spiral sculpture on the earliest teleoconch whorls described by Millet and Brébion are just visible, albeit abraded, and a few very weak cords are present on the siphonal fasciole that do not extend onto the base. As rightly noted by Brébion, the columella bears four folds and not three as described by Millet (1865; see above). We are confident this is the species described by Millet (1865) and figured by Brébion (1964, pl. 12, fig. 40). A few other specimens might represent this species, but they are less elongated (Pl. 54, fig. 2). Brébion (1964, p. 511) recorded *E. s.l. apicina* from the Lower Pliocene Assemblage III locality of Le Pigeon Blanc. This record probably refers to specimens like that figured by Van Dingenen *et al*. (2017, pl. 2, fig. 10) as *Mitra* sp. 1 (Pl. 54, fig. 3), although that shell is not as slender and the base is less excavated. With the material available it is not possible to understand the intraspecific variability and we provisionally restrict the species concept to the slender strongly elongated form. *Episcomitra s.l. apicina* differs from *E. s.l. gravis* (Bellardi, 1887) (see below) in having a more elongated, slender shell and in having a more strongly excavated base. It is possible that they represent extremes of a single species.
Brébion (1964, p. 511) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné), Assemblage III (Le Pigeon Blanc) and Assemblage IV (Gourbesville). However, we restrict the distribution to Assemblage I pending further study.

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

***Episcomitra s.l. gravis* (Bellardi, 1887)**
Plate 55, figs 1-4

*1887a	*Mitra gravis* Bellardi, p. 11, pl. 1, fig. 6.
1964	*Mitra gravis* Bellardi, 1887 – Brébion, p. 501, pl. 12, figs 31, 32.
2017	*Mitra gravis* Bellardi, 1887 – Van Dingenen *et al*., p. 35, pl. 3, figs 1-3.

Material and dimensions – Maximum height 22.8 mm, width 7.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1378-1381 (4), NHMW 2016/0103/1382 (11), LC (5), FVD (15). **Sceaux-d'Anjou**: NHMW 2016/0103/1375 (4), RGM.734980 (50+), RGM.1349188 (2), RGM.1349199 (3 + 3 fragments), RGM.1349202 (8), RGM.1349203 (2), RGM.1352199 (11), FVD (6). **Renauleau**: LC (2).

Discussion – As discussed by Van Dingenen *et al*. (2017, p. 36), we agree with Brébion (1964, p. 501) that this species from Assemblage I and III is closely similar to *Episcomitra s.l. gravis* (Bellardi, 1887), described from the upper Miocene of Italy. These mitrids form part of Bellardi's (1887a, p. 14) '*5ª Serie*', characterised by their relatively long spire in relation to the last whorl, giving them a somewhat turriculate rather than fusiform outline, cords on the early whorl and absence of them over the base, four columellar folds and a short siphonal canal. Of the species included in this group by Bellardi, the French specimens are most like *M. s.l. gravis*, and although we have not seen specimens from Italy and the species was not re-illustrated by Ferrero Mortara *et al*. (1981) nor Davoli (2000), we provisionally consider them conspecific.
Brébion (1964, p. 503) recorded this species widely in the NW French assemblages; from Assemblage I (Thorigné, Sceaux-d'Anjou, St-Clément-de-la-Place, St-Michel, Beaulieu), Assemblage III (La Gauvinière, Le Temple du Cerisier, Le Girondor, Le Pigeon Blanc, Palluau, La Dixmérie) and Assemblage IV (St-Jean-la-Poterie).

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

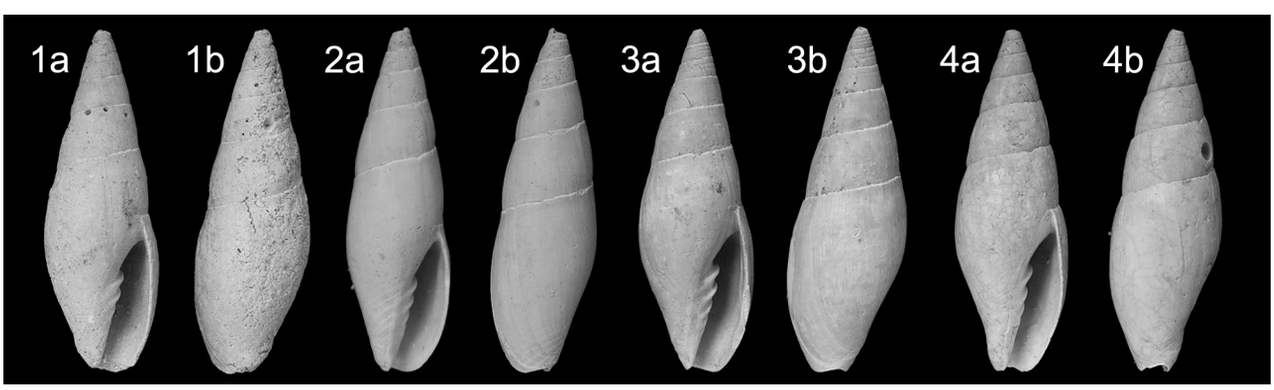


Plate 55. *Episcomitra s.l. gravis* (Bellardi, 1887); 1. NHMW 2016/0103/1378, height 22.0 mm, width 7.3 mm; 2. NHMW 2016/0103/1379, height 22.3 mm, width 7.5 mm; 3. NHMW 2016/0103/1380, height 22.1 mm, width 7.2 mm; 4. NHMW 2016/0103/1381, height 22.8 mm, width 7.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

NW France (Brébion, 1964; Van Dingenen *et al*., 2017). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

***Episcomitra s.l. longula* (Millet, 1865)**
Plate 56, figs 1-4

1854	*Mitra Longula* Millet, p. 159 (*nomen dubium*).
*1865	*Mitra longula* Millet, p. 585.
1964	*Mitra longula* Millet, 1854 [*sic*] – Brébion, p. 503, pl. 12, fig. 33.

Type material – Syntypes: Sceaux-d'Anjou or Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 493).

Material and dimensions – Maximum height 26.2 mm, width 11.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1364-1367 (1), NHMW 2016/0103/1368 (19), FVD (18). **Sceaux-d'Anjou**: NHMW 2016/0103/1371 (5), RGM.718125 (25), RGM.1349171 (1), RGM.1349198 (4), RGM.1349290 (1), RGM.1352264 (1 juvenile), FVD (1). **Renauleau**: LC (12).

Original description – 'Mitra longula, *Millet. Coq. fusiforme, composée de 7-8 tours de spire aplatis, lisses, ou à peine striés transversalement sur les premiers tours, ainsi que sur le dernier. La longueur de l'ouverture fait la moitié de la longueur totale de la coq. Bord columellaire garni de deux plis, rarement, présentant le commencement d'un troisième. Longueur: 24-25 millimètres; diamètre: 8-9 millimètres. Th., Sc*.' (Millet, 1865, p. 585).

Revised description – Shell small to medium size, moderately broad fusiform, biconic. Protoconch multispiral, tall dome-shaped, composed of three smooth whorls, with small nucleus. Teleoconch of five weakly convex whorls, with periphery at abapical suture. Spire regularly conical, relatively narrow, pointed, weakly coeloconoid. Suture impressed, linear. Spiral sculpture of fine, regular, flattened spiral cords separated by narrow grooves over entire shell surface in subadult specimens, weakening or subobsolete on lower half of later whorls and mid-whorl on last whorl in gerontic specimens. On first two whorls, fine axial growth lines visible in spiral interspaces, making interspaces finely punctate or cancellate. Last whorl somewhat inflated, 73% total height, convex, hardly to not constricted at base. Aperture elongate, moderate width, 46% total height; anal canal marked by small notch; siphonal canal short, open, wide. Outer lip thin, extending abapically further than tip of siphonal fasciole, smooth within. Columella weakly excavated, not callused, forming marked depression on venter, bearing three oblique folds at inner edge, adapical fold strongest, weakening abapically. Very weak fourth fold adapical present in some specimens. Siphonal fasciole not developed.

Discussion – We have offered a revised description for this species as the original is insufficient and incorrect. The spiral sculpture extends along the entire surface in subadult specimens, although it weakens or is subobsolete on the lower half of the spire whorls and mid-whorl on the last whorl in the largest specimens, and no mitrids have two columellar folds. The outer lip, which is relatively thick in most mitrids, is thin in *Episcomitra s.l. longula* (Millet, 1865). The pointed coeloconoid spire and rather inflated last whorl separate it from all the Italian mitrids (see Bellardi, 1850, 1887).
According to the generic description given by Fedosov *et al*. (2018, p. 38), the genus *Episcomitra* Monterosato, 1917 has a paucispiral protoconch. Protoconch type is not usually a reliable generic character, and considering that only two extant species of *Episcomitra* are known, both in the Mediterranean, these could be derived from an ancestor with a multispiral protoconch. Other possible placements are in *Isara* H. Adams & A. Adams, 1854 that has such a variable shell that it is hardly possible to use for fossil species, and the West African genus *Ziba* H. Adams & A. Adams, 1854, that is characterised by shells with a multispiral protoconch (Fedosov *et al*., 2018, p. 36), but usually of a larger size, shouldered last whorl and longer siphonal canal. According to the generic description given by those authors *Ziba* has three columellar folds. The French species usually has three, but some specimens have a weak fourth adapical fold. For these reasons we place it in *Episcomitra sensu lato.*

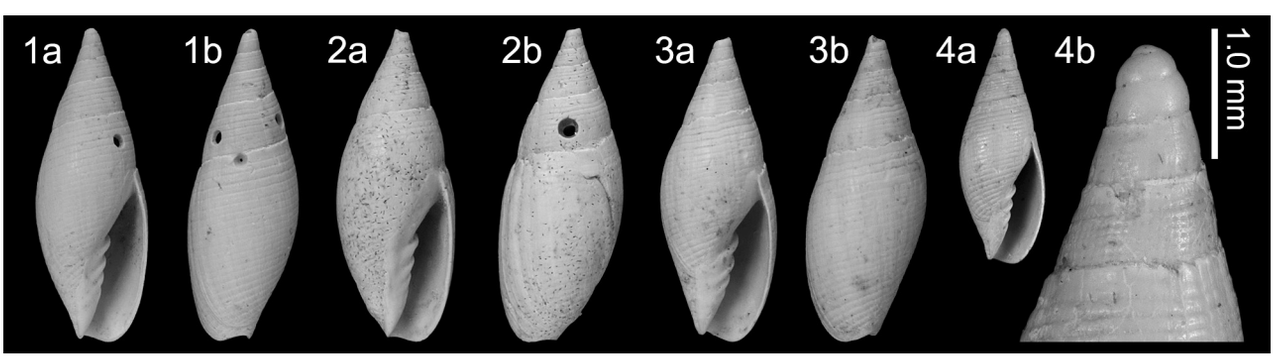


Plate 56. *Episcomitra s.l. longula* (Millet, 1865); 1. NHMW 2016/0103/1364, height 13.5 mm, width 4.8 mm; 2. NHMW 2016/0103/1365, height 12.8 mm, width 4.5 mm; 3. NHMW 2016/0103/1366, height 11.5 mm, width 4.3 mm; 4. NHMW 2016/0103/1367, height 9.5 mm, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

The shell illustrated by Glibert (1952a, pl. 12, fig. 3) as *Mitra* (*Nebularia*) *tenuistria* Dujardin, 1837 (= *M. dautzenbergi* Peyrot, 1938) from the middle Miocene Loire Basin of France has similar spiral sculpture, but differs in having a proportionately higher spire that is cyrtoconoid and not coeloconoid, and having four or five columellar folds, as opposed to three or exceptionally four in *E. s.l. longula* (Millet, 1865).

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

***Episcomitra s.l. silvae* nov. sp.**
Plate 57, figs 1-4

1964 *Mitra angusta* Brébion, p. 506, pl. 12, fig. 36 (*nomen nudum*).

Type material – Holotype NHMW 2016/0103/1370, height 9.3 mm, width 3.5 mm; paratype 1 NHMW 2016/0103/1373, height 9.5 mm, width 3.3 mm; paratype 2 NHMW 2016/0103/1819, height 9.9 mm, width 3.6 mm, paratype 4 RGM.1349113, height 8.7 mm, width 3.4 mm, paratype 5 RGM.1349114, height 10.5 mm, width 3.7 mm, **Sceaux-d'Anjou**. Paratype 3 NHMW 2016/0103/1369, height 10.3 mm, width 3.6 mm, **St-Clément-de-la-Place**.

Other material – Maximum height 11.7 mm, width 4.0 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1374 (4), RGM.719019 (18), RGM.1352215 (9), RGM.1352263 (2), LC (2), FVD (1). **Renauleau**: LC (4).

Etymology – In honour of our good friend and colleague palaeontologist Professor Carlos Marques da Silva from the University of Lisbon. Hardly a paper of BL is published without his help. *Episcomitra* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Episcomitra* species of small size, slender fusiform biconic shape, sculpture of three strong spirals on early spire whorls that weaken rapidly and disappear at beginning of penultimate whorl, four columellar folds, short siphonal canal.

Description – Shell small, solid, slender fusiform, biconic. Protoconch not preserved. Teleoconch of four weakly convex whorls, with periphery at abapical suture. Suture impressed, linear. Spiral sculpture of three strong, broad, rounded spiral cords separated by narrow interspaces on spire whorls. Abapically, cords broaden, flatten and weaken, disappearing progressively from adapical cord upwards on first half penultimate whorl. Last whorl 69% total height, convex, hardly to weakly constricted at base. Aperture elongate, narrow, 44% total height; anal canal marked by small notch; siphonal canal moderately short, open, wide. Outer lip not thickened, smooth within. Columella straight, not callused, forming weak depression on venter, bearing four oblique folds at inner edge, adapical fold strongest, weakening abapically. Siphonal fasciole moderately short, poorly delimited from base, bearing a few poorly developed spiral cords that extend a short distance onto base, weakening adapically.

Discussion – Despite the numerous mitrids described from the European Neogene, *Episcomitra s.l. silvae* nov. sp. is easily distinguished by its very small size and strong spiral cords on the early teleoconch whorls that rapidly weaken and disappear on the first half of the penultimate whorl. Shell form is rather conservative in mitrids, and many of the smaller Italian species are similar in shape; having a small, biconic shell, but they either lack spiral sculpture like *E. s.l. acuta* (Bellardi, 1850) and *E. s.l. optabilis* (Bellardi, 1887) from the lower Miocene of Italy, or they have weaker, but more extensive spiral sculpture, like *E. s.l. bonellii* (Bellardi, 1850) and *E. s.l. zinolensis* (Bellardi, 1887), both from the Pliocene of Italy.

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

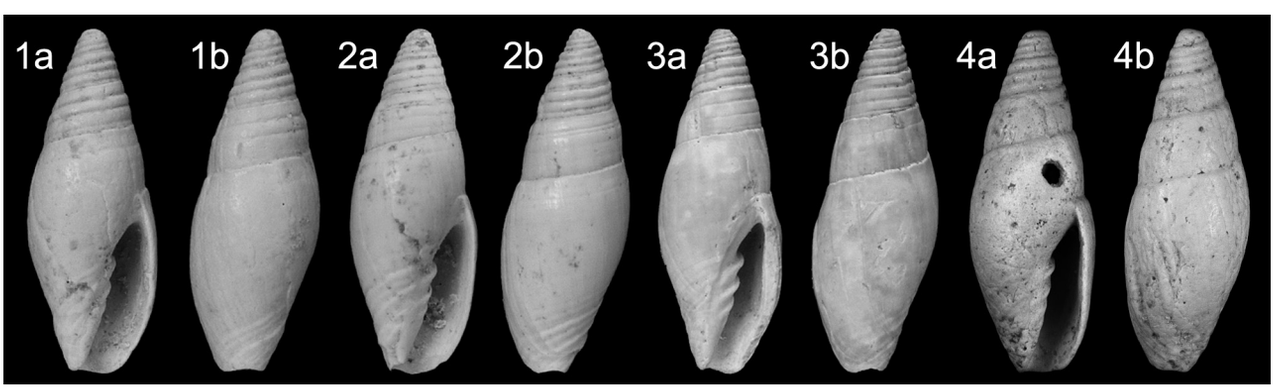


Plate 57. *Episcomitra s.l. silvae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1370, height 9.3 mm, width 3.5 mm; 2. **Paratype 1** NHMW 2016/0103/1373, height 9.5 mm, width 3.3 mm. 3. **Paratype 2** NHMW 2016/0103/1819, height 9.9 mm, width 3.6 mm. La Presselière, Sceaux-d'Anjou. 4. **Paratype 3** NHMW 2016/0103/1369, height 10.3 mm, width 3.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Episcomitra s.l.* sp. 1**
Plate 58, fig. 1

1964 *Mitra acuta* Bellardi, 1850 – Brébion, p. 497, pl. 12, figs 25, ?26.

Material and dimensions – Maximum height 38.8 mm, width 14.8 mm. **Renauleau**: NHMW 2016/0103/1820 (1), NHMW 2016/0103/1821 (1), LC (6), FVD (2 + 2 incomplete).

Discussion – *Episcomitra s.l.* sp. is characterised by having a medium sized, solid shell, squat fusiform shape, with a low, regularly conical, slightly scalate spire and a moderately inflated last whorl. Spiral sculpture is clearly developed on the first three teleoconch whorls that bear five narrow cords, the adapical cord widest. Abapically the cords weaken, so that only the upper two cords, separated by a shallow, narrow groove, are present on the rest of the spire whorls. The last whorl is weakly convex and weakly constricted at the base, totally smooth, devoid of any basal sculpture usually present in *Episcomitra* species. The columella is straight, weakly callused, sharply delimited, and bears five folds. The siphonal fasciole is flattened and separated from the base by a weakly elevated ridge.
This species belongs the the European Neogene *Episcomitra s.l. fusiformis* (Brocchi, 1814) species group, for which a huge number of species have been erected by Bellardi (1850, 1887) amongst others, based on small differences in shape and sculpture, and in need of revision. That is not to say that the group does not include several distinct species, and this NW French species is clearly not *E. s.l. fusiformis* which is much higher spired. At least one of the specimens illustrated by Brébion (1964, pl. 12, fig. 25) we consider conspecific. That author identified it as *Mitra acuta* Bellardi, 1850 from the lower Miocene of Italy, but despite that species being somewhat variable (Sacco, 1904, pl. 18, figs 33-38), it has a less inflated last whorl and spiral sculpture over the base. *Episcomitra s.l. incognita* (de Basterot, 1825) and all its varieties described from the Aquitaine and Loire basins of France are taller spired.
Episcomitra s.l. aperta (Bellardi, 1887) from the Italian Pliocene is much more similar in shape, but that species has spiral sculpture over the base (see Chirli, 2002, pl. 16, figs 1-6). *Episcomitra s.l. turricula* (de Cristofori & Jan, 1832), also from the Italian Pliocene (lectotype illustrated by Pinna & Spezia, 1978, pl. 22, fig. 4), is also similar, but has a higher, more scalate spire composed of shouldered whorls. Despite the enormous number of closely similar forms described, we cannot find one that fits this species. However, in view of the scant material, we do not think it useful to add yet another nominal taxon to this group.

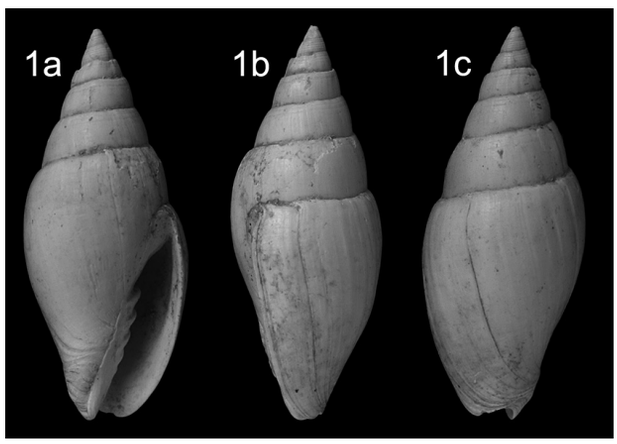


Plate 58. *Episcomitra s.l.* sp. 1; 1. NHMW 2016/0103/1820, height 30.4 mm, width 12.7 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

***Episcomitra s.l.* sp. 2**
Plate 59, figs 1-4

Material and dimensions – Maximum height 18.0 mm, width 6.7 mm. **Renauleau**: NHMW 2016/0103/1822-1825 (4), NHMW 2016/0103/1826 (6), LC (19), FVD (14).

Discussion – We have a group of mitrids from Renauleau that all have in common a relatively thick shell, with a

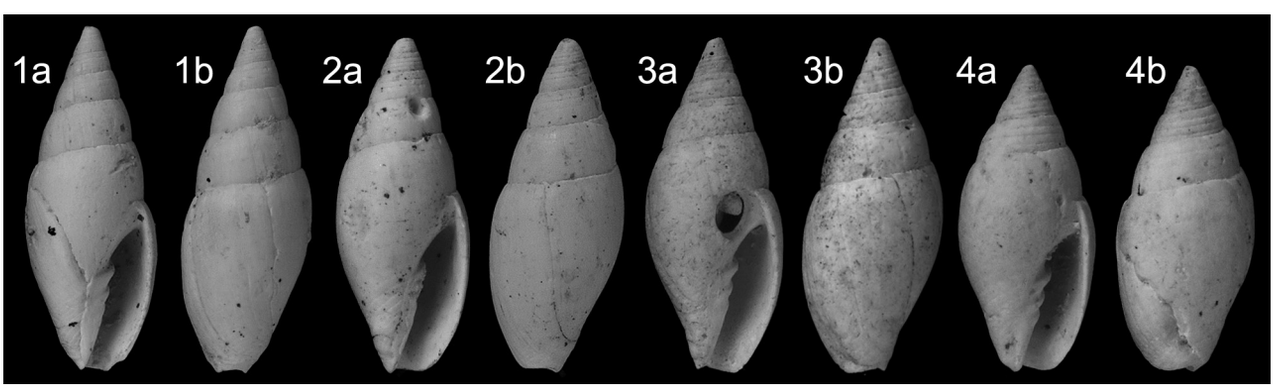


Plate 59. *Episcomitra s.l.* sp. 2; 1. NHMW 2016/0103/1822, height 14.5 mm, width 5.5 mm. 2. NHMW 2016/0103/1823, height 11.8 mm, width 4.7 mm. 3. NHMW 2016/0103/1824, height 12.3 mm, width 5.0 mm. 4. NHMW 2016/0103/1825, height 9.8 mm, width 4.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

thickened outer lip, convex spire whorls with fine spiral sculpture on the early teleoconch whorls, a convex last whorl, weakly constricted at the base, a base bearing very weak spiral sculpture, a short siphonal canal and three stout columellar folds. However, the series illustrated (Pl. 59, figs 1-4) shows a great variability in spire height, if it represents a single species. Brébion (1964) recognised a greater number of species in his material from Assemblage I than we have, but none of his forms had three columellar folds. None of the specimens at hand are well preserved, and we provisionally leave this species in open nomenclature.

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

Genus *Pseudonebularia* Fedosov, Herrmann, Kantor & Bouchet, 2018

Type species (by original designation) – *Mitra tornata* Reeve, 1845, present-day, Indo-Pacific.

2018 *Pseudonebularia* Fedosov, Herrmann, Kantor & Bouchet, p. 46.

***Pseudonebularia hibryda* (Millet, 1865)**
Plate 60, figs 1-3

1854 *Mitra Hybrida* [*sic*] Millet, p. 160 (*nomen nudum*) (*non M. hybrida* Kiener, 1840).
*1865 *Mitra Hibryda* Millet, p. 586.
1964 *Mitra* (*Tiara*) *hybrida* [*sic*] Millet, 1854 [*sic*] – Brébion, p. 512, pl. 10, fig. 41 (*non M. hybrida* Kiener, 1840).

Type material – Syntypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 512).

Material and dimensions – Maximum height 7.6 mm, width 3.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0926 (1), NHMW 2016/0103/0927 (4). **Sceaux-d'Anjou**: NHMW 2016/0103/0928-0929 (2), NHMW 2016/0103/0930 (18), RGM.719018 (50+), RGM.1349180 (3), RGM.1349232 (11), RGM.1349266 (3 + 5 juveniles), RGM.1352206 (18), RGM.1352261 (5), LC (13), FVD (8). **Renauleau**: LC (1).

Original description – 'Mitra hibryda, *Millet. Coq. petite, fusiforme, composée de 7-8 tours de spire, presque plans, mais bien détachés les uns des autres par une suture très prononcée et couverts de stries élevées, arrondies. L'ouverture, qui présente 2-3 plis columellaires égale à peine en longueur le restant de la coq. Longueur: 10-12 millimètres; diamètre: 5 millimètres. Sceaux*' (Millet, 1865, p. 586).

Revised description – Shell small, solid, fusiform, biconic. Protoconch tall, dome-shaped, composed of 2.5 smooth whorls, with small nucleus. Teleoconch boundary marked by beginning of spiral sculpture. Teleoconch of 3.5 straight-sided whorls, with periphery at abapical suture. Suture deeply impressed, linear. Spiral sculpture of 4-5 broad, rounded cords, slightly wider than their interspaces. Close-set, fine axial growth lines seen in interspaces forming finely reticulated pattern. Last whorl about 67% total height, weakly convex, hardly constricted at base, spirals widen mid-whorl in some specimens, separated by narrow interspaces. Aperture elongate, narrow, about 43% total height; anal canal marked by small notch; siphonal canal very short, wide, open, bent slightly to left. Outer lip not thickened, extending abapically slightly beyond tip of siphonal fasciole, smooth within. Columella straight, not callused, forming convex depression on venter, bearing three strong oblique folds at inner edge, adapical fold strongest, that continue as cords over siphonal fasciole. Siphonal fasciole short, not delimited from base.

Discussion – The genus *Pseudonebularia* Fedosov, Herrmann, Kantor & Bouchet, 2018 is characterised by '*Shell small (9-30 mm), fusiform or broadly fusiform to biconical, vividly coloured. Protoconch pointed, narrowly conical, of about three slightly convex, glossy whorls. Suture*

Plate 60. *Pseudonebularia hibryda* (Millet, 1865); 1. NHMW 2016/0103/0928, height 6.3 mm, width 2.8 mm; 2. NHMW 2016/0103/0929, height 6.6 mm, width 2.7 mm; La Presselière, Sceaux-d'Anjou. 3. NHMW 2016/0103/0926 height 5.8 mm (juvenile), 3c. detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

slightly impressed, often indistinct. Teleoconch whorls evenly convex or flattened, sometimes giving the spire a distinctly stepped profile. Sculpture of strong, rounded spiral cords, regularly interspaced and covering the entire shell or, rarely, limited to shell base. Interspaces between cords concave, smooth or bearing fine, dense riblets. Siphonal canal moderately long, stout, siphonal notch shallow or absent. Aperture rather narrow, elongate, with undulating outer lip, sometimes bearing rounded denticles on its inside. Inner lip calloused, often reflected, with three to four strong columellar folds, adapicalmost strongest' Fedosov *et al*., (2018, p. 46). This generic description fits fairly closely with the species description given above, and *P. hibryda* (Millet, 1865) is particularly similar to the Indo-Pacific type species *P. tornata* (Reeve, 1845), from which it differs in being only about one-third of the size, and having the outer lip expanded beyond the tip of the siphonal fasciole abapically. This is the only record of the genus outside the Indo-Pacific region, but it is possible that other fossil species will be reassigned to this newly characterised genus. Having said that, none of the European fossil species consulted are particularly similar. Numerous Miocene and Pliocene spirally striate mitrids have been described from Italian assemblages (see Ferrero Mortara *et al*., 1981, pl. 50), but all of these are much larger with a long siphonal canal, and do not belong within the genus *Pseudonebularia*. They probably belong in the West African genus *Ziba*, as defined by Fedosov *et al*., (2018). Brébion (1964, p. 513) compared *P. hibryda* to *Mitra vasconiensis* Peyrot, 1928, a small species from the middle Miocene Langhian of the Aquitaine Basin. However, that species again has a longer siphonal canal, and should also be placed in the genus *Ziba*.

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

***Pseudonebularia sceauxensis* nov. sp.**
Plate 61, figs 1-3

1964 *Mitra rogeri* Brébion, p. 507, pl. 12, fig. 37 (*nomen nudum*).

Type material – Holotype NHMW 2016/0103/0933, height 11.9 mm, width 4.6 mm; paratype 1 NHMW 2016/0103/0934, height 11.7 mm, width 4.3 mm, paratype 3 RGM.1352216 height 8.4 mm, width 3.6 mm, paratype 4 RGM.1352217, height 11.2 mm, width 4.2 mm, **Sceaux-d'Anjou**. Paratype 2 NHMW 2016/0103/0931, height 10.4 mm, width 3.8 mm, **St-Clément-de-la-Place**.

Other material – Maximum height 11.9 mm, width 4.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0932 (8 juveniles). **Sceaux-d'Anjou**: NHMW 2016/0103/1372 (3), RGM.1352218 (7), RGM.1352262 (1 juvenile), FVD (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pseudonebularia* species of small size, biconic shell shape, large multispiral protoconch, 3.5 teleoconch whorls, spire whorls straight-sided, bearing five weak cords, last whorl roundly angled at periphery, lower half strongly sculptured by spiral cords and axial riblets in intersections, three columellar folds.

Description – Shell small, slender fusiform, biconic. Protoconch large, multispiral dome-shaped, composed of 3-3.5 smooth convex whorls. Junction with teleoconch marked by sinusigeral scar. Teleoconch of 3.5 almost straight-sided whorls, with periphery at abapical suture. Suture superficial, linear. Spiral sculpture weak, composed of five flattened spiral cords separated by narrow punctate interspaces, weakening further abapically. Last whorl 68-71% total height, roundly angled at periphery, hardly to weakly constricted at base. Lower half of last whorl bearing spiral cords that strengthen, broaden, and become more widely spaced towards siphonal fasciole. Interspaces crossed by fine, close-set axial riblets forming finely cancellate sculpture in interspaces. Aperture

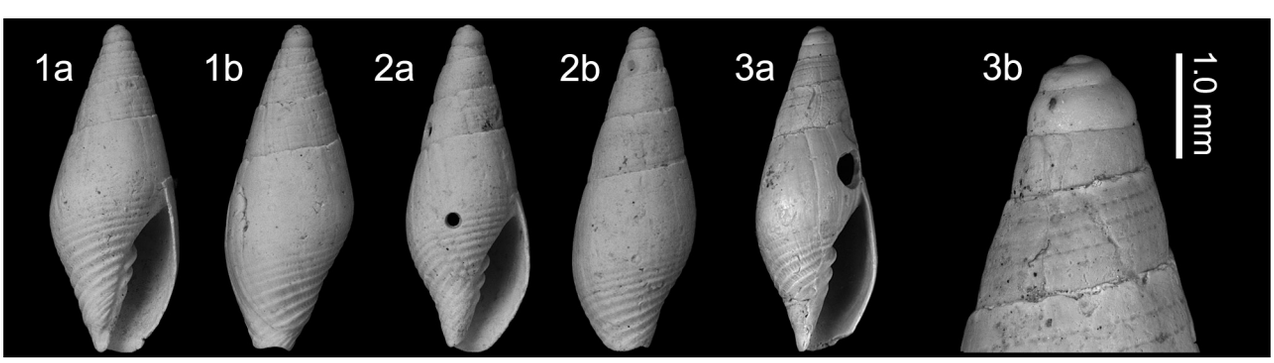


Plate 61. *Pseudonebularia sceauxensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/0933, height 11.9 mm, width 4.6 mm; 2. **Paratype 1** NHMW 2016/0103/0934, height 11.7 mm, width 4.3 mm; La Presselière, Sceaux-d'Anjou. 3. **Paratype 2** NHMW 2016/0103/0931, height 10.4 mm, width 3.8 mm, 3b. detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

elongate, relatively wide, 41-46% total height; anal canal marked by small notch; siphonal canal moderately short, open, wide. Outer lip not thickened, smooth within, extending abapically slightly beyond tip of siphonal fasciole. Columella straight, not callused, forming depression on venter, bearing three oblique folds at inner edge, adapical fold strongest, weakening abapically. Siphonal fasciole not developed.

Discussion – Based on the multispiral protoconch, biconic shape with a short siphonal canal, flat-sided spire whorls, superficial suture, relatively strong cancellate sculpture on the base and the presence of three columellar folds, we have tentatively placed this species in the genus *Pseudonebularia* Fedosov, Herrmann, Kantor & Bouchet, 2018. Although most *Pseudonebularia* species have strong sculpture covering the entire surface, in some extant species, such as *P. maestra* (Reeve, 1845), it is restricted to the early spire whorls and base, like in this NW Franch species. *Pseudonebularia sceauxensis* nov. sp. is immediately separated from *P. hibryda* (Millet, 1865), which is more typical of the genus, in having the strong sculpture covering the entire surface. These two are the only Neogene European records so far of this genus that today is Indo-Pacific.

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

Superfamily Olivoidea Latreille, 1825
Family Olividae Latreille, 1825
Genus *Agaronia* Gray, 1839

Type species (by monotypy) – *Voluta hiatula* Gmelin, 1791, present-day, Atlantic.

1839 *Agaronia* Gray, p. 131.
1831 *Hiatula* Swainson, 73. Junior homonym of *Hiatula* Modeer, 1793 [Bivalvia].
1858 *Anazola* Gray, p. 40. Type species (by subsequent designation; Cossmann, 1899): *Oliva acuminata* Lamarck, 1811, p. 140, present-day, Indo-Pacific.
1847 *Utriculina* Gray, p. 140. Type species (by original designation): *Voluta utriculus* Gmelin, 1791 [= *Voluta gibbosa* Born, 1778], present-day, Caribbean.

***Agaronia vindobonensis* (Csepreghy-Meznerics, 1954)**
Plate 62, figs 1-3

1952a *Olivancillaria clavula* Lamarck, 1810 [*sic*] – Glibert, p. 356, pl. 11, fig. 6 [*non Agaronia clavula* (Lamarck, 1811)].
1964 *Olivancillaria* (*Agaronia*) *clavula* Lamarck, 1810 [*sic*] – Brébion, p. 485 [non *Agaronia clavula* (Lamarck, 1811)].
*1954 *Olivella* (*Lamprodroma*) *clavula vindobonensis* Csepreghy-Meznerics, p. 44, pl. 6, figs 3, 9.
2013 *Anazola vindobonensis* (Csepreghy-Meznerics, 1954) – Landau *et al*., p. 220, pl. 32, figs 5, 6 (*cum syn*.).

Material and dimensions – Maximum height 29.2 mm, width 11.9 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1346-1348 (3), NHMW 2016/0103/1349 (11), RGM.718119 (33), RGM.1349160 (18), RGM.1349161 (5), RGM.1349229 (5), RGM.1349239 (10), RGM.1352222 (4), LC (8), FVD (4). **Renauleau**: NHMW 2016/0103/1677 (4), LC (5 + 6 juveniles), FVD (3). **Beugnon**: RGM.1349131 (4), RGM.1349132 (15 + 10 juveniles), RGM.1349137 (1), LC (7), FVD (6).

Discussion – Landau *et al*. (2013, p. 220) discussed this species under the genus *Anazola* Gray, 1858, which was synonymised with *Agaronia* Gray, 1839 by Kantor *et al*. (2017).
Landau *et al*. separated the lower Miocene *Agaronia clavula* (Lamarck, 1811), which has a slender bullet-shaped shell with a high spire and narrow apical angle, from the middle-upper Miocene *A. vindobonensis* (Csepreghy-Meznerics, 1954), which has a comparatively stouter shell with a broader last whorl and a lower spire. The specimens from Assemblage I are typical for the species, although attaining a smaller maximum size. For fur-

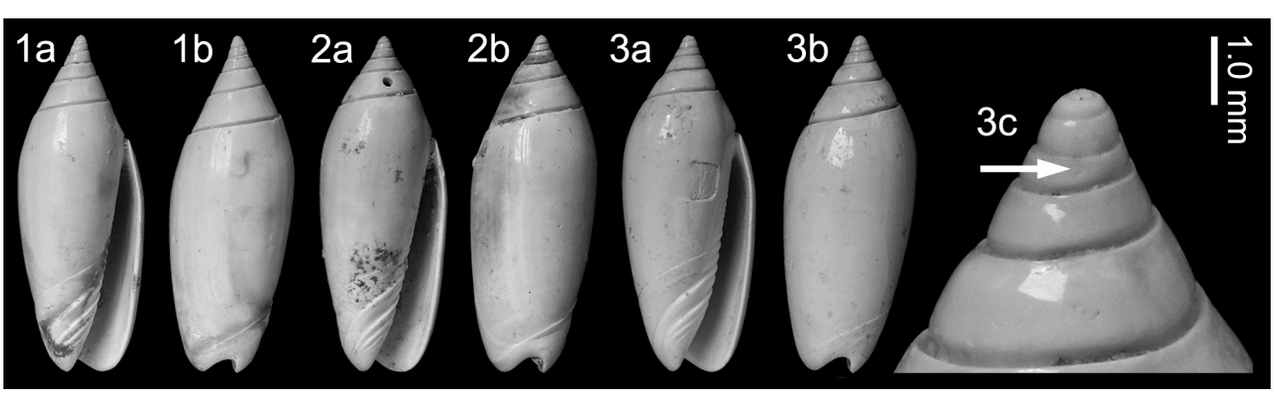


Plate 62. *Agaronia vindobonensis* (Csepreghy-Meznerics, 1954); 1. NHMW 2016/0103/1346, height 25.7 mm, width 9.6 mm; 2. NHMW 2016/0103/1347, height 22.3 mm, width 8.4 mm; 3. NHMW 2016/0103/1349, height 21.7 mm, width 8.5 mm, 3c, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ther discussion see Landau *et al*. (2013, p. 220). Brébion (1964, p. 485) recorded this species from the Assemblage I localities of Sceaux-d'Anjou and Thorigné.

Distribution – Middle Miocene: Atlantic (Langhian): Loire Basin, France (Glibert, 1952a); Paratethys (Langhian-Serravallian): Vienna Basin, Austria (Hörnes, 1852), Poland (Bałuk, 1997), Hungary (Csepreghy-Meznerics, 1954; Strausz, 1966; Kókay, 1966; Bohn-Havas, 1973); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

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

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

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

Amalda glandiformis (Lamarck, 1811) morphotype *elongata*

*1811 *Ancillaria glandiformis* Lamarck, p. 305.
1964 *Ancilla* (*Baryspira*) *glandiformis* Lamarck, 1810 [*sic*] – Brébion, p. 482.
2006 *Amalda glandiformis* (Lamarck, 1810) [*sic*] morphotype *elongata* – Landau & Silva, p. 6, pl. 1, figs 1-8 (*cum syn*.).
2017 *Amalda glandiformis* (Lamarck, 1810) [*sic*] morphotype *elongata* – Van Dingenen *et al*., p. 38, pl. 3, fig. 8.

Material – Thorigné (1), St-Michel (107); fide Brébion (1964, p. 483).

Discussion – This species has been discussed in depth by Landau & Silva (2006), Landau *et al*., (2013) and Van Dingenen *et al*. (2017). The *elongata* morphotype of *Amalda glandiformis* (Lamarck, 1811) is characterised by its tall narrow spire and thin callus. We have not found this morphotype in the collections consulted. Brébion did not find it in the Assemblage I localities sampled by our group, but it seems to be locally abundant at St-Michel. We have no reason to doubt Brébion's identification and include it herein.

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

Discussion

In this paper we record 67 neogastropod species (of which five are left in open nomenclature), representing 26 genera. Eighteen are described as new: *Gibberula ligeriana* nov. sp., *Euthria presselierensis* nov. sp., *Mitrella clava* nov. sp., *Mitrella ligeriana* nov. sp., *Mitrella miopicta* nov. sp., *Mitrella pseudoinedita* nov. sp., *Mitrella pseudoblonga* nov. sp., *Mitrella pseudoturgidula* nov. sp., *Sulcomitrella sceauxensis* nov. sp., *Tritia turtaudierei* nov. sp., *Engina brunettii* nov. sp., *Pisania redoniensis* nov. sp., *Pusia* (*Ebenomitra*) *brebioni* nov. sp., *Pusia* (*Ebenomitra*) *pseudoplicatula* nov. sp., *Pusia* (*Ebenomitra*) *renauleauensis* nov. sp., *Pusia* (*Ebenomitra*) *sublaevis* nov. sp., *Episcomitra s.l. silvae* nov. sp., *Pseudonebularia sceauxensis* nov. sp. *Fusus strigosus* Millet, 1865 is a junior homonym of *F. strigosus* Lamarck, 1822, and is renamed *Polygona substrigosa* nom. nov. Of the 67 neogastropod species recorded here, 44 (66%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. If we include the middle Miocene, 50 (75%) are restricted to northwestern France. Stratigraphically (see Fig. 1), 18 (27%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1952a). Twelve species (18%) are also present in the Assemblage III (sensu Van Dingenen *et al*., 2015) of northwestern France. Three are also found in the North Sea Basin Pliocene. Fifteen species (22%) are relatively cosmopolitan in the Pliocene, found in the Atlantic and Mediterranean. Only three (4%) are still living in European Atlantic and/or Mediterranean waters.

This is the first time in this series that we record fewer species than Brébion (1964), who recorded 73 species from the Assemblage I localities of NW France within the groups covered in this paper. We were unable to verify several of the species recorded by Brébion (1964) of which the most important are listed below uncritically, as identified by Brébion.

Marginella (*Stazzania*) *emarginata* Bonelli, 1825 (1964, pl. 13, fig. 19). The shell figured does indeed seem to be a *Marginella* sp., but is either incomplete or immature as the outer lip is not thickened. Brébion listed one specimen from the Assemblage I locality of St-Michel, but as the specimen figured is from the Assemblage IV locality of Gourbesville we provisionally exclude it from the Assemblage I fauna.

Athleta ficulina Lamarck, 1811 (1964, p. 514, pl. 13, fig. 1). The shell figured is indeed what Landau *et al*. (2013) would have called *Athleta rarispina* (Lamarck, 1811).

Brébion recorded one specimen from the middle Miocene of Louans and one from the Assemblage I locality of St-Michel, and noted that they were both of the *rarispina* variety. However, the specimen figured is the one from Louans. Although this species group is impossible to confuse, it seems their taxonomy is more complicated than previously thought (Lozouet, 2019). In view of this, and not having found a single fragment of *Athleta* in any of the numerous collections consulted, we provisionally exclude it from the Assemblage I fauna pending further material and a revision of the European Neogene *Athleta* species.

Buccinulum (*Euthria*) *corneum* Linné 1766 [*sic*] (1964, p. 418, pl. 10, fig. 14). The shell figured, in lateral view, is from Sceaux-d'Anjou and somewhat worn. It seems to have strong axial ribs on the spire whorls, which would be unusual for *Euthria cornea* and it is more likely to be a large specimen of *E. recurvata* (Millet, 1865).

Euthriofusus burdigalensis Defrance, 1820 [*sic*] (1964, p. 475). Recorded from Sceaux-d'Anjou and Thorigné, but not figured. We have not seen any fragments of this species that was described by de Basterot (1825) and we provisionally exclude it from the Assemblage I fauna.

Fasciolaria (*Pleuroploca*) *nodifera* Dujardin, 1837. (1964, p. 476). Recorded from Sceaux-d'Anjou, but not figured. Now placed in the genus *Aurantilaria* Snyder, Vermeij & Lyons, 2012. Again, we have not seen any fragments of this species and provisionally exclude it from the Assemblage I fauna.

The nassariids
Nassarius instabilis (Bellardi, 1882) (1964, p. 441, pl. 11, fig. 6), Beaulieu.
Hinia reticulata var. *recta* (Dollfus & Dautzenberg, 1886) (1964, p. 442, pl. 11, fig. 9), St-Michel.
Hinia corrugata (Brocchi, 1814) (1964, p. 444, pl. 11, fig. 10), St-Michel.
Hinia (*Tritonella*) *verrucosa* (Brocchi, 1814) (1964, p. 463, not illustrated), Sceaux-d'Anjou, Thorigné, St-Michel.
Hinia (*Uzita*) *prysmatica* (Brocchi, 1814) (1964, p. 449, not illustrated), Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, St-Michel.
Hinia (*Uzita*) *caroli* (Dollfus & Dautzenberg, 1886) (1964, p. 450, not illustrated), Sceaux-d'Anjou, Beaulieu, Thorigné, St-Michel. This is probably a misidentification and represents *Tritia spectabilis* (Nyst, 1845).
Niotha contorta (Dujardin, 1837) (1964, p. 468, not illustrated), Sceaux-d'Anjou.

Some of these species (the first three on the list) originate from localities not represented in the collections used in this work, but the rest are from the same localities sampled. We cannot explain their absence.

Olivancillaria (*Agaronia*) *plicaria* Lamarck, 1810 [*sic*] (1964, p. 484). A single specimen recorded from St-Michel, but not figured. The collections consulted do not contain material from this locality, and the record needs to be confirmed.

Olivancillaria (*Agaronia*) *clavula* Lamarck, 1810 [*sic*] (1964, p. 485). Recorded from Sceaux-d'Anjou and Thorigné. We cannot confirm the occurrence of this species in Assemblage I.

Oliva (*Neocylindrus*) *dufresnei* Basterot, 1825 (1964, p. 486, pl. 12, fig. 11). Widely reported by Brébion in Assemblage I from Renauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, St-Michel and Contigné. The figured specimen from Sceaux-d'Anjou does seem to represent that species. We cannot explain why we cannot verify this record. It is possible that we have failed to recognise it and considered them squatter forms of *Agaronia vindobonensis* (Csepreghy-Meznerics, 1954).

The generic composition is not unusual for European Miocene Atlantic assemblages, but smaller-shelled families like the Cystiscidae and Columbellidae are more abundant in both numbers and species than the larger-shelled groups, in which smaller species are favoured, such as in the nassariids and the Fasciolariidae, where both large and small-shelled species usually co-occur. As we have seen in previous parts of this series, even in the largest-shelled groups in Assemblage I, the species present are far smaller than average for the group. Fragments or abraded larger shells are occasionally found, especially at Renauleau, but these are uncommon and almost without exception show signs of transport. This suggests the large-shelled species did not live in this environment. The dwarfism seen in the fauna, or what Lauriat-Rage (1981) called '*nanisme*', was already commented on in parts 1-3 of this series (Landau *et al*., 2017, 2018, 2019).

The assemblage is highly endemic with 44 (66%) species occurring exclusively in the northwestern French Assemblage I-III. This concurs with the observation that there is a strong predisposition for non-planktotrophic-type protoconchs, especially amongst the endemic species. The rate of endemism is similar to that found in Part 1 of this series (Patellogastropoda and Vetigastropoda) and Part 2 (Caenogastropoda) (63% for both; Landau *et al*., 2017, 2018). Endemism amongst the muricids (Part 3) was lower at 33% (Landau *et al*., 2019).

The neogastropod generic composition is moderately strongly thermophilic, with a considerable number of genera present that do not extend northwards to the latitude of NW France today (i.e. *Gibberula*, *Trigonostoma*, *Pusia* (*Ebenomitra*), *Episcomitra*, *inter alii*.), but with few frankly tropical elements (i.e. *Thala*).

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

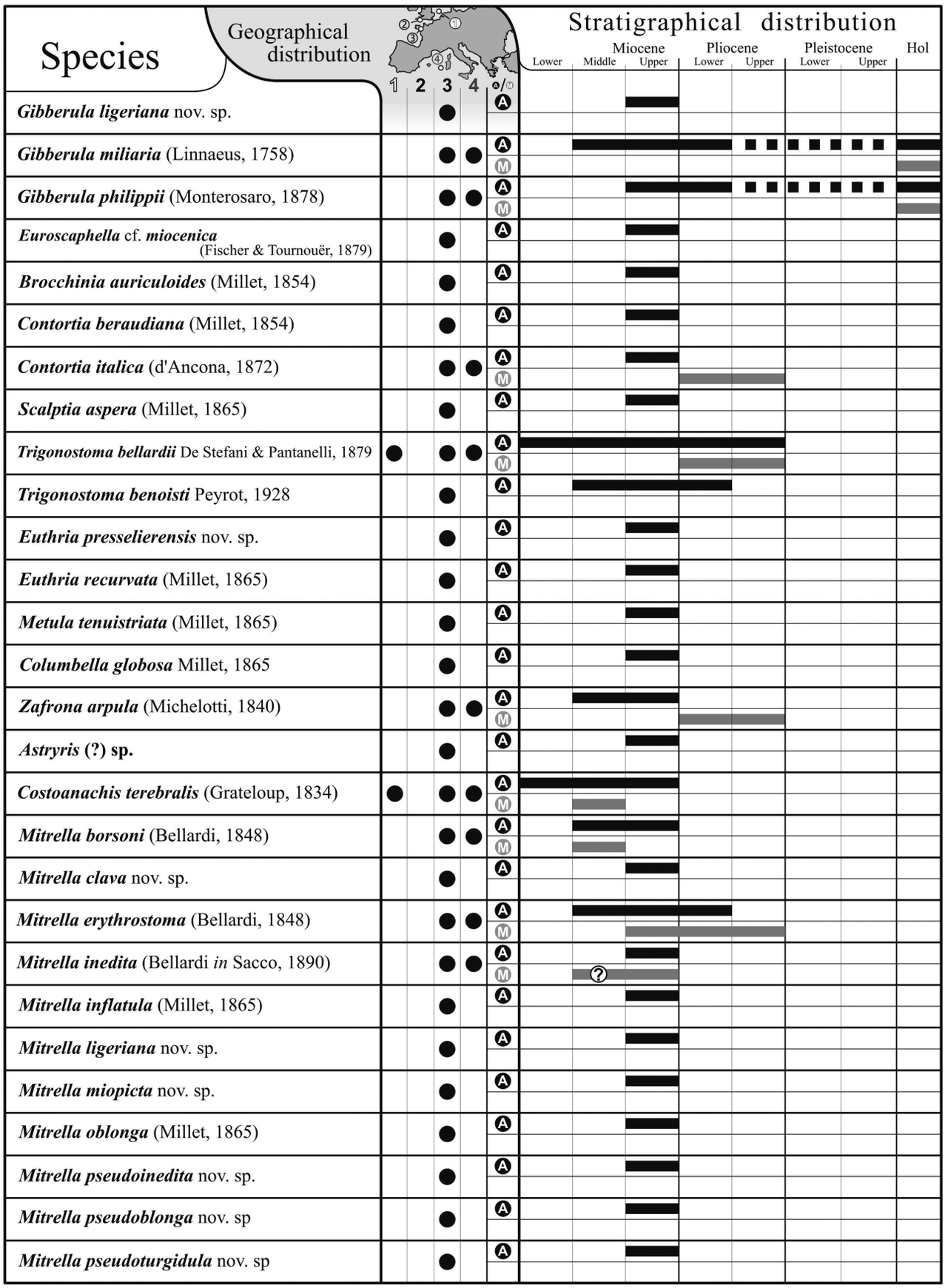
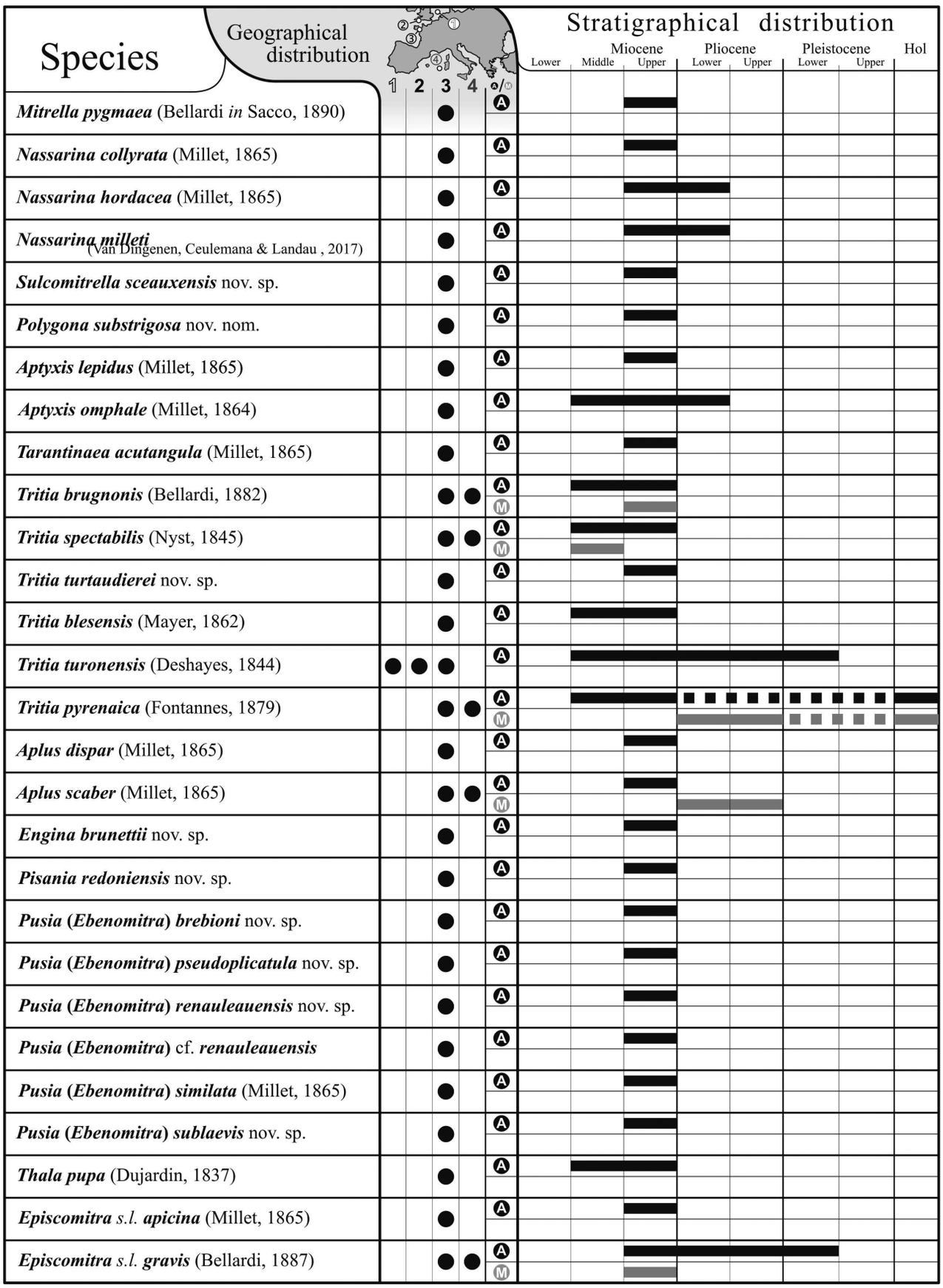
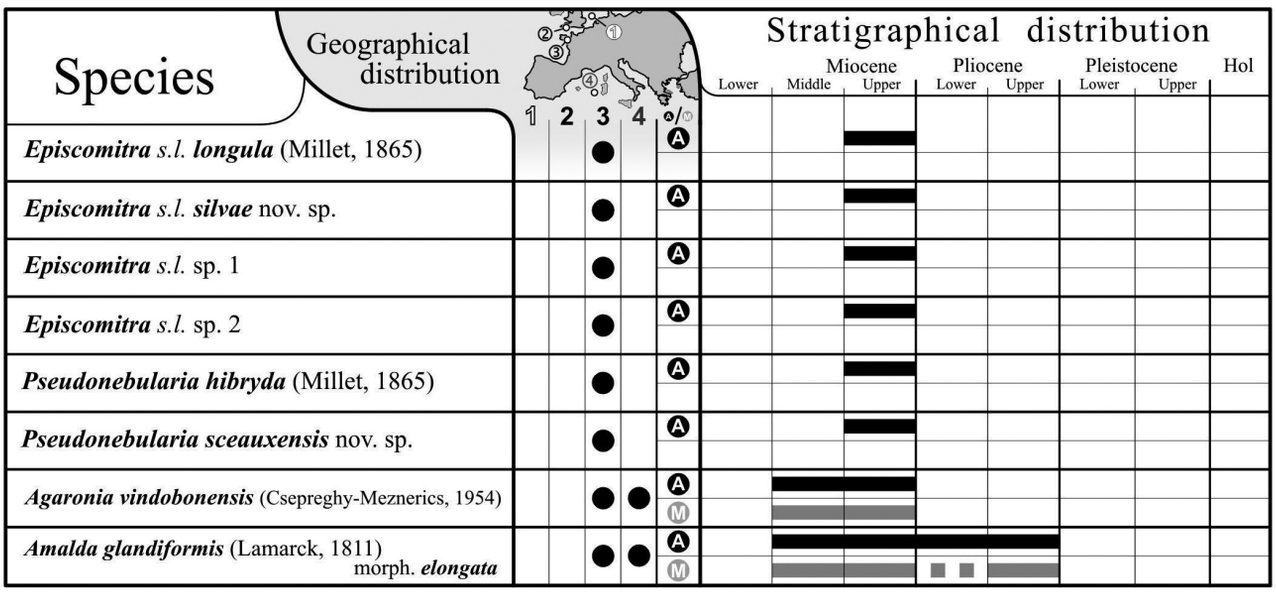


Figure 1. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black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


Species
Geographical distribution
1
2
3
4
♂/♀
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower
Middle
Upper
Lower
Upper
Lower
Upper
Mitrella pygmaea (Bellardi in Sacco, 1890)
Nassarina collyrata (Millet, 1865)
Nassarina hordacea (Millet, 1865)
Nassarina milleti (Van Dingenen, Ceulemana & Landau , 2017)
Sulcomitrella sceauxensis nov. sp.
Polygona substrigosa nov. nom.
Aptyxis lepidus (Millet, 1865)
Aptyxis omphale (Millet, 1864)
Tarantinaea acutangula (Millet, 1865)
Tritia brugnonis (Bellardi, 1882)
Tritia spectabilis (Nyst, 1845)
Tritia turtaudierei nov. sp.
Tritia blesensis (Mayer, 1862)
Tritia turonensis (Deshayes, 1844)
Tritia pyrenaica (Fontannes, 1879)
Aplus dispar (Millet, 1865)
Aplus scaber (Millet, 1865)
Engina brunettii nov. sp.
Pisania redoniensis nov. sp.
Pusia (Ebenomitra) brebioni nov. sp.
Pusia (Ebenomitra) pseudoplicatula nov. sp.
Pusia (Ebenomitra) renauleauensis nov. sp.
Pusia (Ebenomitra) cf. renauleauensis
Pusia (Ebenomitra) similata (Millet, 1865)
Pusia (Ebenomitra) sublaevis nov. sp.
Thala pupa (Dujardin, 1837)
Episcomitra s.l. apicina (Millet, 1865)
Episcomitra s.l. gravis (Bellardi, 1887)



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