The upper Miocene gastropods of northwestern France, 5. Conoidea

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In this paper we review the Conoidea of the Tortonian upper Miocene (Assemblage I of Van Dingenen *et al*., 2015) of northwestern France. Eighty-four species are recorded, of which 42 are new: *Eoconus cambieni* nov. sp., *Eoconus vanhoutenae* nov. sp., *Aphanitoma roesti* nov. sp., *Pleurotomoides barnardi* nov. sp., *Pleurotomoides vanderdoncki* nov. sp., *Mitromorpha* (*s.s.*) *mulderi* nov. sp., *Bactrocythara pascaleae* nov. sp., *Bela henkmulderi* nov. sp., *Bela keukelaari* nov. sp., *Bela pseudomegastoma* nov. sp., *Bela pseudovulpecula* nov. sp., *Bela redoniana* nov. sp., *Bela scarponii* nov. sp., *Bela sceauxensis* nov. sp., *Mangelia burgersae* nov. sp., *Andonia delgadoi* nov. sp., *Buccinaria minuscula* nov. sp., *Clathromangelia daisyae* nov. sp., *Clathromangelia densecostata* nov. sp., *Clathromangelia hakkennesi* nov. sp., *Clathromangelia helwerdae* nov. sp., *Clathromangelia karinneae* nov. sp., *Clathromangelia pereirae* nov. sp., *Clathromangelia vannieulandei* nov. sp., *Clathromangelia wopkeae* nov. sp., *Cyrillia michalidesi* nov. sp., *Daphnella* (*Paradaphne*) *groeneveldi* nov. sp., *Leufroyia annegienae* nov. sp., *Leufroyia hesseli* nov. sp., *Leufroyia ligeriana* nov sp., *Leufroyia renauleauensis* nov. sp., *Leufroyia riccardoi* nov. sp., *Leufroyia seani* nov sp., *Raphitoma breitenbergeri* nov. sp., *Raphitoma dellabellaorum* nov. sp., *Raphitoma soniusae* nov. sp., *Raphitoma vogeli* nov. sp., *Teretia horroi* nov. sp., *Clavatula sceauxensis* nov. sp., *Haedropleura brebioni* nov. sp., *Haedropleura gallica* nov. sp., *Haedropleura ligeriana* nov. sp. The assemblage is highly endemic, with 90% of the species restricted to the Neogene deposits of northwestern France. This probably accounts for the strong predisposition for non-planktotrophic-type protoconchs. This has also been seen in previous parts of this series, but is even more strongly marked amongst the Conoidea.

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, 2017; Landau *et al*., 2017, 2018, 2019a, b): Gastropods of the superfamily Conoidea in the Assemblage I deposits of Van Dingenen *et al*. (2015) of Tortonian upper Miocene age are revised.

In his unpublished thesis, Brébion (1964) of the Centre National de la Recherche Scientifique, Paris, recorded 59 conoidean 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*.

One of the reviewers (Riccardo Giannuzzi-Savelli) brought to our attention the fact that placing the term *nomen nudum* after the names proposed by Brébion (1964) is not correct, as this term is used for published names incorrectly erected, whereas Brébion's thesis was never published. In publishing Brébion's names with a description and illustration the present authors could be considered as making the name available. Indeed, this alternative was proposed to the MNHN (Paris) at the beginning of the series (BL, personal communication J.M. Pacaud, 2015). However, it was felt that to avoid confusion it was best not to use Brébion's names, and therefore throughout this series on the gastropods of northwestern France we have placed the term *nomen nudum* after Brébions names to make it clear that the citation of unpublished names is not intended for taxonomic purposes.

Geological setting and material and methods

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

I (BL) am grateful to the Naturalis Biodiversity Center, Leiden, The Netherlands, for their support over the years in my role as Guest Researcher. I take pleasure in dedicating this work to the many volunteers who work tirelessly in the fossil mollusc section of that institution, and collectors who donated (part of) their collection to Naturalis and name many of the new species after a number of them.

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).

Systematic palaeontology

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

Superfamily Conoidea Fleming, 1822
Family Conidae Fleming, 1822
Genus *Conilithes* Swainson, 1840

Type species – *Conus antidiluvianus* Hwass *in* Bruguière, 1792, by monotypy, Eocene, France.

1840 *Conilithes* Swainson, p. 311.
1847 *Conolithus* Herrmannsen, p. 294. Unjustified emendation of *Conilithes* Swainson, 1840.
1890 *Conospirus* de Gregorio, p. 21. Type species (by original designation): *Conus antidiluvianus* Bruguière, 1792, Eocene, France. Junior objective synonym of *Conilithes* Swainson, 1840.
1896 *Conospira* Cossmann, p. 155. Unjustified emendation of *Conospirus* de Gregorio, 1890.

Conilithes torulosus (Millet, 1865)

Plate 1, figs 1-7

1854 *Conus Torulosus* Millet, p. 160 (*nomen nudum*).
1865 *Conus torulosus* Millet, p. 586.
1952a *Conus* (*Conospira*) *dujardini* Deshayes, 1845 – Glibert (?*partim*), p. 371, pl. 12, fig. 11a (only).
1964 *Conus* (*Conolithus* [*sic*]) *dujardini* Deshayes, 1845 – Brébion, p. 630 [*non* Deshayes, 1845 = *Conilithes exaltatus* (Eichwald, 1830)].
2010 *Conus dujardini* Deshayes, 1845 – Vaessen (*partim*), p. 6, figs 2-4 (only).

Material and dimensions – Maximum height 25.9 mm, width 14.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1297 (1), NHMW 2016/0103/1230 (1 juvenile), NHMW 2016/0103/1298 (5), RGM.1352386 (1), LC (6), FVD (8). **Sceaux-d'Anjou**: NHMW 2016/0103/1299 (13), RGM.718200 (50+), RGM.1352388 (39), RGM.1352470 (25), RGM.1352472 (25), RGM.1352473 (50 + adults and juveniles), LC (30), FVD (38). **Renauleau**: NHMW 2016/0103/1886-1890 (5), NHMW 2016/0103/1886 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1349149 (14 fragments and juveniles), RGM.1352354 (10 juveniles + fragments), RGM.1352409 (6).

Original description – 'Conus torulosus, *Millet. Coq. de moyenne taille, à spire élevée, conique, composée de 11-12 tours creusés en gouttière et bordés chacun d'un cordonnet arrondi; le dernier tour présente à sa base, 7-8 petits sillons placés obliquement. Longueur: 25-26 millimètres; diamèter: 13-14 millimètres, Th, Sc.*' (Millet, 1865, p. 586).

Discussion – This small *Conilithes* species was identified as *Conus dujardini* Deshayes, 1845 by Brébion (1964, p. 630), which was shown to be a junior synonym of *C. exaltatus* Eichwald, 1830 by Harzhauser & Landau (2016, p. 52). It has the same type of tall multispiral protoconch. However, the French Tortonian shells are half the usual size for *C. exaltatus*, the spire is not as tall or scalate and the siphonal canal is shorter. The tubercles present on the neanic whorls of *C. exaltatus* do extend more than the first 3-4 teleoconch whorls, whereas in the French species they persist onto the 6-7 whorl. The spiral grooves cover more of the base in *C. exaltatus*, whereas in the French species they are only present over the lower third of the last whorl. Finally, few shells from Assemblage I preserve any sort of colour pattern, even under UV light. This French cone is an exception with a broad light horizontal band placed mid-whorl on the last whorl enhanced under UV light. This pattern is different from that seen in *C. brezinae* (Hoernes & Auinger, 1879) that has narrow interrupted horizontal stripes (Harzhauser & Landau, 2016, fig. $5H_1$). They are nevertheless closely affiliated species; the couple of fine spiral grooves below the carina on the last whorl described by Harzhauser & Landau (2016) in *C. exaltatus* can also be seen in this species (Pl. 1, fig. 2). *Conilithes exaltatus* is widely distributed in the Miocene Paratethys (Harzhauser & Landau, 2016), and is also present Miocene eastern Atlantic frontage and Proto-Mediterranean, although these records need to be revised as there is confusion in the literature between the various *Conilithes* species such as *C. brezinae*.
Conilithes brezinae differs from *C. exaltatus* in having a stronger shoulder, which is less sharp and placed lower, a wider subsutural ramp on the last whorl, spiral grooves confined to the base, and a shorter siphonal canal that is less constricted. The French species shares with *C. brezinae* the shorter base and the grooves confined to this area, but differs in having a much shorter spire than either *C. exaltatus* or *C. brezinae*, and the tubercles on the early spire whorls persist longer than in either of the other two

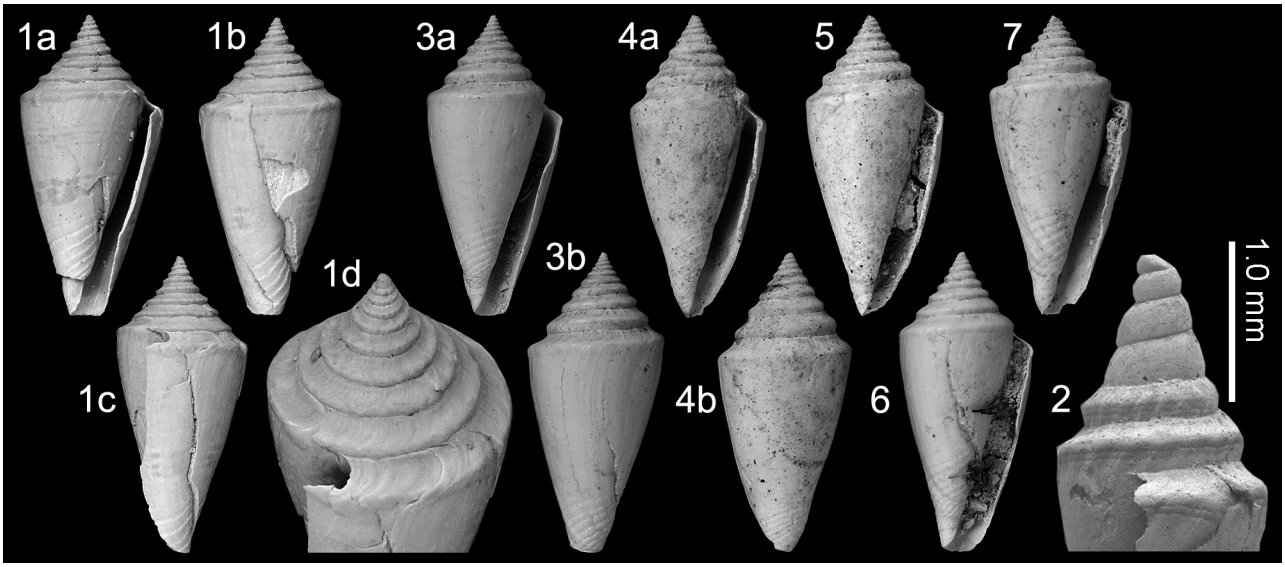

Plate 1. *Conilithes torulosus* (Millet, 1865); 1. NHMW 2016/0103/1297, height 24.2 mm, width 11.7 mm, 1d, detail of subsutural flexure; 2. NHMW 2016/0103/1230 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/1886, height 28.4 mm, width 12.8 mm; 4. NHMW 2016/0103/1887, height 25.1 mm, width 11.2 mm; 5. NHMW 2016/0103/1888, height 23.1 mm, width 10.6 mm; 6. NHMW 2016/0103/1889, height 20.4 mm, width 9.0 mm; 7. NHMW 2016/0103/1890, height 21.1 mm, width 9.9 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

species. *Conilithes brezinae* is also widely distributed in the Miocene Paratethys (Harzhauser & Landau, 2016), and may also be present in the Miocene eastern Atlantic frontage and Proto-Mediterranean, but a revision of the group is required.
In a PCA plot based on shell measurements (Fig. 1a) and a second plot based on shell ratios (Fig. 1b) the three species are well separated.

Fortunately, Millet (1854, 1865) recognised this upper Miocene French form to be distinct and erected the name *C. torulosus* (1854, p. 160; *nomen nudum*), later validated by a description (Millet, 1865, p. 586). We therefore resurrect Millet's name for this French fossil species; *Conilithes torulosus* (Millet, 1865). The specimens from the Atlantic middle Miocene Langhian of the Loire Basin illustrated by Glibert (1952a, pl. 12 figs 11a-c) as *C. dujardini* (= *C. exaltatus*) are problematic and may represent two species. His figure 11a shows a form similar to *C. torulosus* with a relatively low spire and short last whorl and might represent this species. The Loire Basin specimens illustrated by Vaessen (2010, figs 2-4) are almost certainly *C. torulosus*. Glibert (1952a, figs 11b, c) shows a shell with a scalate spire, strongly beaded carina persisting onto the last whorl and relatively long last whorl of which at least the lower two-thirds are spirally grooved. This shell is more like a small form of *C. antidiluvianus.*
Other European Miocene congeners such as *C. allioni*

specimen	SL	MD	AH	AL	HMD	SA	LWA	LW	RD	RSH
NHMW 2016/0103/1297	24.2	11.7	17.6	18.7	16.4	75.9	34.7	2.07	0.66	0.27
NHMW 2016/0103/1886	28.4	12.8	19.9	21.7	18.5	71.1	32.7	2.22	0.64	0.3
NHMW 2016/0103/1887	25.1	11.2	17.6	18.8	16.1	67.5	33.5	2.24	0.64	0.3
NHMW 2016/0103/1888	23.1	10.6	16.6	17.7	15.6	73.2	36.2	2.18	0.64	0.28
NHMW 2016/0103/1889	20.4	9.1	14.9	15.6	13.8	72	33.1	2.27	0.61	0.27
NHMW 2016/0103/1890	21.1	9.9	15.5	16.8	14	80.3	32.9	2.13	0.64	0.27
NHMW (unnumbered)	20	9.7	14.2	15.2	13.2	70.5	36.6	2.06	0.66	0.29
NHMW (unnumbered)	22.6	10.3	15.8	17.4	14.9	68.4	36.6	2.19	0.65	0.3
NHMW (unnumbered)	21.4	9.9	15.7	16.9	14.8	75	33.9	2.16	0.63	0.27

Table 1. *Conilithes torulosus* (Millet, 1865); Shell morphometrics; SL = shell length, MD = maximum diameter, AH = apertural height, AL = apertural length, HMD = height of maximum diameter, SA = spire angle, LWA = angle of last whorl, LW = length/width ratio, RD = relative diameter, RSH = relative height of spire (see Harzhauser & Landau, 2016, p. 8, fig. 2).

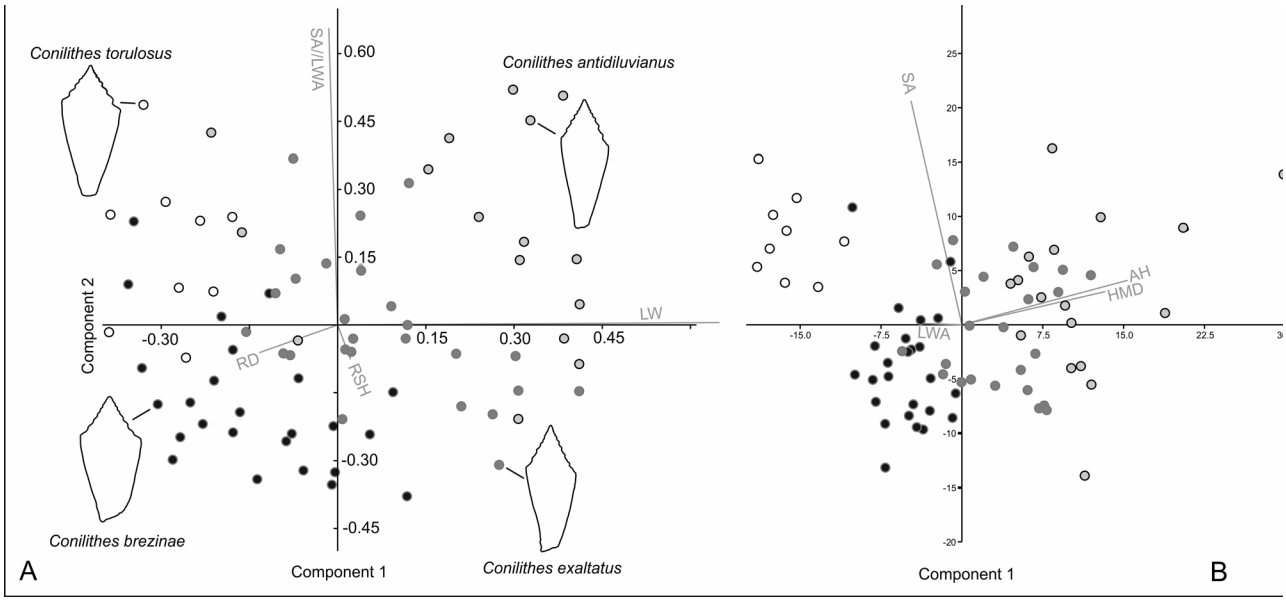

Figure 1. Principal components analysis (PCA) based on shell measurements of specimens of four *Conilithes* species (NHMW collection + Table 1). A: shell ratios, B: shell measurements. A separation of *C. torulosus, C. antidiluvianus*, *C. exaltatus* and *C. brezinae* is evident in both analyses. For measurement abbreviations see legend Table X (adapted from Harzhauser & Landau, 2016, fig. 7).

(Michelotti, 1847), *C. eichwaldi* Harzhauser & Landau, 2016 and *C. sceptophorus* (Boettger, 1887) can be separated by their more rounded shoulder, and hence more pyriform shape. The type species, *C. antidiluvianus* (Bruguière, 1792) is a much larger shell with an elongated last whorl, strongly scalate spire consisting of angular whorls and the strong carina is beaded to the last whorl in most specimens.

As mentioned earlier, this group outside the Paratethys needs revision. It may well be that under closer scrutiny this group consists of allied species rather than one or two variable ones as interpreted by previous authors (i.e. Glibert, 1952a; Vaessen, 2010). We therefore provisionally restrict *C. torulosus* to the middle and upper Miocene of NW France. In Assemblage I it occurs at all localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Beaulieu, les Pierres Blanches; Brébion, 1964, p. 631).

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin (Glibert, 1952a; Vaessen, 2010). Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964).

Genus *Eoconus* Tucker & Tenorio, 2009

Type species – *Conus sauridens* Conrad, 1833, by original designation, present-day, East Pacific.

2009 *Eoconus* Tucker & Tenorio, p. 142.

Note – Two closely similar medium-sized cones occur in Assemblage I characterised by both bearing depressed spires, strong tubercles on early teleoconch whorls, strong spirals on the subsutural platform and a regularly conical last whorl. One has a multispiral protoconch, the other paucispiral. They probably belong to the *Conilithes* group of Tucker & Tenorio (2009) and the *Conasprella* group of Puillandre *et al*. (2014a, b). However, they differ from *Conilithes* species in having a depressed spire (see above) and they differ from *Conasprella* Thiele, 1929 in being lower spired and not having beaded cords on the last whorl. They are closest to the extinct Eocene-Oligocene European and eastern American genus *Eoconus* Tucker & Tenorio, 2009, another member of the *Conilithes*/*Conasprella* group, characterised by having tubercles on early whorls and spirals on the spire whorls. Our only hesitation is that it lacks the dentiform plait on the columella characteristic of the genus. If we are correct in our generic assignment these would be the last known members of the genus and it is possible that this shell trait was lost. Harzhauser & Landau (2016, p. 35) discussed at length the merits of '*One, four or 100 genera*' of Puillandre *et al*. (2014b) and the argument will not be repeated here. However, if all genera in this group were synonymised, as suggested by Puillandre *et al.* (2014a, b) important biogeographic information would be lost, as these two Assemblage I species are not closely related to the species included in either *Conilithes* or *Conasprella* by Harzhauser & Landau (2016).

***Eoconus cambieni* nov. sp.**
Plate 2, figs 1-3

1964 *Conus* (*Lithoconus*) *mercati* var. *sharpeanus* Da Costa, 1866 – Brébion (*partim*?), p. 631 (*non* Pereira da Costa, 1866).

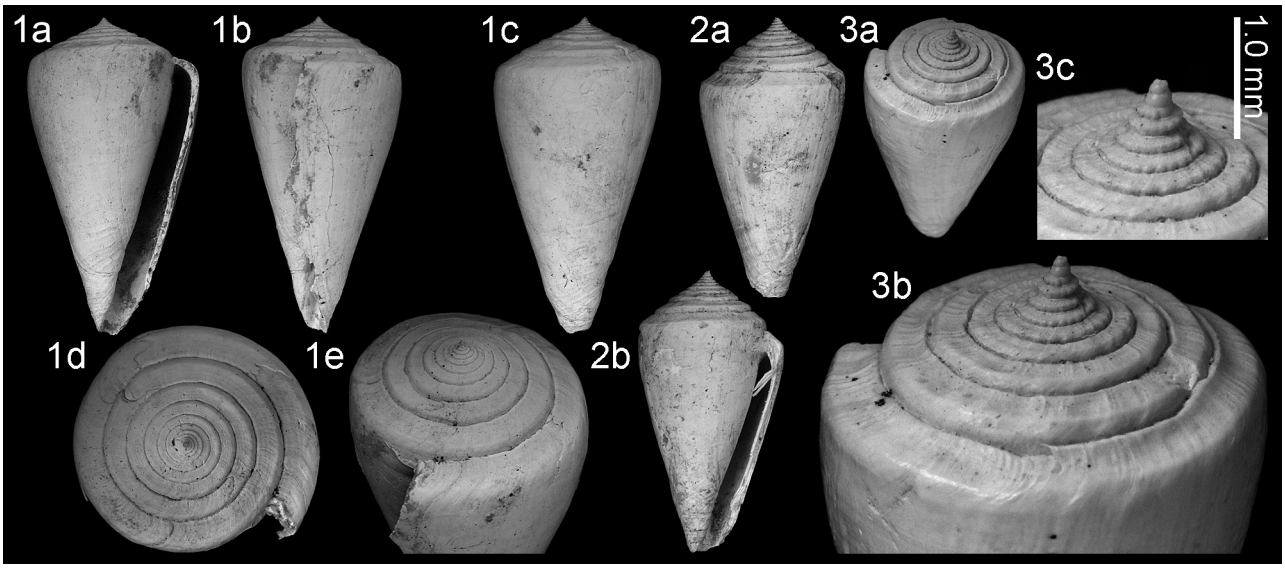

Plate 2. *Eoconus cambieni* nov. sp.; 1. **Holotype** NHMW 2016/0103/1894, height 74.1 mm, width 14.2 mm, 1e detail of subsutural flexure; 2. **Paratype 2** NHMW 2016/0103/1896, height 37.1 mm, 19.2 mm; 3. **Paratype 1** NHMW 2016/0103/1895, 25.1 mm, width 14.6 mm, 3b, detail of subsutural flexure, 3c detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Type material – Holotype NHMW 2016/0103/1894, height 74.1 mm, width 14.2 mm; paratype 1 NHMW 2016/0103/1895, 25.1 mm, width 14.6 mm (juvenile); paratype 2 NHMW 2016/0103/1896, height 37.1 mm, 19.2 mm (juvenile); paratype 3 NHMW 2016/0103/1897, height 26.9 mm, 15.2 mm (juvenile), **Renauleau**. Paratype 4 RGM.1352471, height 29.4, width 15.9 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 35.1 mm, width 18.7 mm. **Sceaux-d'Anjou**: RGM.1352387 (3), FVD (1). **Renauleau**: NHMW 2016/0103/1898 (50+ subadults and juveniles), LC (50+ subadults and juveniles), FVD (50+ subadults and juveniles).

Etymology – Named after Jean-Pierre Cambien from Paris, a passionate collector of the French Tertiary, and good friend of the authors. *Eoconus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Eoconus* species of large size, multispiral protoconch, low spire, whorls with carina placed just above suture, suture deeply impressed, narrowly canaliculated, coarsely beaded early teleoconch whorls and spiral cords on subsutural platform fading by 5-6 whorl, regularly conical last whorl with a few cords restricted to base.

Description – Shell large, with depressed, straight to slightly coeloconoid spire. Protoconch multispiral, tall, consisting of at least three whorls (2.5 whorls preserved). Junction with teleoconch sharply delimited. Teleoconch of up to 11 whorls. Early whorls taller, rapidly becoming depressed. Spire whorls with flat to weakly concave subsutural platform bearing 4-5 weak spirals, roundly angled at beaded carina placed a just above suture, beads prominent extending adapically, crenulating suture. Suture deeply impressed, narrowly canaliculate. Abapically whorls become more depressed, beading and spiral cords weaken, subobsolete by 5-6 whorls where they become broad undulations at shoulder. Last whorl regularly conical with maximum diameter just below shoulder, hardly constricted at base bearing 8-9 narrow cords over base, strengthening abapically. Subsutural flexure initially shallow, deepening towards aperture, strongly curved, strongly asymmetrical. Aperture moderately narrow, anteriorly broadening; siphonal canal medium length, nearly straight; fasciole not well demarcated, weakly swollen with prominent growth lines; inner lip twisted. No colour pattern preserved.

Distribution – *Eoconus cambieni* nov. sp. and *Eoconus vanhoutenae* nov. sp. (see below) are closely similar species. They both have strongly beaded early whorls that fade after 5-6 whorls and spiral cords on the subsutural platform. Indeed, we would probably not have separated them if the protoconch had not been preserved. Despite it being incomplete, in *E. cambieni* it is clearly multispiral, of a planktotrophic type, whilst *E. vanhoutenae*, in which the protoconch is preserved in numerous juveniles, has a paucispiral protoconch typical of direct development. Once the shells are separated, other smaller teleoconch differences become apparent. *Eoconus cambieni* attains a larger maximum size, the spire is even more depressed than in *E. vanhoutenae*, the suture is deeper, even narrowly canaliculated, and the spiral cords on the

subsutural platform are weaker and disappear at about the same time as the beads, on the 5-6 teleoconch whorl, whereas in *E. vanhoutenae* they remain strong on later adult whorls.

These are probably the species identified, but not figured, by Brébion (1964, p. 631) as *Conus* (*Lithoconus*) *mercati* var. *sharpeanus* Pereira da Costa, 1866. However, *Monteiroconus mercati* (Brocchi, 1814) has no beading or spiral cords on the spire whorls (Landau *et al*., 2013, p. 242, 245). *Monteiroconus sharpeanus* does have spiral cords, but does not have tubercles. This is not the species from the middle Miocene Loire Basin described by Peyrot (1938, p. 257) as *Conus mercati ligeriana*, which was synonymised by Glibert (1952a, p. 372) with *C. mercati sharpeanus*, as neither of these authors make any mention of tubercles on the early teleoconch whorls. Vaessen (2010, figs 9, 10B, 11-13) figured further specimens from the Loire Basin as *C. mercati* with spiral sculpture on the subsutural platform, which are not *M. mercati*, but closer to *M. mojsvari* (Hoernes & Auinger, 1879). We have not identified any other species belonging to this group in the European Neogene.

Brébion (1964, p. 632) recorded these two species (as *Conus* (*Lithoconus*) *mercati* var. *sharpeanus*) as occurring in many of the Assemblage I localities (Renauleau, Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place, Beaulieu, les Pierres Blanches, Contigné). It is not possible to tell which of the two he was referring to, but interestingly all the specimens of *E. vanhoutenae*, except one, come from St-Clément-de-la-Place, whereas all the specimens of *E. cambieni* come from Renauleau, where it is not uncommon, but rarely well preserved. Only one specimen of that species attains 74 mm in height, the rest only reach about 35 mm in height. The scarce material at hand from Sceaux-d'Anjou does not have the protoconch preserved, but the cords fade early and are therefore ascribed to *E. cambieni*.

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

***Eoconus vanhoutenae* nov. sp.**
Plate 3, figs 1-2

1964 *Conus* (*Lithoconus*) *mercati* var. *sharpeanus* Da Costa, 1866 – Brébion (*partim*?), p. 631 (*non* Pereira da Costa, 1866).

Type material – Holotype NHMW 2016/0103/1302, height 35.1 mm, width 18.7 mm; paratype 1 NHMW 2016/0103/1303 (juvenile); paratype 2 NHMW 2016/0103/1892, height 33.4 mm, 15.9 mm, **St-Clément-de-la-Place**. Paratype 3 NHMW 2016/0103/1893, height 17.5 mm, 9.3 mm (juvenile), **Renauleau**. Paratype 4 RGM.1352389, height 12.2 mm, width 7.0 mm; paratype 5 RGM.1352390, height 9.5 mm, width 9.3 mm; paratype 6 RGM.1352475, height 11.0 mm, width 5.8 mm; paratype 7 RGM.1352581, height 22.9 mm, width 11.5 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 38.1 mm, width 20.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1304 (10 juveniles), RGM.1352385 (7 juveniles), RGM.1352394 (1 juvenile), RGM.1352431 (3 juveniles), LC (5 juveniles), FVD (12 juveniles). **Sceaux-d'Anjou**: NHMW 2016/0103/1899 (3 subadult + 5 juveniles), RGM.718201 (2 adults + 6 subadults + 50+ juveniles), RGM.1352391 (5), RGM.1352474 (16 juveniles), RGM.1352534 (21 juveniles); RGM.1352582 (2 juveniles), LC (4), FVD (1 adults + 2 subadults + 5 juveniles). **Renauleau**: LC (2).

Etymology – Named after Mieke Visser-van Houten, volunteer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Eoconus* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Eoconus* species of medium size, paucispiral protoconch, angular spire whorls with carina placed just above suture, coarsely beaded early teleoconch whorls,

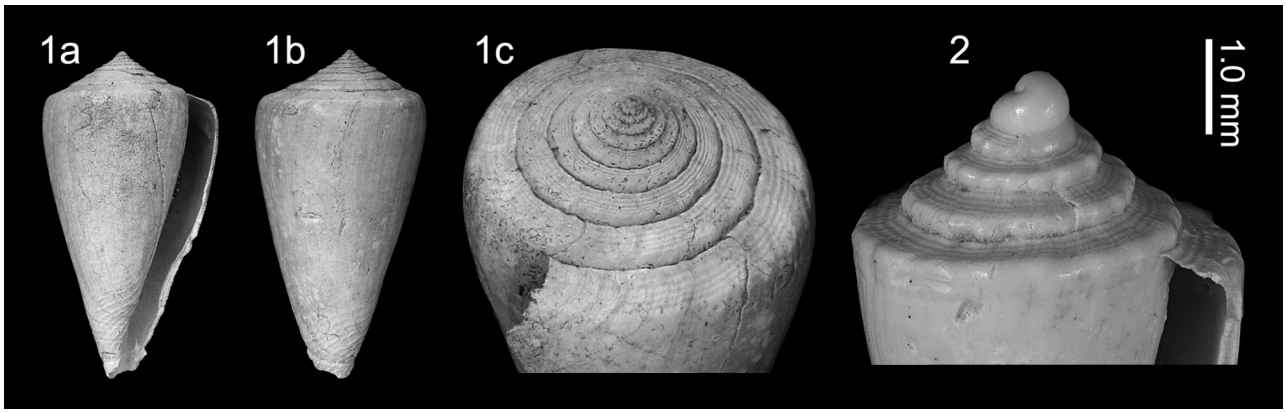

Plate 3. *Eoconus vanhoutenae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1302, height 35.1 mm, width 18.7 mm, 1c, detail of subsutural flexure; 2. **Paratype 1** NHMW 2016/0103/1303 (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fading by 5-6 whorl, strong spiral cords on subsutural platform, regularly conical last whorl with a few cords restricted to base.

Description – Shell medium-sized, with depressed, straight to slightly coeloconoid, scalate spire. Protoconch paucispiral, consisting of two smooth whorls, with large globular first whorl. Junction with teleoconch sharply delimited. Teleoconch of up to eight whorls. Spire whorls with flat to weakly concave subsutural platform bearing 4-5 strong spirals, roundly angled at beaded carina placed a short distance above suture, beads prominent extending adapically, crenulating suture. Suture impressed. Abapically whorls become more depressed, beading weakens, subobsolete by 5-6 whorls where they become broad undulations at shoulder. Last whorl regularly conical with maximum diameter just below shoulder, hardly constricted at base bearing 8-9 narrow cords over base, strengthening abapically. Subsutural flexure of medium depth, strongly curved, strongly asymmetrical. Aperture moderately narrow, anteriorly broadening; siphonal canal moderately short, nearly straight; fasciole not well demarcated, weakly swollen with prominent growth lines; inner lip twisted. No colour pattern preserved.

Discussion – See above under *Eoconus cambieni* nov. sp. We record *Eoconus vanhoutenae* nov. sp. from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

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

Genus *Kalloconus* da Motta, 1991

Type species – *Conus pulcher* Lightfoot, 1786, by original designation, present-day, West Africa.

1991 *Kalloconus* da Motta, p. 12.

***Kalloconus* cf. *pulcher* (Lightfoot, 1786)**
Plate 4, fig. 1

cf. *1810 *Conus pulcher* Lightfoot, p. 179.
1964 *Conus* (*Lithoconus*) *antiquus* Lamarck, 1810 – Brébion, p. 632, pl. 15, figs 15, 16.
cf. *1985 *Conus pulcher* Lightfoot, 1786 – Caretto, p. 185.
cf. *1990 *Conus* cfr. *pulcher* Lightfoot, 1786 – Spadini, p. 320, pl. 3, figs 11, 12.

Material and dimensions – Maximum height 145.0 mm (incomplete). **Sceaux-d'Anjou**: FVD (1 fragment 145.0 mm height), RGM.1352392 (1 fragment 78.4 mm height).

Discussion – This is one of the largest shells found in Assemblage I. Unfortunately only fragments are available to us. Probably due to its large size, Brébion (1964, p. 632) identified this species as *Conus* (*Lithoconus*) *antiquus* Lamarck, 1810. *Monteiroconus antiquus* (Lamarck, 1810) is one of the largest cone shells in the European Neogene. Apart from its large size, it is characterised by its depressed coeleoconoid spire with concave, spirally striate spire whorls, bearing a strongly asymmetrical subsutural flexure, and elongated last whorl. The fragments at hand do not show any spiral striae on the subsutural platform and they therefore do not fit the generic description of *Monteiroconus*. They probably represent *Kalloconus pulcher* (Lightfoot, 1786), however, with the material at hand we cannot make a definitive identification. *Kalloconus pulcher*, now living off West Africa, has been recorded in the Italian Pliocene (Caretto, 1985; Spadini, 1990).
Brébion (1964, p. 633) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and St-Clément-de-la-Place.

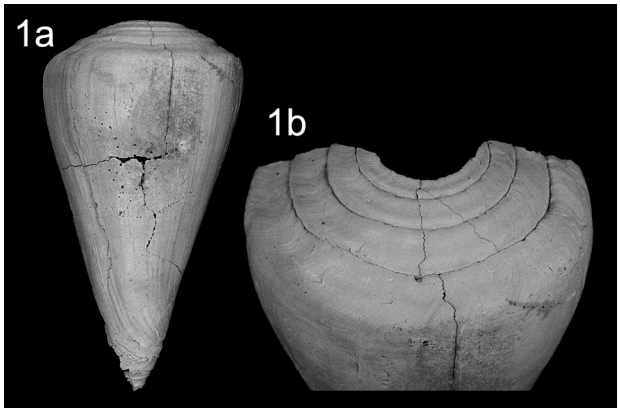

Plate 4. *Kalloconus* cf. *pulcher* (Lightfoot, 1786); 1. FVD coll., height 145.0 mm, width 79.0 mm, 1b, detail of subsutural flexure (photo FVD). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Family Borsoniidae Bellardi, 1875
Genus *Aphanitoma* Bellardi, 1875

Type species – *Turbinella labellum* Bellardi & Michelotti, 1840, by original designation. Miocene, Italy.

1875 *Aphanitoma* Bellardi, p. 22.

***Aphanitoma roesti* nov. sp.**
Plate 5, figs 1-4

1964 *Aphanitoma labellum* Bonelli *in* Bellardi et Michelotti – Brébion, p. 571 [*non Aphanitoma labellum* (Bellardi & Michelotti, 1840)].

Type material – Holotype MNHN.F.A70517, height 8.7 mm, width 3.2 mm; paratype 1 MNHN.F.A70518,

height 8.2 mm, width 3.2 mm; paratype 2 NHMW 2016/0103/1161, height 6.4 mm, width 2.7 mm; paratype 3 NHMW 2016/0103/1162, height 6.1 mm (juvenile); paratype 4 NHMW 2016/0103/1163, height 11.3 mm, width 4.1 mm; paratype 5 NHMW 2016/0103/1164, height 7.4 mm, width 3.0 mm; paratype 6 RGM.1352372, height 8.1 mm, width 3.1 mm; paratype 7 RGM.1352373, height 6.5 mm, width 2.4 mm, **St-Clément-de-la-Place**. Paratype 8 RGM.1352499, height 10.3 mm, width 5.9 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 11.6 mm, width 4.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1165 (32), RGM.1352374 (7), RGM.1352432 (2), LC (24), FVD (40). **Sceaux-d'Anjou**: NHMW 2016/0103/1166 (50+), RGM.718152 (2), RGM.718153 (50+), RGM.718154 (18), RGM.1352439 (11), RGM.1352455 (3), RGM.1352500 (30), LC (6), FVD (50+). **Renauleau**: LC (8). **Beugnon**: RGM.1352347 (2), RGM.1352579 (5).

Etymology – Named after Ben Roest of Silvolde, The Netherlands, who kindly donated his collection to the Naturalis Biodiversity Center, Leiden, The Netherlands, which was used in this work. *Aphanitoma* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Aphanitoma* species of small size, squat fusiform shape, paucispiral protoconch, weakly shouldered teleoconch whorls, 13-15 narrow axial ribs overrun by four primary cords on spire whorls, last whorl regularly convex, narrow aperture, lirate within, two columellar folds, short siphonal canal.

Description – Shell small, squat fusiform, relatively solid. Protoconch low dome-shaped, paucispiral, composed of two smooth whorls. Transition to protoconch sharply delimited by beginning of spiral sculpture. Teleoconch of five convex whorls, weakly angled at shoulder, with periphery a short distance above abapical suture, separated by impressed suture. Axial sculpture of 13-15 narrow opisthocline ribs. Spiral sculpture of four narrow subequal cords, about half width of their interspaces, overrun axials. Secondary thread develops between first and second cord on penultimate whorl and in the occasional interspace on last whorl in some specimens. Last whorl 61-62% total height, regularly convex, weakly constricted at base, axials weaken over base, four widely spaced primary spirals above mid-whorl, about 12 narrower closer-set spirals over base and siphonal fasciole. Aperture 39-42% height, ovate-elongate, outer lip not thickened, lirate a short distance within the aperture; anal sinus not developed; siphonal canal short, open. Columella excavated in upper third, straight below, bearing two prominent, strongly oblique folds mid-columella. Columellar and parietal callus not developed.

Discussion – This species was confused with *Aphanitoma labellum* (Bellardi & Michelotti, 1840) by Brébion (1964, p. 571, pl. 13, fig. 40), a species from the upper Miocene of Italy, but that species is taller and more slender, the shoulder is more angular and the siphonal canal is longer. The lectotype illustrated by Ferrero Mortara *et al*. (1981, pl. 17, fig. 4) seems to have a multispiral protoconch. *Aphanitoma marqueti* Ceulemans, Van Dingenen & Landau, 2018 from the lower Pliocene Assemblage III of NW France also has a paucispiral protoconch of about two whorls, but differs in having predominantly spiral sculpture, the axials weaken and disappear on later teleoconch whorls. Numerous *Aphanitoma* species from the Italian Pliocene were reviewed by Della Bella & Scarponi (2007) of which only those with a paucispiral protoconch need to be compared. *Aphanitoma imperati* (Scacchi, 1835) and *A. pluriplicata* Bellardi, 1877 both have a wider, well-developed, slightly concave subsutural ramp, fewer and broader axial ribs, weaker spiral sculpture, and a longer siphonal canal. The same differences apply to *A. targioniana* d'Ancona, 1872 in which all sculpture is subdued. *Aphanitoma* sp. 2 of Della Bella & Scarponi (2007) is closer in shape to the French species, but has

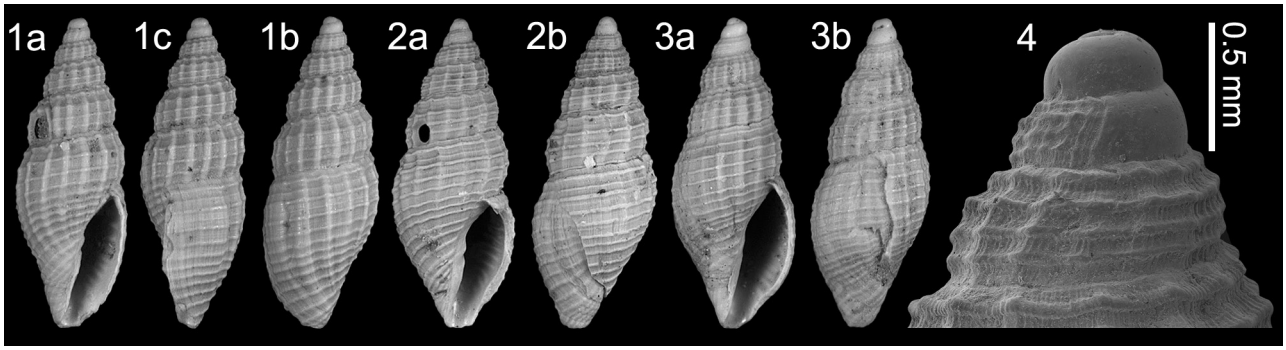

Plate 5. *Aphanitoma roesti* nov. sp.; 1. **Holotype** MNHN.F.A70517, height 8.7 mm, width 3.2 mm; 2. **Paratype 1** MNHN.F.A70518, height 8.2 mm, width 3.2 mm; 3. **Paratype 2** NHMW 2016/0103/1161, height 6.4 mm, width 2.7 mm; 4. **Paratype 3** NHMW 2016/0103/1162, height 5.7 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

a more angular shoulder and broad cords separated by narrow grooves rather than the narrow cords seen in *A. roesti* nov. sp.
We record *A. roesti* nov. sp. from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou, Renauleau and Beugnon.

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

Genus *Asthenotoma* Harris & Burrows, 1891

Type species – Pleurotoma meneghinii Mayer, 1868, by typification of replaced name, Miocene, Italy.

1891 *Asthenotoma* Harris & Burrows, p. 113. *Nom. nov. pro Oligotoma* Bellardi, 1875, *non* Westwood, 1836 [Insecta, Embioptera].

For generic synonymy see Ceulemans *et al*. (2018, p. 90).

***Asthenotoma colus* (Dujardin, 1837)**
Plate 6, figs 1-3

*1837 *Pleurotoma colus* Dujardin, p. 291, pl. 20, fig. 21.
1890 *Pleurotoma* (*Oligotoma*) *ornata* Defr. – Hoernes & Auinger, p. 382, pl. 34, figs 16, 17 [*non Asthenotoma ornata* (Defrance, 1826)].
1891 *Pleurotoma* (*Oligotoma*) *ornata* Defr. – Hoernes & Auinger, pl. 50, fig. 27 [*non Asthenotoma ornata* (Defrance, 1826)].
1931 *Asthenotoma ornata* Defrance – Peyrot, p. 192, pl. 8, figs 35, 36 [*non Asthenotoma ornata* (Defrance, 1826)].
1938 *Asthenotoma ornata* Defrance – Peyrot, p. 279 [*non Asthenotoma ornata* (Defrance, 1826)].
1954 *Asthenotoma colus* Dujardin, 1837 – Glibert, p. 37, pl. 5, fig. 10.
1964 *Asthenotoma colus* Dujardin, 1837 – Brébion, p. 569.

Materials and dimensions – Maximum height 11.6 mm, width 4.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/2005 (1), NHMW 2016/0103/2006 (50+), RGM.1352654 (6), RGM.1352656 (7), RGM.1352657 (14), RGM.1352658 (18), RGM.1352659 (50+), LC (25), FVD (31). **Renauleau**: NHMW 2016/0103/2007-2008 (2), NHMW 2016/0103/2009 (3), LC (2).

Discussion – As discussed by Glibert (1954, p. 38) the description given by Peyrot (1931, p. 192) for *Asthenotoma ornata* (Defrance, 1826) does not refer to that species, but to *A. colus* (Dujardin, 1837). The specimens from Assemblage I have a paucispiral protoconch, like all its congeners in Assemblage I. The teleoconch whorls have a broad, finely beaded subsutural ramp, the shoulder is placed low and is relatively sharply angled. Below the cords are irregular in width, but wider than over the subsutural ramp and more coarsely beaded, most strongly so at the periphery. We have interpreted this species as *A. colus*, although the beading at the periphery is slightly finer than in the specimen from the middle Miocene Loire Basin illustrated by Glibert (1954, pl. 5, fig. 10) and specimens at hand from Le Leroux (Loire Basin).
Brébion (1964, p. 570) recorded this species from the Assemblage I locality of St-Michel and Beaulieu, to which we add Sceaux-d'Anjou and Renauleau and Assemblage II (Apigné, Le Temple du Cerisier). He also listed it from Assemblage III and IV localities, but these records were not confirmed by Ceulemans *et al*. (2018) and we have provisionally excluded these records from the distribution. We have also not seen this species from the Middle Miocene Paratethys, but follow in part the chresonymy given by Gatto (1997, p. 55)

Distribution – Middle Miocene (Langhian): Atlantic, Loire Basin, France (Dujardin, 1837; Peyrot, 1938; Glibert, 1954), Aquitaine Basin (Peyrot, 1931); Paratethys, Austria (Hoernes & Auinger, 1880), Romania (Hoernes & Auinger, 1880). Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964).

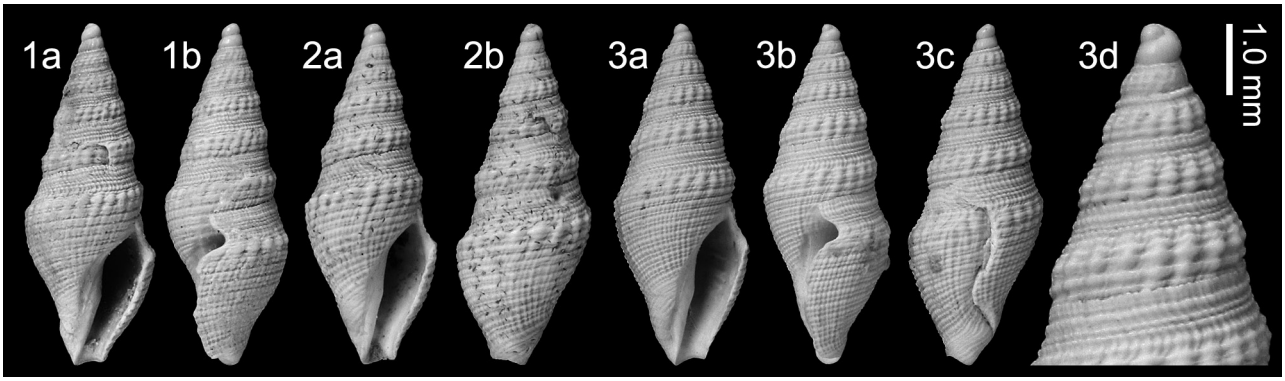

Plate 6. *Asthenotoma colus* (Dujardin, 1837); 1. NHMW 2016/0103/2005, height 10.2 mm, width 3.8 mm. La Presselière, Sceaux-d'Anjou. 2. NHMW 2016/0103/2007, height 10.2 mm, width 3.9 mm; 3. NHMW 2016/0103/2008, height 9.9 mm, width 3.7 mm, 3d, detail of protoconch and early teleoconch whorls. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Asthenotoma falunica* Peyrot, 1938**
Plate 7, figs 1-3

1847 *Pleurotoma pannus* Bast. – Bellardi, p. 27, pl. 2, fig. 1 [*non Asthenotoma pannus* (de Basterot, 1825)].
1877 *Oligotoma pannus* (Bast.) – Bellardi, p. 236, pl. 7, fig. 23 [*non Asthenotoma pannus* (de Basterot, 1825)].
1937 *Asthenotoma intersecta* (Dod.) – Montanaro, p. 166, pl. 7, figs 73, 74 [*non Asthenotoma intersecta* (Bellardi, 1877)].
*1938 *Asthenotoma falunica* Peyrot, p. 280, pl. 5, figs 58, 62.
1954 *Asthenotoma pannus* (Basterot) – Glibert, p. 38, pl. 5, fig. 11[*non Asthenotoma pannus* (de Basterot, 1825)].
1955 *Asthenotoma* (*Asthenotoma*) *micrometrica* Moroni, p. 121, pl. 7, fig. 37.
1959 *Asthenotoma micrometrica* Moroni, 1955 – Moroni, p. 121, pl. 7, fig. 37.
1963 *Asthenotoma* (*Asthenotoma*) *ornata* (Defr.) – Venzo & Pelosio, p. 126, pl. 11, fig. 12 [*non Asthenotoma ornata* (Defrance, 1826)].
1984 *Asthenotoma micrometrica* Moroni, 1955 – Ruggieri & Davoli, p. 70, pl. 5, figs 2-4.
1997 *Asthenotoma falunica* Peyrot, 1938 – Gatto, p. 48, pl. 4, figs 1-10, pl. 7, figs 4-6.

Materials and dimensions – Maximum height 11.6 mm, width 4.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/2024 (1), **Renauleau**: NHMW 2016/0103/2001-2003 (3), NHMW 2016/0103/2004 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1352353 (8).

Discussion – Asthenotoma falunica Peyrot, 1938 is characterised by its paucispiral protoconch, and teleoconch sculpture on the spire whorls composed of four nodose spiral cords per whorl, of which the adapical cord is more finely beaded than the rest. It has been confused with *A. pannus* (de Basterot, 1825) from the Miocene Aquitaine Basin by some authors (Bellardi, 1847, 1877; Glibert, 1954), but that species has a multispiral protoconch (Gatto, 1997, pl. 7, figs 2, 3). The specimens from Assemblage I have regularly beaded sculpture, similar to that seen in the middle Miocene specimen illustrated by Glibert (1954, pl. 5, fig. 11) as *A. pannus* [*non A. pannus* (de Basterot, 1825)]. Most of the specimens from the upper Miocene of Italy figured by Gatto (1997, pl. 4, figs 1-10) have poorly defined axial ribs superimposed on the tubercular teleoconch sculpture. We have not seen this in the French Tortonian population, but follow Gatto in considering them conspecific, as this ribbing does seem to be consistent in the Italian specimens.
It is separated from the other Assemblage I *Asthenotoma* species by its much coarser sculpture. For further discussion see Gatto (1997).
We record this species from the localities of Sceaux-d'Anjou and Renauleau.

Distribution – Middle Miocene (Langhian): Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1954); Paratethys, Austria (Gatto, 1997). Upper Miocene (Tortonian): Atlantic, NW France (this paper); Proto-Mediterranean, Italy (Bellardi, 1847, 1877; Montanaro, 1937; Moroni, 1955, 1959; Venzo & Pelosio, 1963; Ruggieri & Davoli, 1984; Gatto, 1997). Upper Pliocene: Mediterranean, Italy (Gatto, 1997).

***Asthenotoma ligata* (Defrance, 1826)**
Plate 8, figs 1-3

*1826 *Pleurotoma ligata* Defrance, p. 388.
1854 *Pleurotoma Striata* Millet, p. 161 (*nomen nudum*).
1865 *Pleurotoma striata* Millet, p. 161 (*non* Scacchi, 1835; *non* Kiener, 1840).
1954 *Asthenotoma* (*Mitrellatoma*) *ligata* Defrance, 1826 – Glibert, p. 40, pl. 5, fig. 13.
1964 *Asthenotoma* (*Mitrellatoma*) *ligata* Defrance, 1826 – Brébion, p. 570.

Material and dimensions – Maximum height 20.1 mm, width 6.5 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1010-1012 (3), NHMW 2016/0103/1010 (9), RGM.718138 (32), RGM.1352308 (7), RGM.1352565 (8), RGM.1352655 (3),

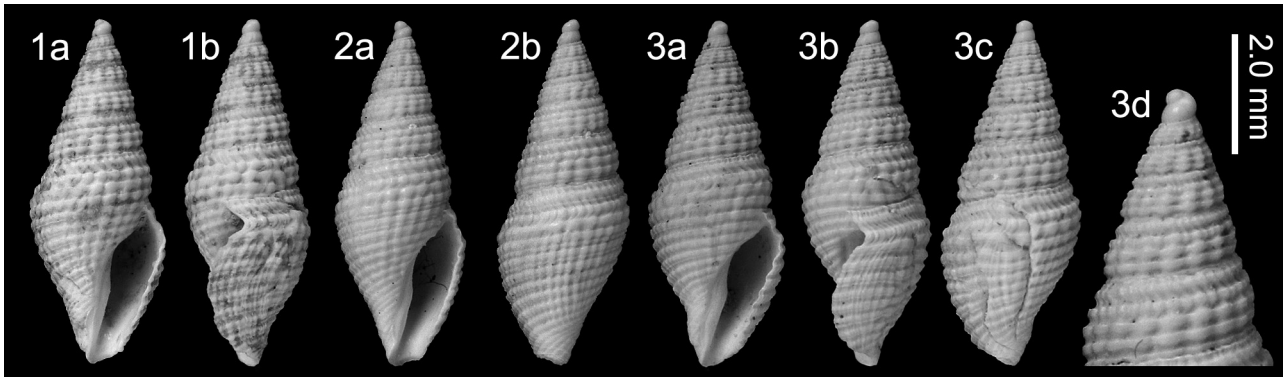

Plate 7. *Asthenotoma falunica* Peyrot, 1938; 1. NHMW 2016/0103/2001, height 9.2 mm, width 3.5 mm; 2. NHMW 2016/0103/2002, height 10.1 mm, width 3.8 mm; 3. NHMW 2016/0103/2003, height 10.0 mm, width 3.8 mm, 3d, detail of protoconch and early teleoconch whorls. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

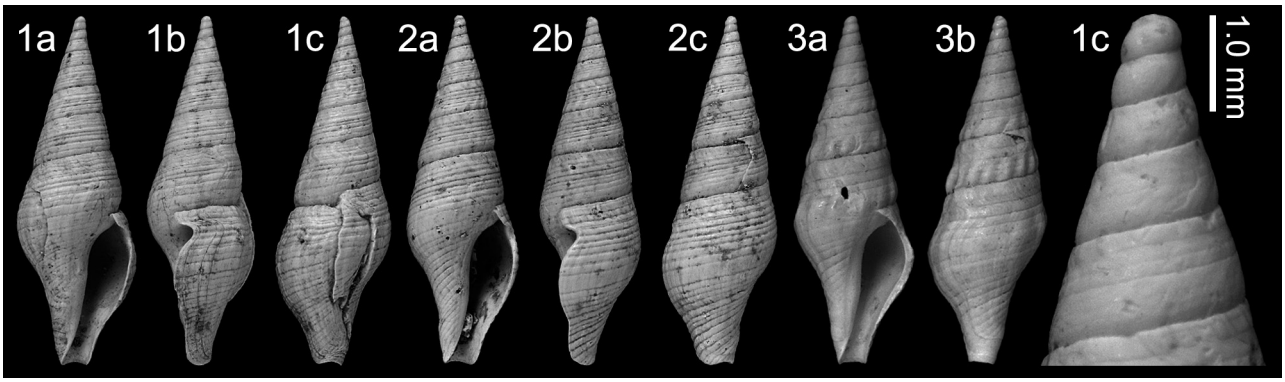

Plate 8. *Asthenotoma ligata* (Defrance, 1826); 1. NHMW 2016/0103/1010, height 19.5 mm, width 6.0 mm, 1c, detail of protoconch; 2. NHMW 2016/0103/1011 height 20.1 mm, width 6.5 mm; 3. NHMW 2016/0103/1011 height 13.7 mm, width 4.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

RGM.1352662 (11), LC (3), FVD (2).

Discussion – Powell (1942) erected the genus *Mitrellatoma* for an antipodean species that superficially resembled a pyrenid. In his turrid revision, Powell (1966) included only two species in the genus, the type from New Zealand *M. angustata* (Hutton, 1886) and *Pleurotoma ligata* Defrance, 1826. Kilburn (1986) added a further species from Mozambique, *Mitrellatoma mitra* Kilburn, 1986 to the genus, but that species was considered a juvenile specimen of *Otitoma cyclophora* (Deshayes, 1863) by Morassi *et al*. (2017), which belongs within the Pseudomelatomidae Morrison, 1965. We agree with Powell that the French middle-upper Miocene shell is at first glance similar to the type from the Pliocene of New Zealand, but this resemblance is probably superficial, as Powell described the anal sinus as '…very shallow, only half as deep as it is wide…' (Powell, 1942, p. 109). The anal sinus in *Pleurotoma ligata* is well-developed, asymmetrically U-shaped, and of almost equal depth and width (Pl. 8, figs 1b, 2b). In his decision to include the French species in this antipodean genus Powell (1966, p. 88) referred to Glibert's (1954, pl. 5, fig. 13) figure that is a dorsal view and does not show the anal sinus. It is more likely that the French species represents an extreme *Asthenotoma* species and we prefer to include it in that genus and avoid the widely disjunct distribution that would arise from attribution to *Mitrellatoma*.
Asthenotoma ligata is separated from all its congeners by its absence of axial sculpture, although some specimens develop axial ribs on the abapical half of later teleoconch whorls and mid-whorl on the last whorl (Pl. 8, fig. 3). We note that *Pleurotoma ligata* Edwards, 1861 from the upper Eocene of England is a junior homonym and was renamed *Bathytoma ligatoides* Amitrov & Mironova in Amitrov, 1973.
Brébion (1964, p. 570) recorded *A. ligata* from the Assemblage I localities of Sceaux-d'Anjou, Renauleau and Thorigné.

Distribution – Middle Miocene (Langhian): Atlantic, Loire Basin, France (Glibert, 1954). Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964).

***Asthenotoma ornata* (Defrance, 1826)**
Plate 9, figs 1-4

*1826	*Pleurotoma ornata* Defrance, p. 390.
1854	*Pleurotoma Ornata* Defr. – Millet, p. 161.
1964	*Asthenotoma ornata* Defrance, 1826 – Brébion, p. 568.
2018	*Asthenotoma ornata* (Defrance, 1826) – Ceulemans *et al*., p. 90, pl. 1, figs 3-5 (*cum syn*.).

Material and dimensions – Maximum height 19.0 mm, width 6.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1005-1006 (2), NHMW 2016/0103/1999-2000 (2), NHMW 2016/0103/1007 (50+), RGM.1352298 (50), RGM.1352418 (41), RGM.1352698 (7), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1009 (50+), RGM.734983 (6), RGM.1348804 (15), RGM.1348916 (31), RGM.718150 (50+), RGM.1352282 (50+), RGM.1352290 (2), RGM.1352295 (50+), RGM.1352299 (36), RGM. 1352309 (26), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1008 (10), LC (20), FVD (16). **Beugnon**: RGM. 1349130 (5 juveniles and fragments).

Discussion – *Asthenotoma ornata* (Defrance, 1826) is characterised by its moderate size, slender biconic shape, paucispiral protoconch and the sculpture, although strongly variable, is relatively fine compared to that of many of its congeners. For further discussion see Ceulemans *et al*. (2018, p. 91).

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (Millet, 1854; Glibert, 1954; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018); North Sea Basin, Coralline Crag, England (Harmer, 1915). Upper Pliocene: North Sea Basin, Red Crag, England (Harmer, 1915); Oorderen Sands, Belgium (Marquet, 1997, 1998). Pliocene

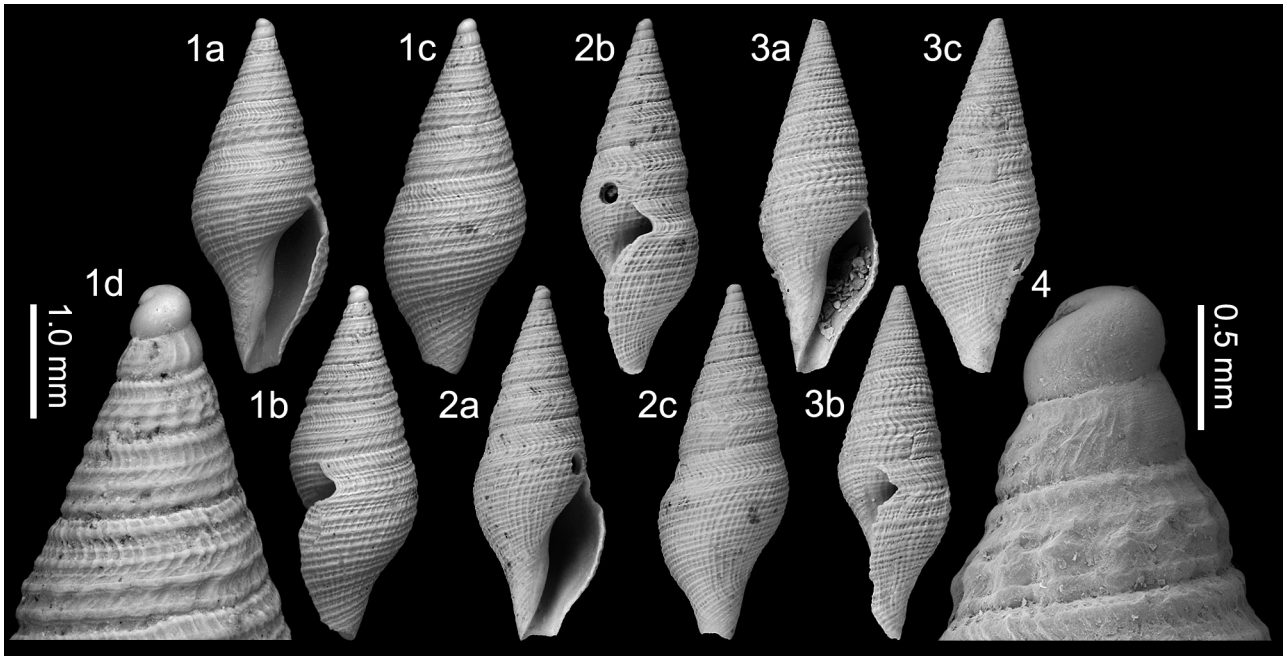

Plate 9. *Asthenotoma ornata* (Defrance, 1826); 1. NHMW 2016/0103/1005, height 9.8 mm, width 3.8 mm, 1d, detail of sculpture early spire whorls; 2. NHMW 2016/0103/1999, height 11.9 mm, width 4.2 mm; 3. NHMW 2016/0103/2000, height 15.1 mm, width 5.0 mm; 4. NHMW 2016/0103/1006 height 8.3 mm, width 3.3 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(indeterminate): North Sea Basin, Netherlands (Beets, 1946).

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

Type species – Murex mitriformis W. Wood, 1828, by original designation, present-day, West Africa.

1853 *Genota* H. Adams & A. Adams, p. 89.

For generic synonymy see Ceulemans *et al.* (2018, p. 92).

***Genota maximei* Ceulemans, Van Dingenen & Landau, 2018**

Plate 10, figs 1-3

1854 *Pleurotoma Insignis* Millet, p. 161 (*nomen nudum*).

1865 *Pleurotoma insignis* Millet, p. 587 (*non* Edwards, 1861).

1954 *Genota ramosa* cf. *valeriae* (Hörnes & Auinger) – Glibert, p. 22, pl. 4, fig. 6 [*non Genota valeriae* (Hoernes & Auinger, 1891)].

1964 *Genota ramosa* Basterot, 1825 – Brébion, p. 628 [*non Genota ramosa* (de Basterot, 1825)].

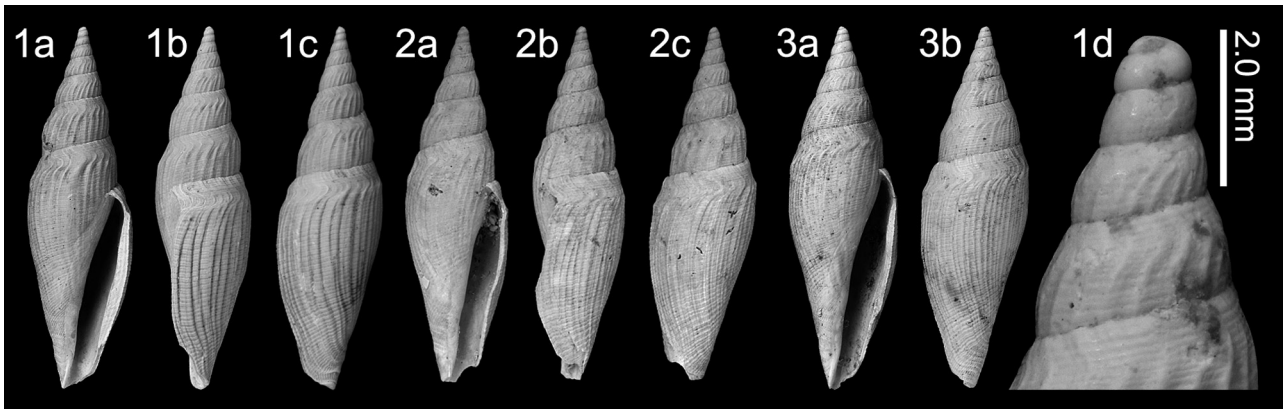

Plate 10. *Genota maximei* Ceulemans, Van Dingenen & Landau, 2018; 1. NHMW 2016/0103/1305, height 35.5 mm, width 10.3 mm, 1d, detail of protoconch; 2. NHMW 2016/0103/1306, height 29.8 mm, width 8.4 mm; 3. NHMW 2016/0103/1885, height 32.9 mm, width 9.9 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

*2018 *Genota maximei* Ceulemans, Van Dingenen & Landau, p. 92, pl. 1, figs 8, 9 (*nom. nov. pro Pleurotoma insignis* Millet, 1865, *non* Edwards, 1861).

Material and dimensions – Maximum height 35.5 mm, width 10.3 mm. **St-Clément-de-la-Place**: LC (2 incomplete). **Sceaux-d'Anjou**: NHMW 2016/0103/1305-1306 (2), NHMW 2016/0103/1307 (1), NHMW 2016/0103/1885 (1), RGM.1352416 (3 + fragments), RGM.1352521 (2 fragments), RGM.1352538 (9 fragments), RGM.739229 (2 + 3 juveniles), LC (5), FVD (4).

Discussion – This species was fully discussed in Ceulemans *et al*. (2018, p. 93).
Millet (1854, p. 161) recorded this species from Assemblage I localities (Thorigné, St-Michel, Sceaux-d'Anjou,). Brébion (1964, p. 569) added Beaulieu and we add St-Clément-de-la-Place, and Assemblage III (Le Pigeon Blanc, Palluau).

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Glibert, 1954; Brébion, 1964; Ceulemans *et al*., 2018).

Family Clathurellidae H. & A. Adams, 1858
Genus *Pleurotomoides* Bronn, 1831

Type species – Defrancia pagoda Millet, 1827, by typification of replaced name, Miocene, France.

1827 *Defrancia* Millet, p. 437. Type species (by subsequent designation; Dall, 1908): *Defrancia pagoda* Millet, 1827, Miocene, France. Junior homonym of *Defrancia* Bronn, 1825 [Bryozoa].
1831 *Pleurotomoides* Bronn, p. 555. Type species (by typification of replaced name): *Defrancia pagoda* Millet, 1827, Miocene, France. *Nom. nov. pro Defrancia* Millet, 1827, *non* Bronn, 1825 [Bryozoa].
1848 *Lora* Gistel, 1848, p. ix. Type species (by typification of replaced name): *Defrancia pagoda* Millet, 1827, Miocene, France. *Nom. nov. pro Defrancia* Millet, 1827, *non* Bronn, 1825 [Bryozoa].

***Pleurotomoides barnardi* nov. sp.**
Plate 11, figs 1-3

Type material – Holotype MNHN.F.A70519, height 10.1 mm, width 4.2 mm; paratype 1 MNHN.F.A70520, height 9.5 mm, width 4.2 mm; paratype 2 NHMW 2016/0103/1327, height 8.8 mm, width 3.9 mm; paratype 3 NHMW 2016/0103/1328, height 10.1 mm, width 4.7 mm; paratype 4 NHMW 2016/0103/1329, height 9.0 mm, width 4.2 mm, **Renauleau**. Paratype 5 RGM.1352401, height 10.1 mm, width 4.4 mm, **Beugnon**.

Other material – Maximum height 11.6 mm, width 4.2 mm. **Renauleau**: NHMW 2016/0103/1330 (29), LC (42), FVD (42). **Beugnon**: RGM.1352413 (2).

Etymology – Named after Charles Barnard, former collection assistant and presently volunteer at the Naturalis Biodiversity Center, Leiden. *Pleurotomoides* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Pleurotomoides species of small size, stocky shell with inflated last whorl and relatively short siphonal canal, protoconch of two whorls, last half carinate, 10-11 broad rounded ribs, narrow equal cords, small parietal tubercle.

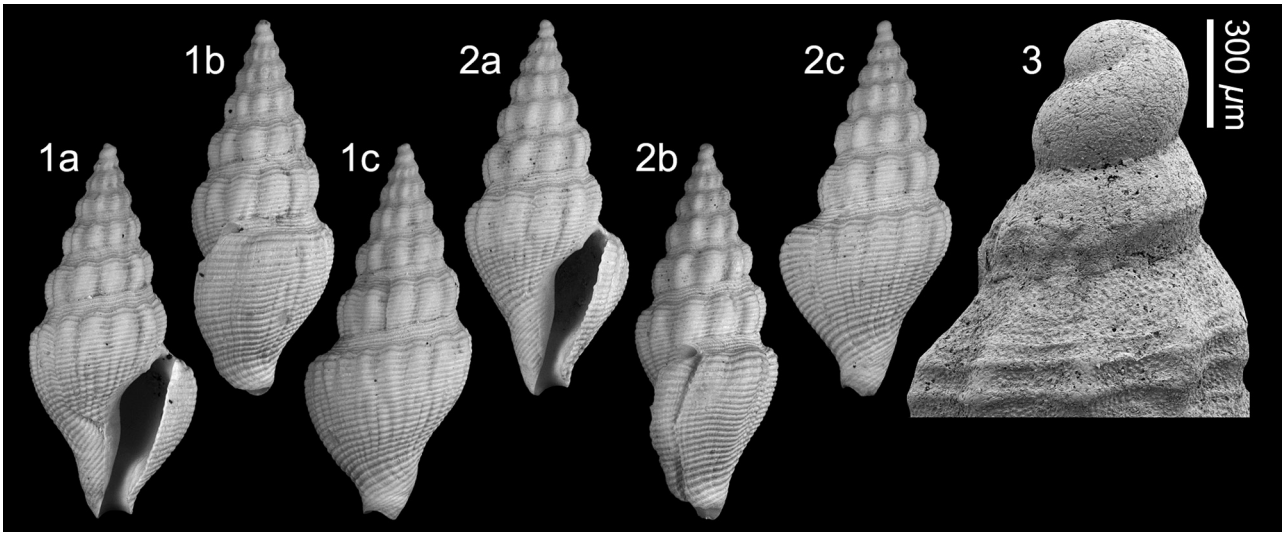

Plate 11. *Pleurotomoides barnardi* nov. sp.; 1. **Holotype** MNHN.F.A70519, height 10.1 mm, width 4.2 mm; 2. **Paratype 2** NHMW 2016/0103/1327, height 8.8 mm, width 3.9 mm; 3. **Paratype 1** MNHN.F.A70520, height 9.5 mm, width 4.2 mm, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell small, relatively stocky and solid. Protoconch paucispiral, consisting of two whorls with carina placed mid-whorl on last half whorl, nucleus large, surface sculpture abraded. Teleoconch of six convex whorls with relatively narrow, concave subsutural ramp, rounded at poorly defined shoulder, convex below. Suture linear, impressed. Sculpture of 10-11 broad, rounded axial ribs, slightly wider than their interspaces, commencing at shoulder, merging abapically with suture, overrun by narrow, subequal spiral cordlets covering entire surface. Last whorl moderately inflated and squat, narrow subsutural ramp, rounded at high-placed shoulder, convex below, weakly constricted at base. Aperture short, narrow; anal sinus deeply U-shaped; outer lip expanded, convex in profile, smooth within; siphonal canal moderately short, open, recurved, notched at tip. Columella excavated in upper third. Columella callus not thickened, forming narrow indented callus rim; small parietal tubercle developed. Siphonal fasciole rounded, not delimited.

Discussion – Pleurotomoides barnardi nov. sp. is similar to *Pleurotomoides hordaceus* (Millet, 1827) (see below), but differs in having a paucispiral protoconch, a slightly greater number or more prominent axial ribs, more regular spiral sculpture and much weaker apertural dentition. It is also similar to *Pleurotomoides suturalis* (Millet, 1827), but differs in having a stockier, more solid shell, with broader axial ribs and a more inflated last whorl. The last half protoconch whorl bears a stout carina mid-whorl (Pl. 11, fig. 3), whereas in *P. suturalis* it has two carinae (Pl. 15, figs 3a, b). *Comarmondia gracilis* (Montagu, 1803) is immediately separated by its multispiral planktotrophic-type protoconch. *Pleurotomoides casilorica* (Boettger, 1906) from the middle Miocene Paratethys and eastern Mediterranean (see Landau *et al*., 2013, p. 260) has a teleoconch shape and sculpture that is almost indistinguishable from that of *P. barnardi*, but differs in having a multispiral protoconch.

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

***Pleurotomoides hordaceus* (Millet, 1827)**
Plate 12, figs 1-3

*1827	*Defrancia hordacea* Millet, p. 440, pl. 9, fig. 3.
1854	*Defrancia Hordacea* Millet – Millet, p. 161.
1865	*Defrancia hordacea* Millet – Millet, p. 589.
1954	*Pleurotomoides hordaceus* (Millet, 1826 [*sic*]) – Glibert, p. 56, pl. 7, fig. 2.
1964	*Pleurotomoides hordaceus* Millet, 1826 [*sic*] – Brébion, p. 617.
2018	*Pleurotomoides hordaceus* (Millet, 1827) – Ceulemens *et al*., p. 94, pl. 6, figs 1, 2.

Material and dimensions – Maximum height 11.0 mm, width 4.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1251-1252 (2), NHMW 2016/0103/1254 (20), LC (15), FVD (18). **Sceaux-d'Anjou**: NHMW 2016/0103/1253 (1), NHMW 2016/0103/1255 (23), RGM.718176 (50+), RGM.1352311 (15), RGM.1352458 (13), RGM.1352517 (32), LC (10), FVD (16). **Renauleau**: NHMW 2016/0103/1256, NHMW 2016/0103/1255 (8), LC (20), FVD (11).

Discussion – Pleurotomoides hordaceus (Millet, 1827) is characterised by its relatively slender shell, round shouldered whorls and sculpture composed of broad rounded ribs, 9-10 on the penultimate whorl; on the last whorl the ribs are obsolete on the subsutural platform and base, swollen mid-whorl, crossed by fine close-set spiral cords of alternate strength. The outer lip is alate, the aperture has a strong tooth on outer lip and on the parietal portion of the columella, delimiting a deep, U-shaped anal sinus. Numerous elongated denticles are developed below these stout teeth on either side of the aperture. The protoconch is multispiral, composed of about 3-3.5 whorls, with the last two whorls carinate.
Pleurotomoides strombillus (Dujardin, 1837) from the middle Miocene Loire Basin is larger, taller spired, with a broader, steeper subsutural ramp, the outer lip is less strongly alate and thickened, and the apertural denticulations are weaker. Bałuk (2003, pl. 11, fig. 1) illustrated a specimen from the middle Miocene of Poland, which he tentatively assigned to *P. strombillus*, and considered

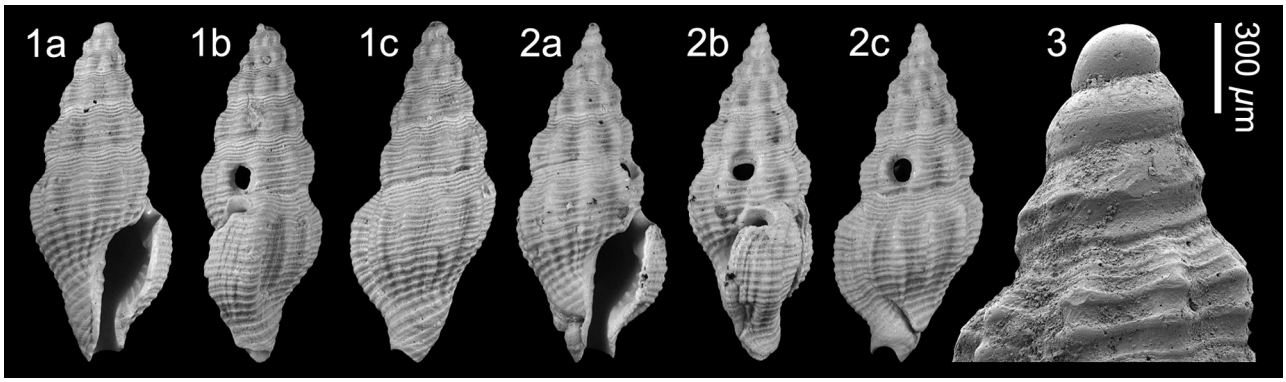

Plate 12. *Pleurotomoides hordaceus* (Millet, 1827); 1. NHMW 2016/0103/1251 height 9.7 mm, width 4.1 mm; 2. NHMW 2016/0103/1252, height 7.9 mm, width 3.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/1253, height 8.0 mm, width 3.5 mm, detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

it's a 'dwarf' form. The specimen is closely similar to *P. hordaceus*, differing in having a more angular shoulder on the last two whorls and finer spiral sculpture. We have not seen any specimens like these from the Paratethys and are unclear if this is a freak specimen as suggested by Bałuk (2003, p. 45), or if it represents another species or possibly *P. hordaceus*.
Pleurotomoides ringens (Bellardi, 1847) from the lower Pliocene of Italy is similar in shape and teleoconch sculpture, but differs in having stronger spiral cords, the shoulder is angular and the protoconch is strongly sculptured by micropustules above the carina and riblets below. The protoconch surface is somewhat worn in our material and no clear sculpture is seen. For further discussion see Ceulemans *et al*. (2018, p. 95).
Millet (1854) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou, Renauleau), to which Brébion (1964, p. 618) added St-Clément-de-la-Place and Assemblage III (Le Pigeon Blanc).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1827, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Glibert, 1954; Brébion, 1964; Ceulemens *et al*., 2018).

***Pleurotomoides milletii* (Millet, 1827)**
Plate 13, figs 1-3

*1827	*Defrancia Milletii* Millet, p. 440, pl. 9, fig. 5a, b.
1854	*Defrancia Milletii* Millet – Millet, p. 161.
1865	*Defrancia milletii* Millet – Millet, p. 589.
1954	*Pleurotomoides milleti* [*sic*] (Millet, 1826 [*sic*]) – Glibert, p. 57, pl. 7, fig. 3.
1964	*Pleurotomoides milleti* [*sic*] Millet, 1826 [*sic*] – Brébion, p. 621, pl. 15, fig. 11.

Material and dimensions – Maximum height 17.3 mm, width 7.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1257-1258 (2), NHMW 2016/0103/1259 (7), LC (11), FVD (9). **Sceaux-d'Anjou**: NHMW 2016/0103/1260 (1), NHMW 2016/0103/1261 (18), RGM.718196 (50+), RGM.1352333 (3), RGM.1352566 (8), LC (12), FVD (15).

Original description – '*Coquille à neuf tours de spire convexes, marqués de petites côtes longitudonales, coupées par des stries, et rudes. Canal un peu alongé, quelquefois oblique. Bourrelet comprimé et très arqué. Longueur, 21 millimètres (9 lignes et demie). Assez commune*' (Millet, 1827, p. 441).

Discussion – *Pleurotomoides milletii* (Millet, 1827) is characterised by its tall multispiral protoconch composed of 3.5 whorls, the last two whorls strongly carinate. The entire surface is covered in dense micropustules. The teleoconch whorls are strongly shouldered, with a broad concave subsutural ramp above bearing 5-6 narrow close-set cords, and convex below bearing three primary cords and 16 opisthocline axial ribs, roughly equal in width to their interspaces. The last whorl is moderately inflated, regularly convex below the shoulder; a single secondary cord appears in each of the interspaces and further cords cover the base and siphonal canal, the axial ribs weaken over the base. The outer lip is strongly flared and rounded in profile, moderately thickened by labial varix, delimited by a deep anal sinus filling the subsutural area, devoid of denticles within, and the siphonal canal is long and slightly posteriorly recurved.
Pleurotomoides robbai (Della Bella & Scarponi, 2007) from the Italian Pliocene differs in having a more slender shell, fewer axial ribs, and different protoconch sculpture, with strong riblets below the carina. We note that Della Bella & Scarponi (2007) used the genus *Clathurella* Carpenter, 1857 (type species *Clavatula rava* Hinds, 1843, tropical western America) for a group of species very much like those discussed here under *Pleurotomoides* Bronn, 1831. Powell (1966) considered the most important characters in *Clathurella* [in comparison with *Glyphostoma* Gabb, 1873] to be the short siphonal canal, weaker apertural dentition and less impressed anal sinus. Whilst *Clathurella ringens* (Bellardi, 1847) might fit this generic description, all the other species included in that genus by Della Bella

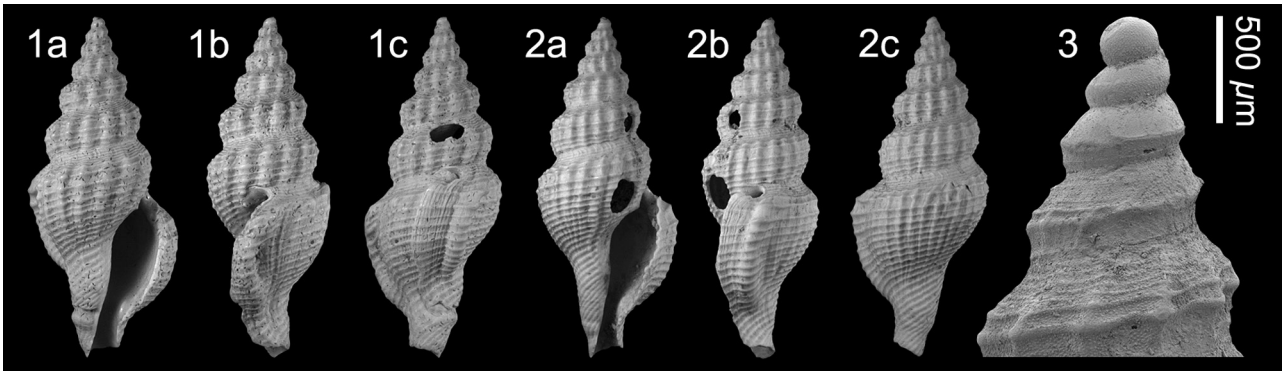

Plate 13. *Pleurotomoides milletii* (Millet, 1827); 1. NHMW 2016/0103/1257 height 14.1 mm, width 5.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 2. NHMW 2016/0103/1260, height 16.2 mm, width 6.6 mm. La Presselière, Sceaux-d'Anjou. 3. NHMW 2016/0103/1258, height 8.0 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

& Scarponi (2007) have a long siphonal canal and are probably better placed in *Pleurotomoides*. Landau *et al*. (2013) followed Powell (1966) in placing species within this group with a multispiral protoconch in the genus *Clathurella* and those with a paucispiral protoconch in the genus *Pleurotomoides*. However, with the review herein of these species that were included by Millet (1827) in the genus *Defrancia* Millet, 1827 (= *Pleurotomoides*), we see that both protoconch types occur. Therefore we include all these European Neogene species within the genus *Pleurotomoides*. We note that all the Italian Pliocene species illustrated by Della Bella & Scarponi (2007) have a multispiral protoconch with the last whorls carinate and axial riblets below the carina. This protoconch type is not seen in the Assemblage I species.

It is unusual for a species to be dedicated to the author and there is a note at the end of the species description '*N.B. La Société Linnéenne dédie cette espèce à M. Millet lui-même, afin de l'encourager à continuer ses savants recherches*' (Millet, 1827, p. 441). Despite this, the species description is clearly written by Millet and therefore authorship goes to him (ICZN 1999, Art. 50.1).

Millet (1854, 1865) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou), to which Brébion (1964, p. 618) added Renauleau, St-Michel and Beaulieu, and we add St-Clément-de-la-Place.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1827, 1854, 1865; Glibert, 1954; Brébion, 1964).

***Pleurotomoides pagoda* (Millet, 1827)**
Plate 14, figs 1-6

*1827	*Defrancia pagoda* Millet, p. 439, pl. 9, fig. 1a, b.
1854	*Defrancia Pagoda* Millet – Millet, p. 161.
1865	*Defrancia pagoda* Millet – Millet, p. 588.
1964	*Pleurotomoides pagoda* Millet, 1826 [*sic*] – Brébion, p. 618, pl. 15, fig. 9.

Material and dimensions – Maximum height 16.1 mm, width 8.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1246-1248 (3), NHMW 2016/0103/1249 (50+), RGM.1352679 (2), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1262-1263 (2), NHMW 2016/0103/1250 (16), NHMW 2016/0103/1900 (1), RGM.718178 (50+), RGM.718179 (50+), RGM.1352293 (15), RGM.1352312 (17), RGM.1352334 (15), RGM.1352452 (3), RGM.1352461 (11), RGM.1352488 (46), RGM.1352672 (8 juveniles), LC (16), FVD (7). **Renauleau**: NHMW 2016/0103/1455 (5), LC (47), FVD (10). **Beugnon**: RGM.1352283 (1).

Original description – '*Coquille turriculée, à huit ou neuf tours de spire anguleux, garnis de côtes élevées, longitudonales, surmontées par des stries saillantes et transverses, alternant dans leurs grosseurs, et dont la première, qui est la plus forte de toutes, est placée au tiers et sur l'angle qu'éprouve la partie supérieure de chaque tour de spire. On remarque aussi dans le type de cette espèce une forte dent sur la partie interne du bord droit qui avoisine le sinus. Longueure, 18 millimètres (7 lignes et demie). Rare*' (Millet, 1827, p. 439).

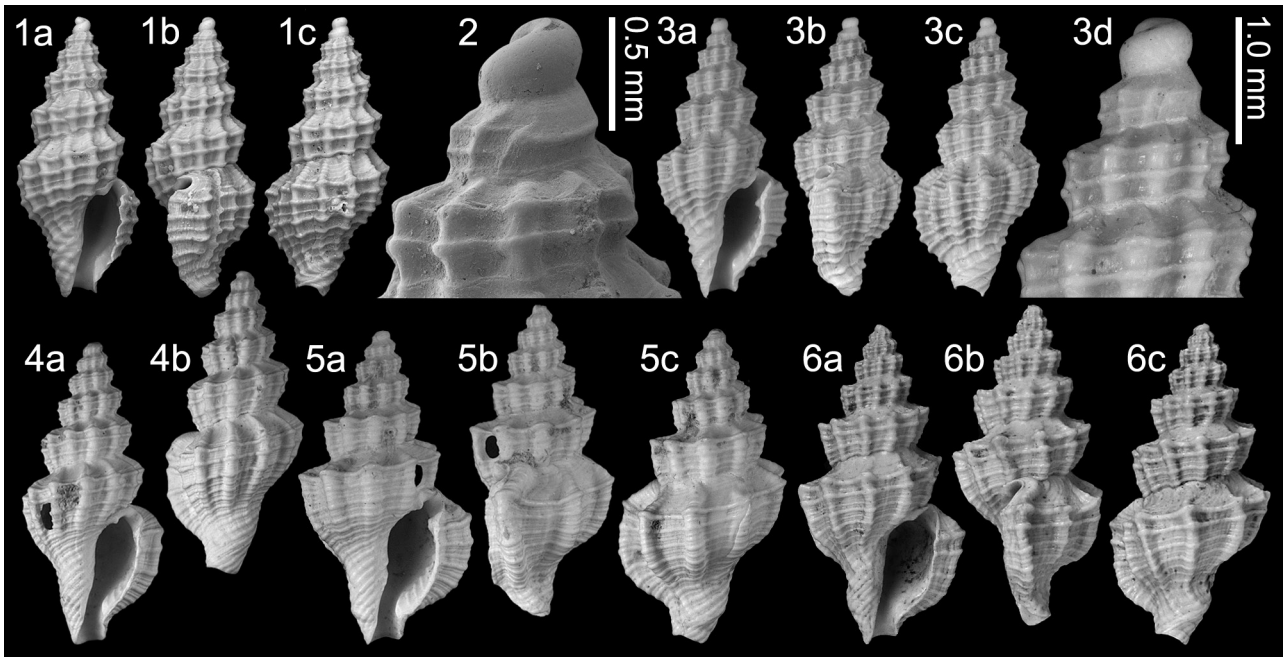

Plate 14. *Pleurotomoides pagoda* (Millet, 1827); 1. NHMW 2016/0103/1246, height 8.7 mm, width 3.5 mm; 2. NHMW 2016/0103/1248, height 6.0 mm (juvenile), detail of protoconch (SEM image); 3. NHMW 2016/0103/1247, height 8.8 mm, width 4.2 mm, 3d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 4. NHMW 2016/0103/1262, height 12.0 mm, width 6.5 mm; 5. NHMW 2016/0103/1263, height 11.4 mm, width 5.4 mm; 6. NHMW 2016/0103/1900, height 15.8 mm, width 8.0 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Pleurotomoides pagoda* (Millet, 1827) is one of the most striking species found in Assemblage I. It is characterised by its paucispiral protoconch composed of two whorls, the last whorl carinate. No microsculpture is preserved. The spire is strongly scalate, for which it earned the apt trivial name '*pagoda*'. Sculpture consists of about nine strong elevated axial ribs and narrow spiral cords that overrun the ribs. The outer lip is strongly varicose and denticulate within, the adapical labial tooth is strongest opposite a stout parietal tooth. This is the largest *Pleurotomoides* species in Assemblage I attaining 15.8 mm in height. Having said this, many specimens seem to be fully adult, with a thickened outer lip and strong apertural dentition, and yet attain only half the size. The apical angle is also variable as is the sculpture. In most specimens the subsutural platform is smooth, but some specimens bear strong to weakly developed secondary spiral cords, and whilst there is no secondary sculpture in most specimens, some develop secondary and even tertiary spirals. During the review process it was suggested to us that the plate represented more than one species. However, we consider all these forms to represent a single species in which there are important changes with ontogeny. As the shells get larger the subsutural platform widens, becomes more horizontal and the sculpture on the platform weakens. In the material at hand a continuous growth series with gradually changing characters can be constructed.

Pleurotomoides pouweri Landau, Harzhauser, İslamoğlu and Silva, 2013 from the middle Miocene eastern Mediterranean Karaman Basin has a teleoconch shape and sculpture that is almost indistinguishable from that of the fully adult form of *P. pagoda*, but differs in having a multispiral protoconch. *Pleurotomoides fuschi* (Bellardi, 1877) from the upper Miocene of Italy is very similar to *P. pagoda*. It differs in having more convex whorls, giving the spire a less angularly scalate appearance. The smaller adult forms are similar to *P. fascinellus* (Dujardin, 1837) from the middle Miocene of the Loire Basin, but in that species the whorls are less angular.

Brébion (1964, p. 619) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place) and Assemblage II (Apigné, Le Temple du Cerisier).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1827, 1854, 1865; Brébion, 1964).

***Pleurotomoides suturalis* (Millet, 1827)**
Plate 15, figs 1-3

*1827	*Defrancia suturalis* Millet, p. 440, pl. 9, fig. 4a, b.
1854	*Defrancia Suturalis* Millet – Millet, p. 161.
1865	*Defrancia suturalis* Millet – Millet, p. 589.
1964	*Comarmondia gracilis* Montagu, 1803 – Brébion, p. 598, pl. 14, fig. 27 (*non* Montagu, 1803)
1964	*Comarmondia milleti* Brébion, p. 600, pl. 14, fig. 28 (*nomen nudum*).

Type material – Locality not specified; lost (*fide* Brébion, 1964, p. 601).

Material and dimensions – Maximum height 14.0 mm, width 5.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1014-1016 (3), NHMW 2016/0103/1017 (50+), RGM.1352342 (50+), RGM.1352408 (50+), RGM.1352686 (6), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1018 (50+), RGM.718168 (50+), RGM.718181 (50+), RGM.1352310 (18), RGM.1352336 (9), RGM.1352460 (46), RGM.1352613 (20), LC (50+), FVD (50+).

Original description – '*Coquille fusiforme, aiguë au sommet, à neuf tours de spire convexes, et garnis de petites côtes longitudinales peu saillantes, moins prononcées sur le dernier tour; ces petites côtes sont croisées par des stries fines et rapprochées. Une gouttière spirale près de la suture, et finement striée, n'est que la trace du sinus du bord droit. Le bourrelet extérieur est moins prononcé que dans les espèces précédentes* [D. pagoda, D. varia-

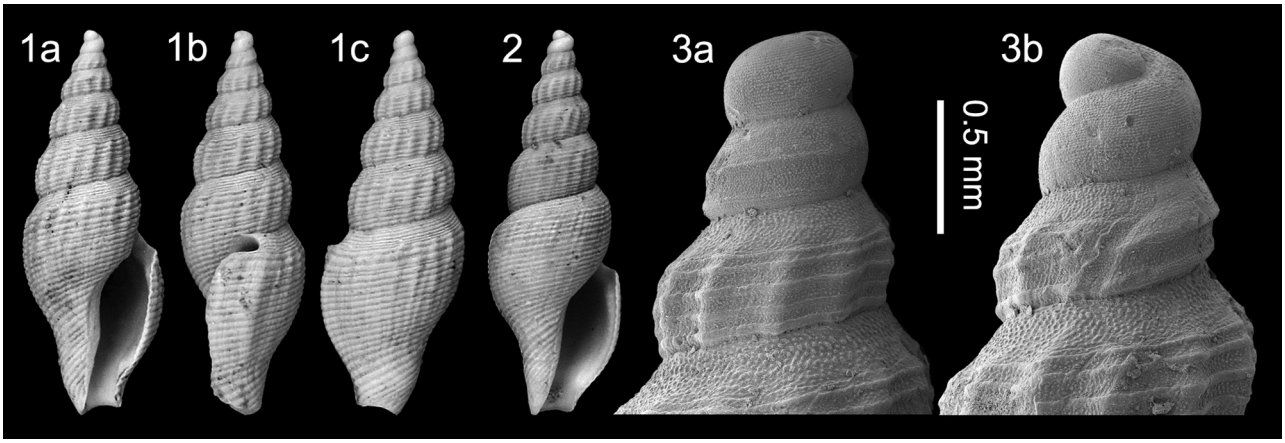

Plate 15. *Pleurotomoides suturalis* (Millet, 1827); 1. NHMW 2016/0103/1014, height 9.5 mm, width 3.3 mm; 2. NHMW 2016/0103/1015, height 9.3 mm, width 3.1 mm; 3. NHMW 2016/0103/1016 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

bilis, D. hordacea] *et souvent n'est indiqué que par un renflement du bord droit. Longueur. 14 à 16 millimètres (6 à 7 lignes). Assez commune*.' (Millet, 1827, p. 440).

Discussion – This species was synonymised with the European late Miocene to present-day *Comarmondia gracilis* (Montagu, 1803) by Brébion (1964, p. 598). Della Bella & Scarponi (2007) considered *Comarmondia* Monterosato, 1884 a junior subjective synonym of *Clathurella* Carpenter, 1857, however this opinion was not supported by molecular studies (Bouchet *et al*., 2011). *Clathurella* has *Clavatula rava* Hinds, 1843 from tropical West America as type species. It is therefore likely that the other species similar to *C. gracilis* included by Della Bella & Scarponi in *Clathurella* represent *Comarmondia* species. *Comarmondia* species differ in all having a multispiral protoconch with axial riblets on the abapical half of postnuclear whorls. This type of protoconch is not seen in any of the species here described in *Pleurotomoides*. The protoconch of the French shell has just over two whorls with a large nucleus, which we consider a non-planktotrophic protoconch. Apart from the protoconch characters, the French fossil species has weaker axial sculpture than any specimen of *C. gracilis* we have seen and the ribs are narrower.

Glibert (1964, p. 600) separated some small slender specimens with subobsolete sculpture as *Comarmondia milleti* nov. sp. (*nomen nudum*). The protoconch is identical to that of *C. suturalis* and, as already commented by Brébion, intermediate forms exist. We consider this form to fit within the specific variability of *C. suturalis.*

Millet (1854, p. 161) recorded this species from the Assemblage I localities of Thorigné, Sceaux-d'Anjou, Renauleau, to which Brébion (1964, p. 600) added St-Michel. Brébion also recorded a specimen from the middle Miocene of the Loire Basin from the locality of La Beurelière. Taking account of the discussion above we provisionally exclude this record until its protoconch is known.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (Millet, 1827; Brébion, 1964).

***Pleurotomoides vanderdoncki* nov. sp.**
Plate 16, figs 1-5

Type material – Holotype NHMW 2016/0103/1958, height 7.7 mm, width 2.9 mm; paratype 1 NHMW 2016/0103/1959, height 8.2 mm, width 3.4 mm; paratype 2 NHMW 2016/0103/1960, height 8.8 mm, width 3.9 mm; paratype 3 NHMW 2016/0103/1961, height 6.2 mm, width 2.5 mm; paratype 4 NHMW 2016/0103/1988, height 7.5 mm, width 2.8 mm, paratype 7 RGM.1352567, height 9.0 mm, height 3.2 mm; paratype 8 RGM.1352568, height 8.1 mm, height 2.9 mm, **Sceaux-d'Anjou**. Paratype 5 RGM.1352436, height 7.4 mm, height 3.0 mm; paratype 6 RGM.1352437, height 5.6 mm, height 2.6 mm, **St-Clément-de-la-Place**.

Other material – Maximum height 10.1 mm, width 3.9 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1962 (45), RGM.1352438 (1), RGM.1352459 (2), RGM.1352568 (50+), RGM.718177 (50+), LC (50+), FVD (50+).

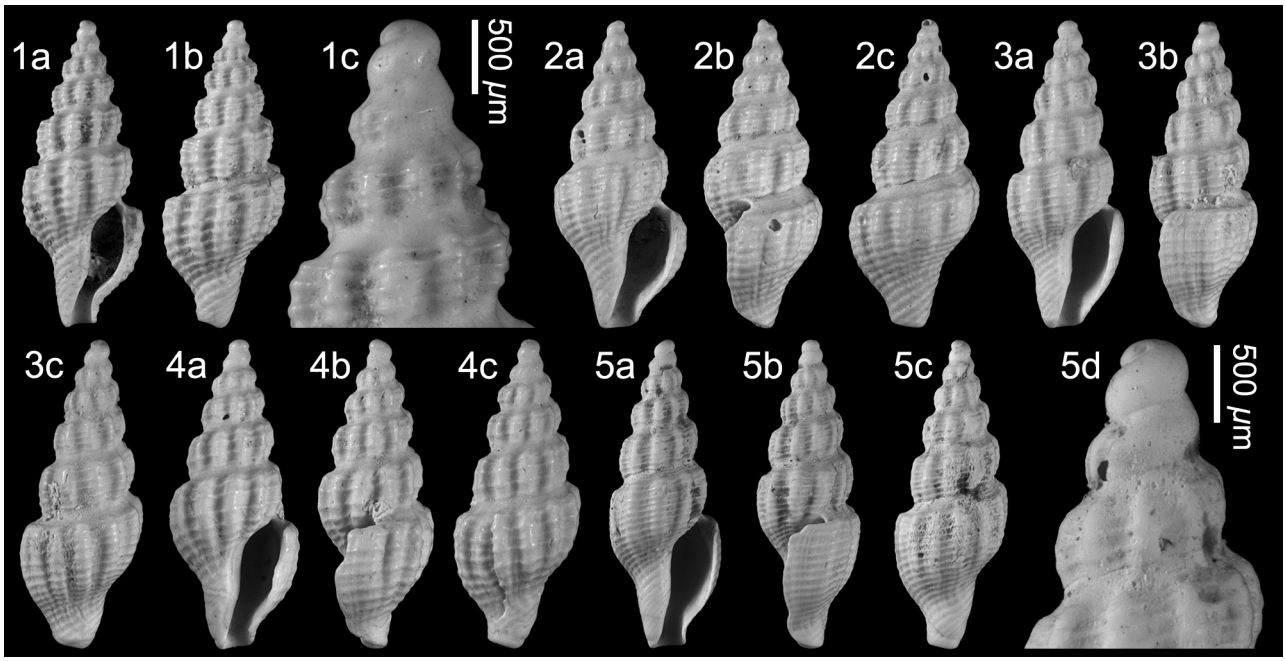

Plate 16. *Pleurotomoides vanderdoncki* nov. sp.; 1. **Holotype** NHMW 2016/0103/1958, height 7.7 mm, width 2.9 mm, 1c, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1959, height 8.2 mm, width 3.4 mm; 3. **Paratype 2** NHMW 2016/0103/1960, height 8.8 mm, width 3.9 mm; 4. **Paratype 3** NHMW 2016/0103/1961, height 6.2 mm, width 2.5 mm; 5. **Paratype 4** NHMW 2016/0103/1988, height 7.5 mm, width 2.8 mm, 5d, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Etymology – Named after Peter van der Donck, volunteer at the Naturalis Biodiversity Center, Leiden. *Pleurotomoides* gender masculine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Pleurotomoides* species of small size, slender, strongly scalate spire, protoconch of two tall whorls, last half carinate, 11-14 broad rounded ribs, narrow widely spaced spiral cords, outer lip not expanded.

Description – Shell small, slender fusiform, strongly scalate spire. Protoconch paucispiral, consisting of two tall whorls with carina placed just below mid-whorl on last half whorl, nucleus large, surface sculpture abraded. Teleoconch of 4.5 angular whorls with relatively narrow, shallow, smooth, concave subsutural ramp, delimited by sharp shoulder, convex below. Suture weakly undulating, impressed. Sculpture of 11-14 broad, rounded, orthocline axial ribs, equal in width to interspaces, commencing at shoulder, merging abapically with suture, overrun by narrow, widely spaced spiral cords, three on first teleoconch whorl, five on penultimate whorl. Last whorl 57% total height, narrow, shallow, subsutural ramp, sharply angled at high-placed shoulder, convex below, strongly constricted at base. Aperture short, 39% total height; anal sinus deeply U-shaped; outer lip not expanded, convex in profile, smooth within; siphonal canal moderately short, open, recurved, notched at tip. Columella excavated in upper third. Columellar callus not thickened, forming narrow indented callus rim; no parietal tubercle developed. Siphonal fasciole rounded, not delimited.

Discussion – *Pleurotomoides vanderdoncki* nov. sp. is the smallest of its congeners in Assemblage I and relatively uncommon. It also differs from most of the other NW French upper Miocene *Pleurotomoides* species in not having an expanded and thickened outer lip. The most similar is *P. suturalis* (Millet, 1827), in which the outer lip is also not expanded and not, or weakly thickened, but that species has much weaker axial sculpture and crowded spiral cords (see above).
We record *P. vanderdoncki* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Pleurotomoides variabilis* (Millet, 1827)**
Plate 17, figs 1-3

*1827	*Defrancia variabilis* Millet, p. 439, pl. 9, fig. 2a, b.
1854	*Defrancia Variabilis* Millet – Millet, p. 161.
1865	*Defrancia variabilis* Millet – Millet, p. 589.
1964	*Pleurotomoides variabilis* Millet, 1826 [*sic*] – Brébion, p. 620, pl. 15, fig. 10.

Type material – Holotype: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 620).

Material and dimensions – Maximum height 11.2 mm, width 5.3 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1264-1265 (2), NHMW 2016/0103/1266 (12), RGM.1352332 (7), RGM.1352516 (7), RGM.1352526 (10 fragments), LC (4), FVD (4).

Original description – '*Coquille ovale, oblongue, composée de sept tours de spire, plus ou moins anguleux, selon les variétés, garnis de côtes longitudonales et de stries élevées, transverses, légèrement renfrées dans leur junction avec les côtes. La partie supérieure de chaque tour de spire est ordinairement dépourvue de stries, et l'on n'y voit que le prolongement des côtes qui vont se rendre à la suture. Longueure, 9 millimètres (4 lignes).*' (Millet, 1827, p. 439).

Discussion – *Pleurotomoides variabilis* (Millet, 1827) is characterised by its tall multispiral protoconch composed of 3.5 whorls, the last two whorls strongly carinate. The entire surface is covered in dense micropustules. The teleoconch whorls are strongly shouldered, with a broad concave subsutural ramp above bearing 5-6 nar-

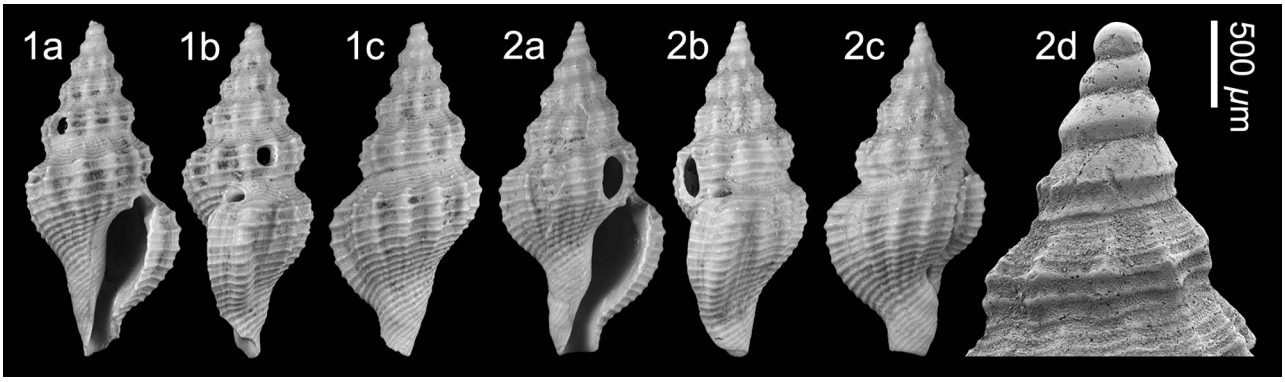

Plate 17. *Pleurotomoides variabilis* (Millet, 1827); 1. NHMW 2016/0103/1264, height 8.9 mm, width 4.4 mm; 2. NHMW 2016/0103/1265, height 9.6 mm, width 4.1 mm, 2d, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

row close-set cords, and convex below bearing 3-4 primary cords and 9-10 opisthocline axial ribs, roughly half the width of their interspaces. The last whorl is strongly inflated, regularly convex below the shoulder; a single secondary thread appears in each of the interspaces and further cords cover the base and siphonal canal, the axial ribs weaken over the base. The outer lip is strongly flared and rounded in profile, strongly thickened by labial varix, delimited by a very deep anal sinus filling the subsutural area; the anal sinus is delimited by two denticles, one on the outer lip and one on the parietal callus. In most fully adult specimens some further weaker denticles are developed variably within the outer lip. The siphonal canal is long and slightly posteriorly recurved.
This species is closely similar to *Pleurotomoides milletii* (Millet, 1827), with which it co-occurs, but differs in having fewer axial ribs (9-10 vs. 16), in having a more inflated last whorl, in having the labial varix more strongly developed, and in having denticles delimiting the anal sinus developed in fully adult specimens. *Pleurotomoides serventii* (Pelosio, 1967) and *P. robbai* (Della Bella & Scarponi, 2007), both from the Italian Pliocene, have similar sculpture, but both are more slender elongated in shape and differ in their protoconch microsculpture.
Millet (1854, 1865) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou), to which Brébion (1964, p. 618) added St-Clément-de-la-Place.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1827, 1854, 1865; Brébion, 1964).

Family Mitromorphidae Casey, 1904
Genus and subgenus *Mitromorpha* Carpenter, 1865

Type species – Daphnella filosa Carpenter, 1864, *non* Dujardin, 1837 (= *Mitromorpha carpenteri* Glibert, 1954), by monotypy, present-day, California.

1865 *Mitromorpha* Carpenter, p. 182.

Synonyms of the subgenus *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883 omitted by Ceulemans *et al*. (2018, p. 104).

1888 *Clinomitra* Bellardi, p. 10. Type species (by monotypy): *Clinomitra rovasendae* Bellardi, 1888, Miocene, Italy.
1888 *Diptychomitra* Bellardi, p. 10. Type species (by subsequent designation, Pace, 1902): *Diptychomitra eximia* Bellardi, 1888, Miocene, Italy.
1904 *Helenella* Casey, p. 167. Type species (by subsequent designation, Cossmann, 1906): *Pleurotoma multigranosa* E.A. Smith, 1890, present-day, St. Helena.
1922 *Mitrithara* Hedley, p. 233. Type species (by original designation): *Columbella alba* Petterd, 1879, present-day, Tasmania, Australia.

Note – Species in the subgenus *Mitromorpha* Carpenter, 1865 lack well defined columella folds, whereas species in *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883 have two columellar folds. *Mitrolumna* was relegated to subgenus rank by Kilburn (1986) and Drivas & Jay (1986) based on having similar radular formulae.

***Mitromorpha* (*s.s.*) *mulderi* nov. sp.**
Plate 18, figs 1-3

1964 *Mitrolumna lardeauxi* Brébion, p. 573, pl. 14, figs 1-3 (*nomen nudum*).

Type material – Holotype MNHN.F.A70522, height 6.4 mm, width 2.6 mm; paratype 1 MNHN.F.A70523, height 6.5 mm, width 2.5 mm; paratype 2 NHMW 2016/0103/1157, height 6.2 mm, width 2.4 mm; paratype 3 NHMW 2016/0103/1158, height 6.8 mm, width 2.5 mm; paratype 4 NHMW 2016/0103/1159, height 6.3 mm, width 2.4 mm.

Other material – Maximum height 7.4 mm, width 2.8 mm. **St-Clément-de-la-Place**: NHMW NHMW 2016/0103/1160 (19), LC (8), FVD (25). **Sceaux-d'Anjou**: NHMW 2016/0103/1789 (3), RGM.735000 (15), RGM.735001 (4 juveniles).

Etymology – Named after Aad Mulder of Maarssen, The Netherlands, who kindly donated his collection to the Naturalis Biodiversity Center, Leiden, The Netherlands, which was used in this work. *Mitrolumna* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Mitromorpha species of small size, biconic, smooth protoconch of two whorls, sculpture of very narrow spiral cords separated by wide interspaces, suggestion of axial ribs on first two teleoconch whorls, outer lip simple, smooth to weakly lirate within, poorly developed columellar fold.

Description – Shell small, biconic. Protoconch paucispiral dome-shaped, composed of two smooth convex whorls, with medium sized nucleus. Junction with teleoconch sharp, marked by beginning of adult sculpture. Teleoconch of four moderately convex whorls, with periphery just above abapical suture. Suture linear, impressed. Sculpture of narrow subequal spiral cords, about one quarter width of their interspaces, five on first whorl, a further primary develops on second whorl intercalated between the adapical two cords, strengthening to become equal in strength to others, six cords on penultimate whorl. Axial sculpture weak, subobsolete, restricted to first two teleoconch whorls. Prominent, close-set, axial growth lines cover entire surface. Last whorl 65% total height, regularly convex, base hardly constricted, not de-

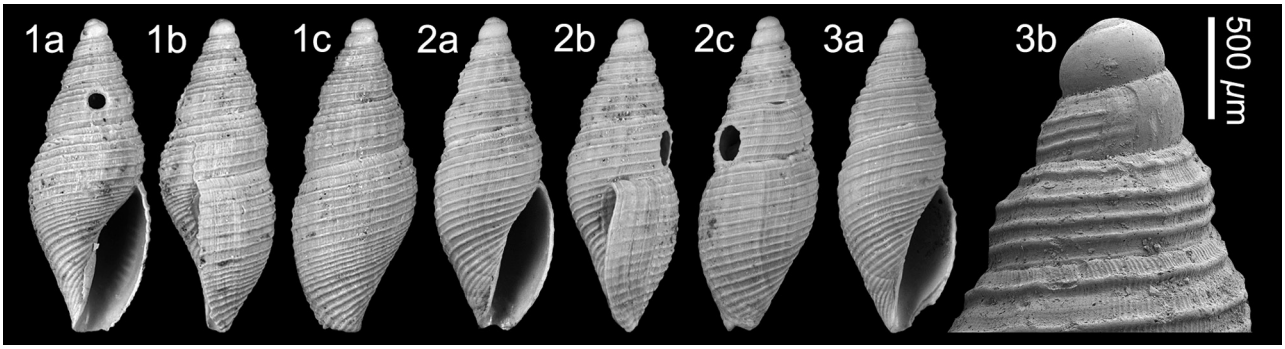

Plate 18. *Mitromorpha* (*s.s.*) *mulderi* nov. sp.; 1.**Holotype** MNHN.F.A70522, height 6.4 mm, width 2.6 mm; 2. **Paratype 2** NHMW 2016/0103/1157, height 6.2 mm, width 2.4 mm; 3. **Paratype 1** MNHN.F.A70523, height 6.5 mm, width 2.5 mm, 3b, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fined. Aperture 45% total height, elongate-ovate, outer lip not thickened, smooth to subobsoletely lirate within; anal sinus not developed; siphonal canal short, wide. Columella weakly excavated mid-height, bearing suggestion of fold just below excavation. Columellar callus forming narrow rim, slightly thickened abapically. Siphonal fasciole not developed.

Discussion – *Mitromorpha* (*s.s.*) *mulderi* nov. sp. is characterised by its protoconch of two smooth whorls, its predominantly spiral sculpture, with just a suggestion of axials on the first two teleoconch whorls, and its closeset axial growth lines that give the surface a somewhat rough appearance. The columella bears a slight fold midheight, placing it in the genus *Mitromorpha* Carpenter, 1865, rather than the subgenus *Mitrolumna* Bucquoy, Dautzenberg & Dollfus, 1883 (see generic note). A couple of similar species occur in the older middle Miocene assemblages of the Loire Basin, of which *Mitromorpha (Mitrolumna) dollfusi* (Peyrot, 1938) has stronger axial sculpture and the spirals are wider than their interspaces in contrast to the very narrow spirals in *M.* (*s.s.*) *mulderi*. We have placed these species in the subgenus *Mitrolumna* as Glibert (1954, p. 44) described the presence of two weak columellar folds. Glibert described a second form co-occurring with *M. (M.) dollfusi*, which he called forma *peyroti*. It differs from the nominal taxon in being more slender, in having finer spiral sculpture, and in the absence of any axial sculpture. '*Formas*' no longer have any taxonomic status, so the two forms either represent extremes of a single species or separate species. We have not seen enough material to settle this issue. All extant European mitromorphids reviewed by Mifsud (2001) have two columellar folds and therefore belong to the subgenus *Mitrolumna*. Species of the subgenus *Mitromorpha* occur off West Africa; *M. saotomensis* (Rolán & Boyer, 2001), *M. hernandezi* Rolán & Gori, 2012 and *M. annobonensis* Rolán & Gori, 2012 all have much coarser sculpture with a stronger axial component.
Brébion (1964, p. 574) recorded this species from Assemblage I (Sceaux-d'Anjou, Thorigné, St-Michel), to which we add St-Clément-de-la-Place, and Assemblage II (Apigné).

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

Family Mangeliidae Fischer, 1883b
Genus *Agathotoma* Cossmann, 1899

Type species – *Mangelia angusta* Bellardi, 1847, by typification of replaced name, Pliocene, Italy.

1877 *Ditoma* Bellardi, p. 295. Type species (by monotypy): *Mangelia angusta* Bellardi, 1847, Pliocene, Italy (*non* Illiger, 1807, p. 320 [Coleoptera]).
1899 *Agathotoma* Cossmann, p. 45. *Nom. nov. pro Ditoma* Bellardi, 1877, *non* Illiger, 1807 [Coleoptera].

***Agathotoma pherousae* (Glibert, 1960)**
Plate 19, figs 1-3

1938 *Mangelia* (*Agathotoma*) *angustus* [*sic*] Jan. – Peyrot, p. 294 [*non Agathotoma angusta* (Bellardi, 1847)].
*1960 *Mangelia* (*Agathotoma*) *pherousae* Glibert, p. 26, pl. 5, fig. 12.

Material and dimensions – Maximum height 6.3 mm, width 2.6 mm. **Renauleau**: NHMW 2016/0103/1167-1169 (3), NHMW 2016/0103/1170 (25), RGM.1348999 (6), LC (46), FVD (31).

Discussion – There is little doubt that this is *Agathotoma pherousae* (Glibert, 1960), originally described from the middle Miocene of the Loire Basin of France, and its range is herein extended into the Tortonian of NW France. It differs from *A. angusta* (Bellardi, 1847), which is widely distributed in the European Neogene from lower Miocene to lower Pleistocene deposits in the Paratethys and Mediterranean. The French species has fewer and wider axial ribs (9-10 vs. 14-15, finer spiral sculpture and a weaker stromboid notch on the abapical portion of the outer lip than *A. angusta*. However, Glibert (1960,

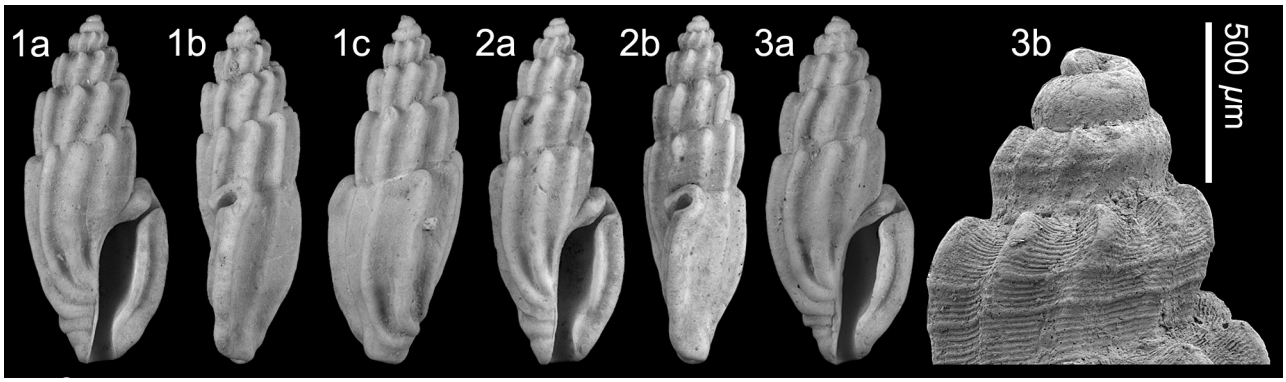

Plate 19. *Agathotoma pherousae* (Glibert, 1960); 1. NHMW 2016/0103/1167, height 6.1 mm, width 2.6 mm; 2. NHMW 2016/0103/1168, height 6.1 mm, width 2.3 mm; 3. NHMW 2016/0103/1169, height 6.1 mm, width 2.5 mm, 3b, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

p. 27) described the protoconch as paucispiral, which is clearly not the case (Pl. 19, fig. 4). In the figured holotype the apex seems to be missing, but it is difficult to be certain. We have re-examined the type from St. Catherine de Fierbois (IRSNB 5081) and confirm that the protoconch is incomplete. Our efforts to track down further specimens from the Loire Basin assemblages was unsuccessful. Therefore, it unlikely that the holotype has a paucispiral protoconch and consider them conspecific. This species and its European Neogene congeners were fully discussed by Landau *et al*. (2013, p. 264).
In Assemblage I this species has only been found at Renauleau.

Distribution – Middle Miocene (Langhian): Atlantic, Loire Basin, France (Glibert, 1960). Upper Miocene (Tortonian): Atlantic, NW France (this paper).

Genus *Bactrocythara* Woodring, 1928

Type species – Cythara obtusa Guppy *in* Guppy & Dall, 1896, by original designation, Pliocene, Jamaica.

1928 *Bactrocythara* Woodring, p. 174.

***Bactrocythara pascaleae* nov. sp.**
Plate 20, figs 1-4

Type material – Holotype MNHN.F.A70521, height 2.2 mm, width 730 μm; paratype 1 NHMW 2016/0103/0974, height 2.3 mm, width 990 μm; paratype 2 NHMW 2016/0103/1764, height 2.8 mm, width 1.1 mm; paratype 3 NHMW 2016/0103/1765, height 1.1 mm, width 650 μm, **St-Clément-de-la-Place**. Paratype 4 RGM 1352545, height 2.4 mm, width 1.0 mm; paratype 5 RGM 1352597, height 3.1 mm, width 800 μm; paratype 6 RGM 1352598, height 2.2 mm, width 720 μm, **Sceaux-d'Anjou**.

Other material – Maximum height 3.1 mm, width 800 μm. **St-Clément-de-la-Place**: NHMW 2016/0103/1905 (32), LC (3), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/2190 (1), RGM.719026 (1 + 2 fragments).

Etymology – It gives me great pleasure to name this remarkable little species after my (BL) partner, Pascale Muriel Paques. *Bactrocythara* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Bactrocythara species of minute size, paucispiral protoconch of 1.25 smooth whorls, subcylindrical teleoconch of two whorls with fine reticulated surface sculpture, axial component weakly predominant, narrow aperture, almost straight outer lip, weak anal sinus, short, wide siphonal canal.

Description – Shell minute, cylindrical-fusiform, protoconch paucispiral, composed of 1.25 smooth whorls, with large nucleus. Junction with teleoconch marked by beginning of adult sculpture, not sharply delimited. Teleoconch of just over two whorls. Suture impressed, becoming more deeply so towards aperture. First teleoconch rapidly develops rounded shoulder, subsutural ramp moderately wide, whorl profile almost straight-sided below. Sculpture of 16-19 narrow sinuous axial ribs extend between sutures, crossed by 19-20 narrow spiral cords forming fine reticulated pattern. Ribs and cords about one-third width of their interspaces. Last whorl 66-73% total height, subcylindrical, weakly shouldered, hardly to moderately constricted at base; shoulder and base poorly delimited. Aperture elongate 45-51% total height, outer lip weakly thickened by varix, weakly convex in profile, smooth within; anal canal weakly developed, shallow, siphonal canal open, wide, short, notched at tip. Columella weakly excavated to almost straight, smooth, Columellar callus not thickened, restricted to narrow rim bordering medial side of aperture. Siphonal fasciole not delimited.

Discussion – Bactrocythara pascaleae nov. sp. has an

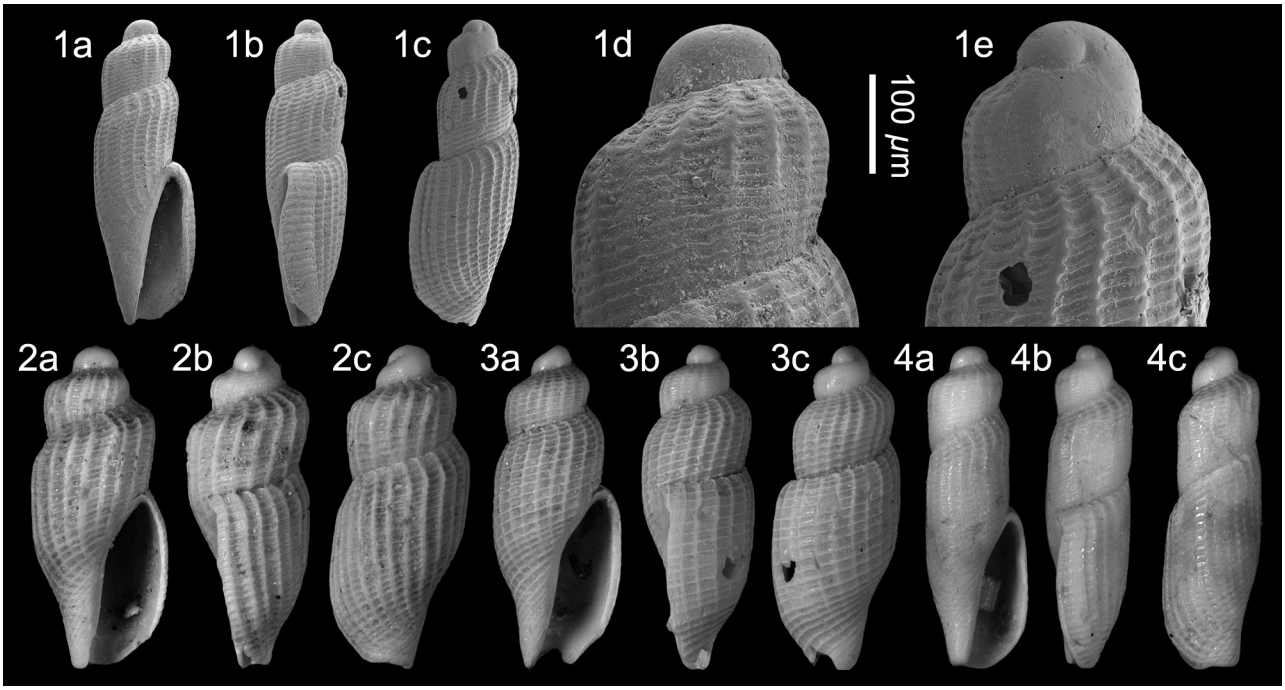

Plate 20. *Bactrocythara pascaleae* nov. sp.; 1. **Holotype** MNHN.F.A70521, height 2.2 mm, width 730 μm, 1c, d. detail of protoconch (SEM image); 2. **Paratype 1** NHMW 2016/0103/0974, height 2.3 mm, width 990 μm; 3. **Paratype 2** NHMW 2016/0103/1764, height 2.8 mm, width 1.1 mm; 4. **Paratype 3** NHMW 2016/0103/1765, height 1.1 mm, width 650 μm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

usual looking shell and we have not found any species with which to compare. It shows important variability in relation to width; some specimens are exceedingly slender and bullet-shaped (Pl. 20, figs 1, 4), whilst others are broader (Pl. 20, figs 1, 2), and hence variable in apertural width, broader shells having wider apertures. There are also small differences in sculptural detail; in all specimens axials are dominant, but in some more strongly so (Pl. 20, fig. 2).

Its generic placement is problematic. In our opinion the teleoconch shell is most similar to that of mangeliid species in the genera *Bactrocythara* Woodring, 1928 and *Kyllinia* Garilli & Galletti, 2007, in having a subcylindrical shell shape, almost straight-sided spire whorls, a narrow aperture and a moderate to weak anal sinus. It lacks a stromboid notch typical of *Kyllinia* and the axial sculpture is stronger than any known *Kyllinia* species, but then again only two species of that genus are known, possibly resulting in a rather narrow generic concept. *Bactrocythara*, like *Kyllinia*, is recorded from West Africa ((Rolán *et al*., 1994). The West African species all have a considerably stronger and deeper developed anal sinus, but have similar sculpture, especially *B. labiosa* (E.A. Smith, 1872) from Angola.

The protoconch does not conform to that of *Bactrocythara* or *Kyllinia*. Both have a multispiral protoconch (Rolán *et al*., 1994; Rolán *et al*., 1998 [although they placed the species in the genus *Diaugasma* Melvill, 1917]; Garilli & Galletti, 2007). The original generic description of *Kyllinia* described crenulations at the adapical protoconch suture as a generic characteristic. Therefore the protoconch of this French species is quite wrong for these genera. Indeed Mangeliidae typically have multispiral protoconchs, and if paucispiral, it is usually spirally striate (Bouchet *et al*., 2011, p. 281).

The truncated paucispiral protoconch seen in this French species is similar in shape to that of many of the Assemblage I *Raphitoma* species, although in those it is always sculptured. Its shell shape is not unlike that of *Diaugasma*, which is placed in the Raphitomidae (Bouchet *et al*., 2011), but that also has a multispiral protoconch (Powell, 1966, p. 123). Another raphitomid genus with narrow subcylindrical shells with appressed whorls and a high truncated protoconch devoid of reticulate sculpture is *Exomilus* Hedley, 1918 (Powell, 1966; Kilburn, 2009). This is a Western Pacific and Antipodean genus and although the protoconch is devoid of sculpture and truncated as in the French species, it is still multispiral.

In view of the difficulties discussed, we have asked the advice of several malacologists. Opinions have been split between the Mangeliidae and the Raphitomiidae, so we have taken the advice of the majority and placed it in the Mangeliidae, genus *Bactrocythara*, but stress the uncomfortable position of this taxonomic placement. It is quite possible that a new genus may need to be erected for this small species. My thanks to all the colleagues who offered an opinion.

We record *B. pascaleae* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

Genus *Bela* Leach *in* Gray, 1847a [October]

Type species – *Murex nebula* Montagu, 1803, by subsequent designation (Gray, 1847b [November]), present-day, British Isles.

1847a *Bela* Leach *in* Gray, p. 270.

For generic synonymy see Ceulemans *et al*. (2018, p. 100).

***Bela henkmulderi* nov. sp.**
Plate 21, figs 1-2

Type material – Holotype NHMW 2016/0103/1223, height 5.1 mm, width 1.9 mm; paratype 1 NHMW 2016/0103/1224, height 4.5 mm, width 1.7 mm; paratype 2 NHMW 2016/0103/2015, height 6.4 mm, width 2.1 mm; paratype 3 NHMW 2016/0103/2016, height 6.1 mm, width 2.0 mm; paratype 4 NHMW 2016/0103/2017, height 6.2 mm, width 2.1 mm; paratype 5 RGM.1352649, height 5.8 mm, width 2.1 mm; paratype 6 RGM.1352650, height 5.4 mm, width 1.8 mm; paratype 7 RGM.1352651, height 5.4 mm, width 1.9 mm.

Other material – Maximum height 6.4 mm, width 2.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2018 (12), RGM.1352674 (3), LC (1), FVD (5). **Sceaux-d'Anjou**: RGM.734984 (8).

Etymology – Name after Henk Mulder, enthusiastic collector of fossil molluscs and friend of the first author (BL). *Bela* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mangelia* species of small size, multispiral protoconch of three whorls with tuberculate second whorl and reticulate third whorl, teleoconch slender fusiform, whorls bearing 12-13 sharp arcuate ribs and fine beaded spirals, aperture narrow, siphonal canal medium length, siphonal fasciole not distinct.

Description – Shell small, slender fusiform. Protoconch multispiral, composed of three convex whorls, second whorl bearing four rows of tubercles, last half whorl bearing six spiral cords and arcuate riblets forming rectangular reticulate pattern. Junction with teleoconch sharp. Teleoconch of four whorls, with narrow sutural ramp, bluntly angled at high-placed shoulder, weakly convex below, periphery mid-whorl. Suture impressed, linear. Axial sculpture extending between sutures consisting of sharp, narrow, prosocline axials, strongly arcuate over subsutural ramp, weakly curved below, 12 on second teleoconch whorl, 13 on last whorl. Spiral sculpture overrides axials, consists of numerous fine, subequal, irregularly beaded threads. Last whorl 60% total height, slightly convex narrow subsutural ramp, bluntly angled at shoulder, weakly convex below, weakly constricted at base; axial sculpture extending over base; spiral sculpture of fine threads over entire last whorl, slightly strengthened over siphonal fasciole; siphonal fasciole not delimited. Aperture elongate, narrow, 40% total height; outer moderately thickened; anal sinus broad, shallow U-shaped, apex placed at shoulder; siphonal canal medium length, open, bent slightly adaxially. Columella moderately excavated in upper third. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – The teleoconch of this species is similar to that of several *Mangelia* species, however, the protoconch suggests placement in the genus *Bela*. The *Mangelia*-like teleoconch shape and very close-set axial ribs separate it from its Assemblage I congeners as well as the numerous species from the Italian Pliocene reviewed by Della Bella *et al*. (2015).
In Assemblage I we record *B. henkmulderi* only from St-Clément-de-la-Place.

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

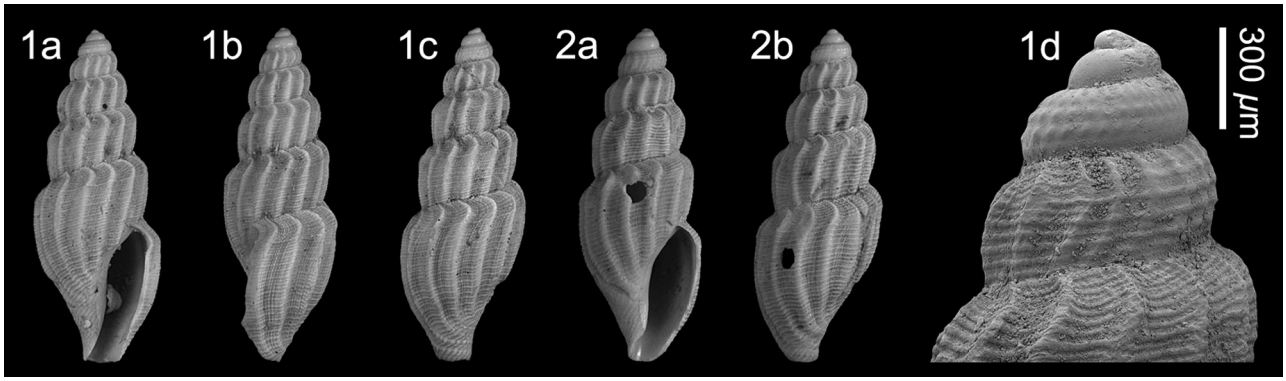

Plate 21. *Bela henkmulderi* nov. sp.; 1. **Holotype** NHMW 2016/0103/1223, height 5.1 mm, width 1.9 mm, 1d, detail of protoconch (SEM image); 2. **Paratype 1** NHMW 2016/0103/1224, height 4.5 mm, width 1.7 mm, Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Bela keukelaari* nov. sp.**
Plate 22, figs 1-4

1854 *Pleurotoma subcostellata* d'Orb – Millet (*partim*), p. 161.
1964 *Cythara* (*Mangelia*) *couffoni* Brébion, p. 591, pl. 14, figs 21, 22 (*nomen nudum*).

Type material – Holotype MNHN.F.A70524, height 8.5 mm, width 3.3 mm; paratype 1 MNHN.F.A70525, height 11.2 mm, width 3.9 mm; paratype 2 NHMW 2016/0103/1171, height 9.3 mm, width 3.5 mm; paratype 3 NHMW 2016/0103/1172, height 4.7 mm (juvenile); paratype 4 NHMW 2016/0103/1173, height 8.5 mm, width 3.2 mm; paratype 5 NHMW 2016/0103/1175, height 8.4 mm, width 3.4 mm, **St-Clément-de-la-Place**. Paratype 6 RGM.1352507, height 8.2 mm, width 3.5 mm; paratype 7 RGM.1352508, height 7.5 mm, width 3.2 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 11.2 mm, width 3.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1174 (50+), RGM.1352365 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1940 (50+), RGM.718158 (50+), RGM.1352337 (9), RGM.1352509 (44), RGM. 1352647 (50+), LC (50+), FVD (50+). **Beugnon**: NHMW 2016/0103/1941 (3).

Etymology – Named after Hans Keukelaar of Nieuwpoort, The Netherlands, who kindly donated his collection to the Naturalis Biodiversity Center, Leiden, The Netherlands, which was used in this work. *Bela* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Bela species of small size, fusiform-biconic shape, protoconch of 3.5 convex whorls, last whorl with arcuate riblets, teleoconch whorls weakly convex, subsutural ramp and shoulder poorly developed, sculpture of low axial ribs, 11-14 on last whorl developed only mid-whorl, fine regular spiral threads over entire surface, anal sinus broad and shallow, siphonal canal short, siphonal fasciole indistinct.

Description – Shell small, fusiform-biconic. Protoconch multispiral, composed of 3.5 convex whorls, weak arcuate riblets on last half whorl. Junction with teleoconch sharp. Teleoconch of 4.5 weakly convex whorls, with periphery at or just above suture, subsutural ramp and shoulder poorly developed. Suture impressed, linear. Sculpture of low, rounded, prosocline axial ribs, sinuous over subsutural ramp, weakening towards sutures, 11-14 on penultimate whorl, overrun by numerous very fine subequal spiral threads. Last whorl barrel-shaped, 60-71% total height, slightly convex narrow subsutural ramp, broadly rounded at shoulder that is hardly developed, regularly and broadly convex below, weakly constricted at base; axial sculpture developed only mid-whorl, not extending over base, weakening towards outer lip; spiral sculpture of fine threads over entire last whorl; siphonal fasciole not delimited. Aperture relatively wide, 51% total height; outer lip thin, regularly convex; anal sinus broad, shallow U-shaped, apex placed at shoulder; siphonal canal short, open. Columella weakly excavated mid-aperture. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – Bela keukelaari nov. sp. is quite distinctive in having a regularly conical spire, the subsutural ramp and shoulder poorly developed making the shell rather barrel-shaped and in having subdued sculpture consisting of low axial ribs that on the last whorl are only developed mid-whorl and tend to weaken towards the outer lip and fine spiral threads of equal strength covering the entire shell surface. Most *Bela* species are more strongly shouldered. *Bela nevropleura* (Brugnone, 1862), with which it co-occurs in Assemblage I is also weakly shouldered, but has more convex whorls and fewer but stronger ribs, and a longer and more constricted siphonal fasciole. Other weakly shouldered species such as *B. proxima* (Cocconi, 1873) and *B. vulpecula* (Brocchi, 1814), both

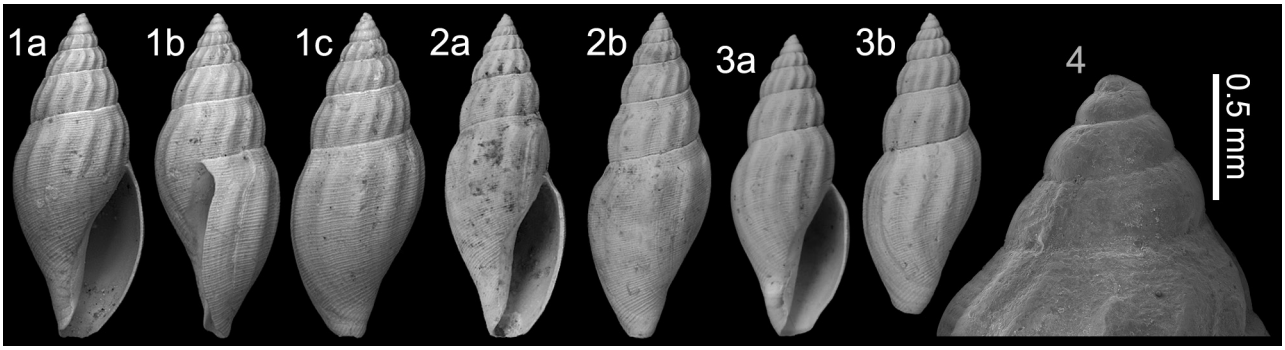

Plate 22. *Bela keukelaari* nov. sp.; 1. **Holotype** MNHN.F.A70524, height 8.5 mm, width 3.3 mm; 2. **Paratype 1** MNHN.F.A70525, height 11.2 mm, width 3.9 mm; 3. **Paratype 2** NHMW 2016/0103/1171, height 9.3 mm, width 3.5 mm; 4. **Paratype 3** NHMW 2016/0103/1172, height 4.7 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

from the Mediterranean Pliocene, also differ in having stronger axial sculpture.
Brébion (1964, p. 592) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and St-Michel, to which we add Clément-de-la-Place and Beugnon.

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

***Bela nevropleura* (Brugnone, 1862)**
Plate 23, figs 1-2; Plate 24, figs 1-3

*1862	*Pleurotoma nevropleurum*	Brugnone, p. 33, pl. 1, fig. 24.
1877	*Raphitoma nevropleura*	(Brugn.) – Bellardi, p. 310, pl. 9, fig. 22.
1914	*Daphnella* (*Raphitoma*) *nevropleura*	Brugnone – Cipolla, p. 165, pl. 14, fig. 13.
1954	*Mangelia* (*s.s.*) *nevropleura*	Brugnone, 1862 – Glibert, p. 50, pl. 6, fig. 11.
1964	*Cythara* (*Mangelia*) *nevropleura*	Brugnone, 1862 – Brébion, p. 585.
1997	*Raphitoma nevropleura*	(Brugnone, 1862) – Chirli, p. 84, pl. 24, figs 5-7.
2015	*Bela nevropleura*	(Brugnone, 1862) – Della Bella *et al*., p. 39, figs 101-108.

Material and dimensions – Typical form: Maximum height 7.1 mm, width 2.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1206-1208 (3), NHMW 2016/0103/1209 (6), LC (3), FVD (6). **Sceaux-d'Anjou**: NHMW 2016/0103/1939 (6), RGM.1352510 (2), LC (1), FVD (2).
Variety: Maximum height 13.0 mm, width 5.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1186-1188 (3), NHMW 2016/0103/1189 (5), LC (2), FVD (4). **Sceaux-d'Anjou**: NHMW 2016/0103/2191 (4), RGM.718185 (1), RGM.1352583 (17), FVD (1).

Discussion – *Bela nevropleura* (Brugnone, 1862) is characterised by its multispiral protoconch, with a few arcuate axial riblets on the last quarter whorl and its slender shell with about eight relatively narrow axials. Spiral sculpture is very weak, only visible under magnification. The specimens illustrated here (Pl. 23, figs 1-2) are similar to that illustrated by Della Bella *et al*. (2015, figs 102-104) and considered by those authors to be the typical form. A second form (Pl. 24, figs 1-3) co-occurs at St-Clément-de-la-Place that differs from the type in being broader, having a more strongly developed subsutural ramp, delimited by a slightly strength-

Plate 23. *Bela nevropleura* (Brugnone, 1862) typical form; 1. NHMW 2016/0103/1206, height 7.1 mm, width 2.6 mm, 1d, detail of protoconch; 2. NHMW 2016/0103/1207, height 6.3 mm, width 2.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

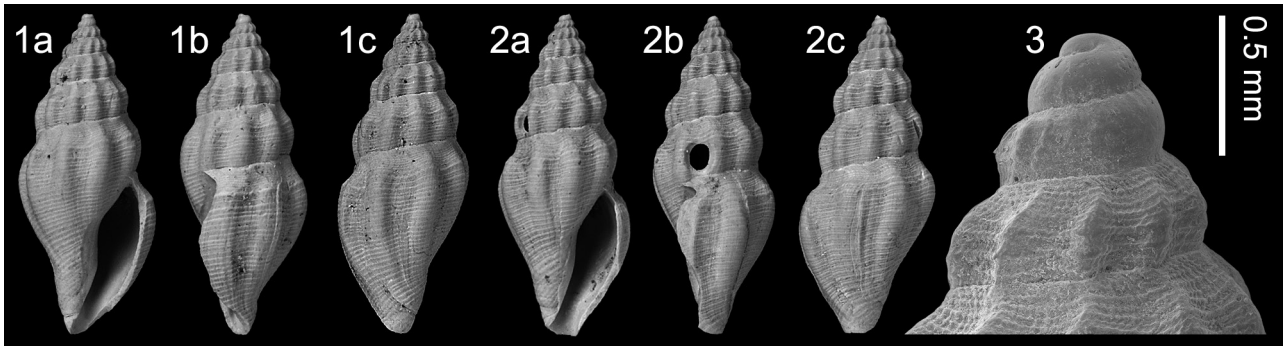

Plate 24. *Bela nevropleura* (Brugnone, 1862) variety with sharper and stronger sculpture; 1. NHMW 2016/0103/1186, height 13.0 mm, width 5.5 mm; 2. NHMW 2016/0103/1187, height 13.9 mm, width 6.0 mm; 3. NHMW 2016/0103/1188, height 9.1 mm, width 3.9 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ened spiral cord at the shoulder, more prominent spiral sculpture and thicker axial ribs. They are very similar to the specimens illustrated by Della Bella *et al*. (2015, figs 106-108) described as a form of *B. nevropleura*. The protoconch is similar (albeit slightly taller in the typical form; Pl. 23, fig. 1d) in that they are smooth with axial riblets on the last half whorl. We follow Della Bella *et al*. (2015) in considering them forms of a single species. This second form is similar to *B. vulpecula* (Brocchi, 1814) but in that species the last two protoconch whorls are tuberculose, the subsutural ramp and shoulder are better developed, and the siphonal canal is longer.
Bela nevropleura was recorded by Glibert (1954, p. 50) from the Assemblage I locality of Beaulieu, we here add St-Clément-de-la-Place and Sceaux-d'Anjou.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (Glibert, 1954; Brébion, 1964). Lower Pliocene: central Mediterranean, Italy (Chirli, 1997; Della Bella *et al*., 2015). Upper Pliocene: central Mediterranean, Italy (Brugnone, 1862; Bellardi, 1877; Cipolla, 1914; Della Bella *et al*., 2015).

***Bela peyroti* Glibert, 1960**
Plate 25, figs 1-3

1938 *Mangelia* (*Clathurella*) *turonensis* Peyrot, p. 292, pl. 5, fig. 51 (*non Mangelia turonensis* Peyrot, 1938, p. 283, pl. 5, figs 2, 64).
*1960 *Bela peyroti* Glibert, p. 28 (*nom. nov. pro Mangelia* (*Clathurella*) *turonensis* Peyrot, 1938).

Material and dimensions – Maximum height 7.7 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1202-1204 (3), NHMW 2016/0103/1205 (13), LC (12), FVD (18). **Sceaux-d'Anjou**: NHMW 2016/0103/1947 (17), RGM.718184 (43), RGM.1352457 (3), RGM.1352497 (20), RGM.1352617 (2), RGM.1352629 (1), RGM.1352669 (6), LC (1), FVD (11). **Renauleau**: NHMW 2016/0103/1201 (3), LC (12), FVD (7).

Revised description – Shell small, stout fusiform, very solid. Protoconch paucispiral, composed of 1.5-1.7 depressed convex whorls with microsculpture of fine crowded spiral threads. Junction with teleoconch sharp. Teleoconch of 4.5 shouldered whorls, with periphery just below mid-whorl, subsutural ramp broad, concave, shoulder well developed. Suture impressed, undulating. Sculpture of broad, rounded, prosocline axial ribs, equal in width to their interspaces, weakening over subsutural ramp, not reaching adapical suture, 11 on second whorl, ten on last whorl, overrun by fine subequal spiral cords, about one-quarter width of their interspaces; four spirals on first teleoconch whorl, two on subsutural ramp, two below shoulder, secondary spirals intercalated on second teleoconch whorl. Last whorl 64-69% total height, broad, concave subsutural ramp, rounded at shoulder, convex below, strongly constricted at base; axial sculpture extends weakened over base; spirals broadening over base and siphonal; siphonal fasciole distinct. Aperture ovate, 44-47% total height; outer lip thickened; anal sinus wide, moderately deep U-shaped, apex placed mid subsutural ramp; siphonal canal medium length, relatively wide, open. Columella moderately excavated mid-aperture. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – We have offered a revised description for this species as the type figured by Peyrot (1938) is worn. The protoconch is composed of 1.5-1.7 whorls and bears fine spiral sculpture. This type of protoconch microsculpture is common in mangeliids with paucispiral protoconchs (Bouchet *et al*., 2011, p. 281). *Bela peyroti*

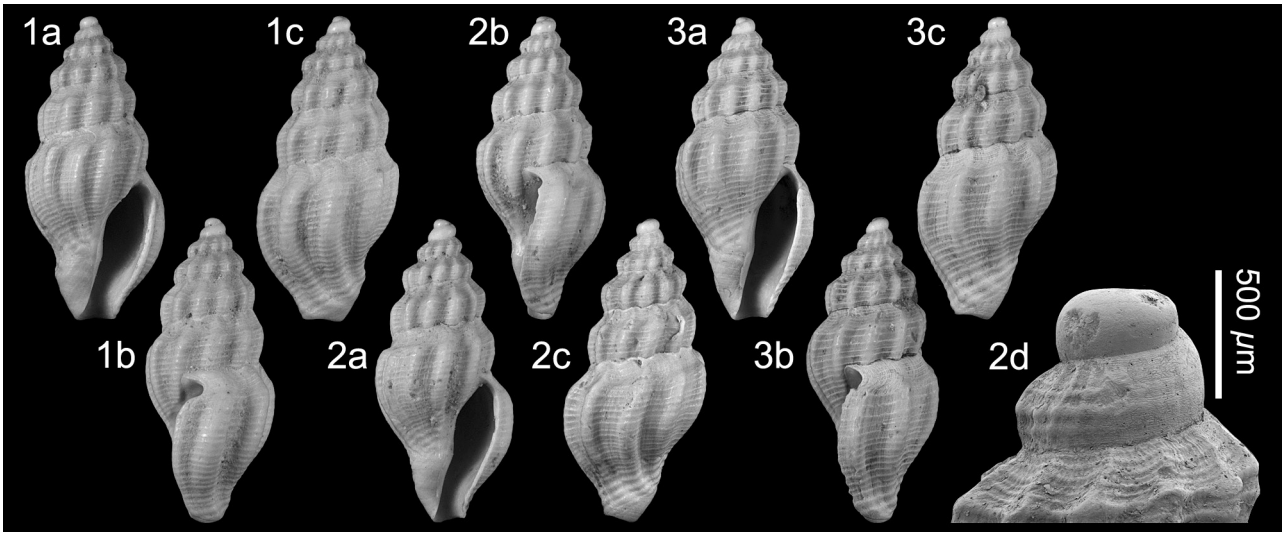

Plate 25. *Bela peyroti* Glibert, 1960; 1. NHMW 2016/0103/1202, height 7.2 mm, width 3.3 mm; 2. NHMW 2016/0103/1203, height 7.0 mm, width 3.1 mm, 2d, detail of protoconch (SEM image); 3. NHMW 2016/0103/1204, height 6.6 mm, width 3.0 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Glibert, 1960 is similar to the stockier forms of *B. quadrata* (Peyrot, 1938), with which it co-occurs in Assemblage I, but the teleoconch differs in being even thicker, in having a better developed shallower and subsutural platform, a more strongly developed shoulder, a distinct siphonal fasciole and having the spiral sculpture more strongly developed.
We record *B. peyroti* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Peyrot, 1938; Glibert, 1960). Upper Miocene: Atlantic (Tortonian): NW France (this paper).

***Bela pseudomegastoma* nov. sp.**
Plate 26, figs 1-3

1964 *Cythara* (*Mangelia*) *submarginata* Bonelli in Bellardi, 1877 [*sic*] – Brébion, p. 587, pl. 14, figs 16-18 [*non Bela submarginata* (Bellardi, 1847)].

Type material – Holotype NHMW 2016/0103/1984, height 13.1 mm, width 5.7 mm; paratype 1 NHMW 2016/0103/1985, height 11.9 mm, width 5.1 mm; paratype 2 NHMW 2016/0103/1986, height 9.3 mm, width 4.3 mm (subadult); paratype 3 NHMW 2016/0103/2022, height 12.1 mm, width 5.6 mm; paratype 4 NHMW 2016/0103/2023, height 11.7 mm, width 5.4 mm; paratype 5 RGM.1352620, height 11.3, width 5.0 mm; paratype 6 RGM.1352621, height 11.3, width 4.9 mm.

Other material – Maximum height 13.1 mm, width 5.7 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1987 (2 subadults), RGM.1352630 (1). **Renauleau**: NHMW 2016/0103/1991 (1), LC (?1).

Etymology – Named reflecting the close similarity to *B. megastoma* (Brugnone, 1862). *Bela* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Bela* species medium-sized for genus, relatively broad fusiform, protoconch of 2.8 whorls, with axial riblets last whorl, teleoconch with roundly shouldered whorls, 9-11 broad axials, weakening over subsutural ramp, fine spiral sculpture of alternating strength, relatively short siphonal canal, siphonal fasciole indistinct.

Description – Shell medium-sized for genus, relatively broadly fusiform. Protoconch multispiral, composed of 2.8 convex whorls, weak arcuate riblets on last whorl. Junction with teleoconch sharp. Teleoconch of 5.5 roundly shouldered whorls, with periphery between mid-whorl and lower suture, subsutural ramp broad, concave, shoulder well developed, rounded. Suture impressed, weakly undulating. Sculpture of broad, rounded, prosocline axial ribs, extending between sutures, weakened over subsutural ramp, 9-11 on last whorl, overrun by extremely fine spiral threads of alternating strength over entire surface. Last whorl 61-65% total height, concave subsutural ramp, obtusely angled at soulder, convex below, weakly to moderately constricted at base; axial sculpture weakens over base; siphonal fasciole not delimited. Aperture relatively short, 43-46% total height; outer lip thin; anal sinus broad, moderate depth, U-shaped, apex placed mid subsutural ramp; siphonal canal relatively short, open. Columella moderately excavated mid-aperture. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – *Bela pseudomegastoma* nov. sp. is very similar to the Italian Pliocene-Pleistocene *B. megastoma* (Brugnone, 1862). They share the same type of multispiral protoconch with axial riblets on the last protoconch whorl, although slightly fewer whorls [2.8 whorls vs 3.1 in *B. megastoma*; fide Della Bella *et al*. (2015, fig. 141)]. This form is common to many *Bela* species. They are both scultured by 9-11 broad axial ribs and fine spiral cords. The shapes of the subsutural ramp and sinus are also similar. The only difference between the two is in shell shape; the Assemblage I species is broader than any specimen seen of *B. megastoma* and the siphonal canal is slightly shorter. Although the number of specimens available from Assemblage I is rather small, these differences appear to be constant.

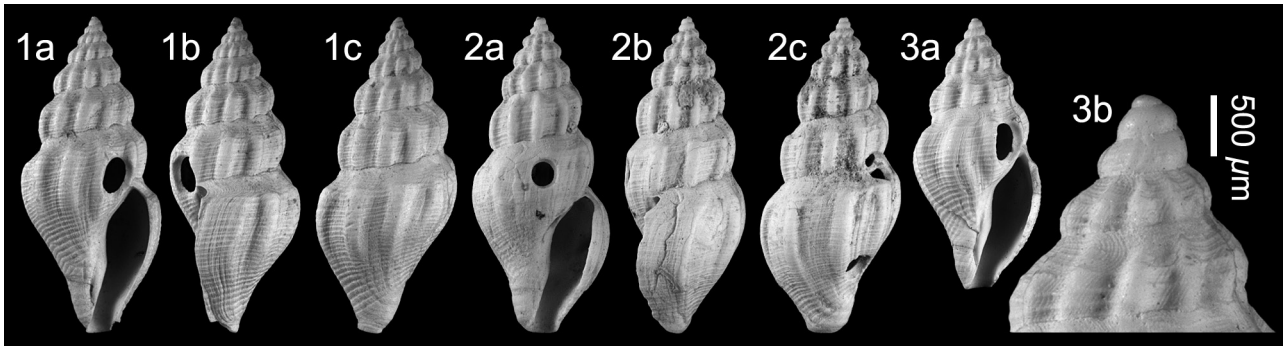

Plate 26. *Bela pseudomegastoma* nov. sp.; 1. **Holotype** NHMW 2016/0103/1984, height 13.1 mm, width 5.7 mm; 2. **Paratype 1** NHMW 2016/0103/1985, height 11.9 mm, width 5.1 mm; 3. **Paratype 2** NHMW 2016/0103/1986, height 9.3 mm, width 4.3 mm, 3b, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Brébion (1964, p. 587) confused this species with the Mediterranean Pliocene *Bela submarginata* (Bellardi, 1847) (syntype figured by Ferrero Mortara *et al*., 1981, pl. 18, fig. 12), but that species is more slender, with a taller spire and longer siphonal canal and the base is more constricted. These differences between the French and Italian specimens were highlighted by Brébion himself in his discussion of the species.
It was recorded by Brébion (1964, p. 588) from the Assemblage I localities of Sceaux-d'Anjou, Thorigné, St-Clément-de-la-Place and St-Michel, to which we add Renauleau.

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

***Bela pseudovulpecula* nov. sp.**
Plate 27, figs 1-7

1954 *Mangelia* (*s.s*.) *vulpecula* Brocchi, 1814 – Glibert, p. 49, pl. 6, fig. 9 [*non Bela vulpecula* (Brocchi, 1814)].
1964 *Cythara* (*Mangelia*) *milleti* Brébion, p. 589 (*nomen nudum*) [*nom. nov. pro Mangelia* (*s.s*.) *vulpecula* Glibert, p. 49, pl. 6, fig. 9; *non Bela vulpecula* (Brocchi, 1814)].

Type material – Holotype MNHN.F.A70526, height 13.1 mm, width 5.3 mm; paratype 1 MNHN.F.A70527, height 11.1 mm, width 4.1 mm; paratype 2 NHMW 2016/0103/1176, height 14.6 mm, width 5.6 mm; paratype 3 NHMW 2016/0103/1177, height 11.3 mm, width 5.0 mm; paratype 4 NHMW 2016/0103/1178, height 11.7 mm, width 4.8 mm; paratype 5 NHMW 2016/0103/1179, height 12.4 mm, width 4.9 mm; paratype 6 NHMW 2016/0103/1943 (juvenile), **St-Clément-de-la-Place**. Paratype 7 RGM.1352504, height 13.8 mm, width 5.4 mm; paratype 8 RGM.1352505, height 10.8 mm, width 4.6 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 14.6 mm, width 5.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1180 (39), RGM.1352677 (1), LC (35), FVD (39). **Sceaux-d'Anjou**: NHMW 2016/0103/1944 (37), RGM.718160 (32), RGM.1352506 (29), RGM.1352646 (1), LC (12), FVD (20). **Renauleau**: NHMW 2016/0103/1992 (3), LC (8), FVD (2).

Etymology – Named reflecting the close similarity to *B. vulpecula* (Brocchi, 1814). With which it has been confused by authors. *Bela* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Bela* species medium-sized for genus, fusiform, protoconch of 2.5 whorls, with axial riblets last half whorl, teleoconch with shouldered whorls, 8-12 axials extending between sutures, extremely fine spiral sculp-

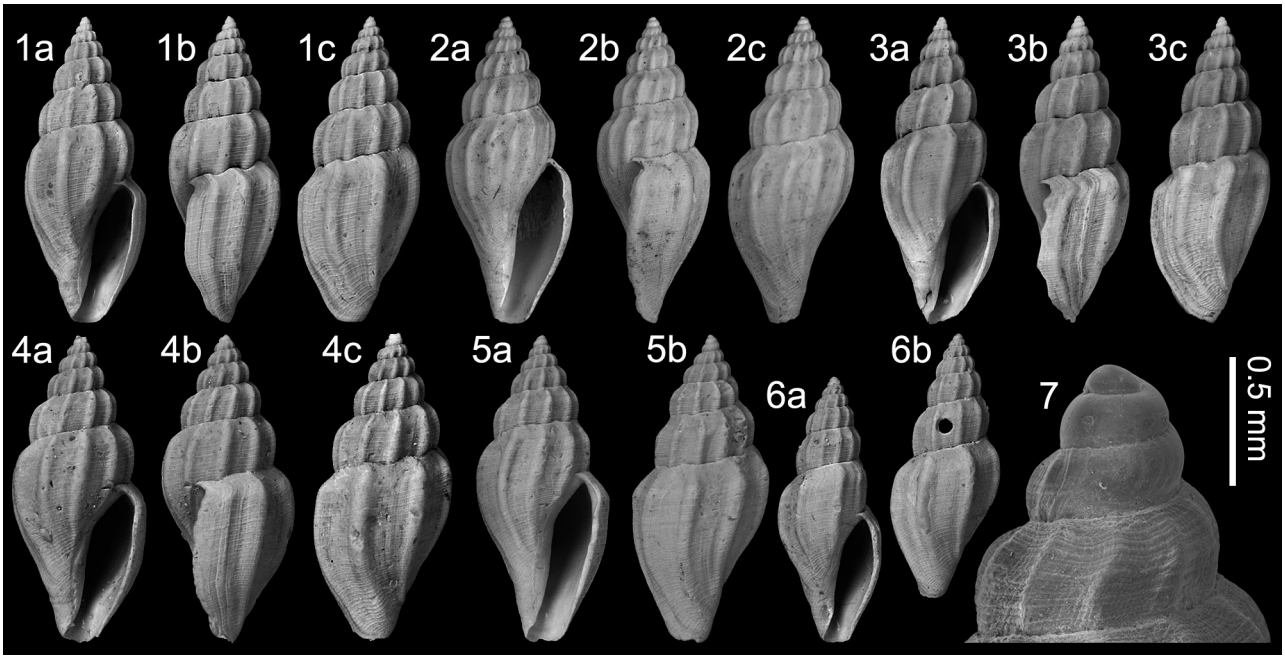

Plate 27. *Bela pseudovulpecula* nov. sp.; 1. **Holotype** MNHN.F.A70526, height 13.1 mm, width 5.3 mm; 2. **Paratype 1** MNHN.F.A70527, height 11.1 mm, width 4.1 mm; 3. **Paratype 2** NHMW 2016/0103/1176, height 14.6 mm, width 5.6 mm; 4. **Paratype 3** NHMW 2016/0103/1177, height 11.3 mm, width 5.0 mm, 5. **Paratype 4** NHMW 2016/0103/1178, height 11.7 mm, width 4.8 mm; 6. **Paratype 5** NHMW 2016/0103/1179, height 12.4 mm, width 4.9 mm; 7. **Paratype 6** NHMW 2016/0103/1943 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ture of alternate strength, medium length siphonal canal, siphonal fasciole indistinct.

Description – Shell medium-sized for genus, fusiform. Protoconch multispiral, composed of 2.5 convex whorls, weak arcuate riblets on last half whorl. Junction with teleoconch sharp. Teleoconch of five weakly shouldered whorls, with periphery just below mid-whorl, subsutural ramp broad, shoulder moderately developed. Suture impressed, linear. Sculpture of rounded, prosocline axial ribs, extending between sutures, sinuous over subsutural ramp, 8-12 on last whorl, overrun by extremely fine spiral threads, usually of alternating strength over entire surface. Last whorl 69% total height, slightly concave to slightly convex wide subsutural ramp, obtusely angled at soulder, convex below, weakly to moderately constricted at base; axial sculpture extends over base; siphonal fasciole not delimited. Aperture relatively wide, 52% total height; outer lip thin; anal sinus broad, shallow U-shaped, apex placed mid sutural ramp; siphonal canal medium length, open. Columella weakly excavated mid-aperture. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion –Della Bella *et al*. (2015, p. 44) were correct to exclude the Assemblage I specimen from Sceaux-d'Anjou illustrated by Glibert (1954, pl. 6, fig. 9) from their chresonymy of *Bela vulpecula* (Brocchi, 1814). Indeed, Brébion (1964, p. 589) also realised the two were not conspecific and suggested the replacement name *Cythara* (*Mangelia*) *milleti* for Glibert's species. However as his thesis was never published that name must be considered *nomen nudum*.
The protoconch has a similar number of whorls as *B. vulpecula*, but in that species, the last whorl, riblets and fine cords form a reticulated pattern with small beads developed at the intersections (Della Bella *et al*., 2015, figs 117, 121), whereas in the Assemblage I species the axial riblets are relatively weak and there is no spiral sculpture (Pl. 27, fig. 4). The teleoconch of the two species is of similar shape, with a distinct, but not sharp shoulder, but *Bela pseudovulpecula* nov. sp. has fewer axial ribs (usually 8-11, exceptionally 12; vs. 12-13 in *B. vulpecula*) and the spiral sculpture is much finer, composed of threads separated by wider interspaces, whereas in *B. vulpecula* the narrow cords are wider than their interspaces. Brébion (1964, p. 587) confused this species with the Mediterranean Pliocene *Bela submarginata* (Bellardi, 1877) (syntype figured by Ferrero Mortara *et al*., 1981, pl. 18, fig. 12), but that species is more slender, with a taller spire and longer siphonal canal and the base is more constricted. These differences between the French and Italian specimens were highlighted by Brébion himself in his discussion of the species. *Bela sceauxensis* nov. sp., with which it oc-occurs in Assemblage I, differs in being small, more slender, weaker shouldered and in having more numerous axial ribs (see below).
Glibert (1954, 49) recorded this species from the Assemblage I locality of Sceaux-d'Anjou, to which Brébion (1964, p. 588) added Thorigné, St-Clément-de-la-Place and St-Michel, and we add Renauleau. Glibert also recorded it from the Assemblage III locality of Le Pigeon Blanc, but we were unable to confirm this record in Ceulemans *et al*. (2018). As the specimen illustrated by Glibert is from Sceaux-d'Anjou, we provisionally exclude this species from the Assemblage III distribution.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (Glibert, 1954; Brébion, 1964).

***Bela quadrata* (Peyrot, 1938)**
Plate 28, figs 1-6

1854	*Pleurotoma Hordeola* Millet (*partim*), p. 161 (*nomen nudum*).
1865	*Pleurotoma hordeola* Millet (*partim*), p. 588.
1938	*Daphnella* (*Raphitoma*) *quadrata* Peyrot, p. 297, pl. 5, figs 59, 61.
non 1960	*Bela quadrata* Peyrot, 1938 – Glibert, p. 33, pl. 5, fig. 13.
1964	*Cythara* (*Mangelia*) *quadrata* Peyrot, 1939 – Brébion, p. 588, pl. 14, figs 19, 20.

Material and dimensions – Maximum height 7.5 mm, width 3.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1181-1184 (4), NHMW 2016/0103/1198-1199 (3), NHMW 2016/0103/1185 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/2019 (3), RGM. 718161 (50+), RGM.718162 (5), RGM.1352511 (7), FVD (1).

Discussion – *Bela quadrata* (Peyrot, 1938) is characterised by its small size, solid shell, protoconch composed of 2-2.25 smooth convex whorls, teleoconch with shouldered whorls, about ten prosocline to orthocline axial ribs and very fine, crowded spiral threads of equal size. The anal sinus is moderately deep, U-shaped, with the apex placed mid subsutural ramp, and the siphonal canal is short to medium length. There is some intraspecific variability, some specimens are squatter than others and the shoulder more or less sharp. The sculpture is relatively constant. We doubt that the specimen illustrated by Glibert (1960, pl. 5, fig. 13) from the Loire Basin is conspecific. That shell is biconic, the last whorl strongly angled mid-whorl. Brébion (1964, p. 589) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, St-Clément-de-la-Place and possibly Thorigné.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Peyrot, 1928; Glibert, 1960). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964).

***Bela redoniana* nov. sp.**
Plate 29, figs 1-5

1964	*Cythara* (*Mangelia*) *turgida* Forbes, 1843 [*sic*] – Brébion (?*partim*), p. 584, pl. 14, fig. 14 (Assemblage I specimens) [*non Bela turgida* (Reeve, 1844)].

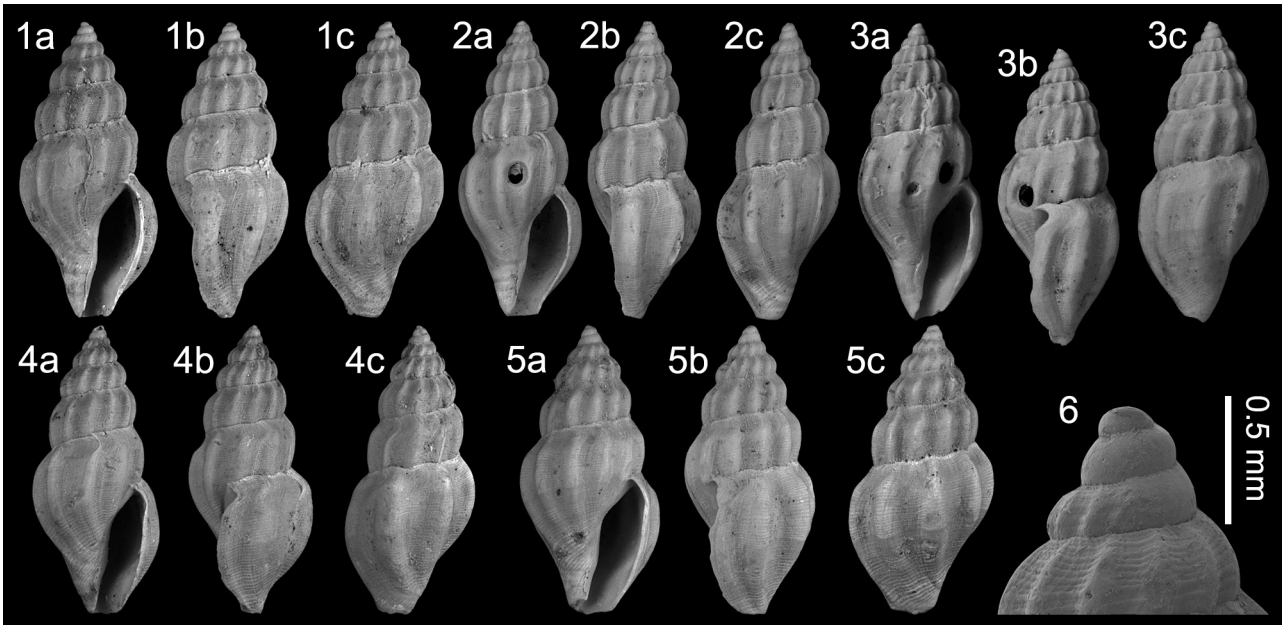

Plate 28. *Bela quadrata* (Peyrot, 1938); 1. NHMW 2016/0103/1181, height 6.4 mm, width 2.8 mm; 2. NHMW 2016/0103/1182, height 7.5 mm, width 3.0 mm; 3. NHMW 2016/0103/1183, height 6.6 mm, width 2.9 mm; 4. NHMW 2016/0103/1198, height 7.2 mm, width 3.1 mm; 5. NHMW 2016/0103/1199, height 6.2 mm, width 3.0 mm; 6. NHMW 2016/0103/1184, height 6.1 mm, width 2.1 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Type material – Holotype MNHN.F.A70528, height 7.2 mm, width 3.5 mm; paratype 1 MNHN.F.A70529, height 6.1 mm, width 2.6 mm; **St-Clément-de-la-Place**. Paratype 2 NHMW 2016/0103/1195, height 9.0 mm, width 4.0 mm; paratype 3 NHMW 2016/0103/1196, height 8.0 mm, width 3.9 mm; paratype 4 NHMW 2016/0103/1197, height 7.9 mm, width 3.8 mm; paratype 5 NHMW 2016/0103/1945, (juvenile). **Renauleau**. Paratype 6 RGM.1352610, height 7.4 mm, width 3.3 mm; paratype 7 RGM.1352615, height 9.3 mm, width 3.9 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 9.0 mm, width 4.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1194 (9), LC (6), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/2021 (2), RGM.719027 (8 juveniles). **Renauleau**: NHMW 2016/0103/1946 (39), LC (50+), FVD (44). **Beugnon**: RGM.1352580 (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Bela* species of small size, squat-biconic, protoconch of 3.5 whorls, with axial riblets last half whorl, teleoconch with shouldered whorls, subsutural platform wide, shoulder nodulose, nine axials second teleoconch whorl, seven last whorl, extending between sutures, extremely fine subequal spiral sculpture, medium length siphonal canal, siphonal fasciole indistinct.

Description – Shell small, biconic, very solid. Protoconch tall multispiral, composed of 3.5 convex whorls, weak arcuate riblets on last half whorl. Junction with teleoconch sharp. Teleoconch of five shouldered whorls, with periphery just below mid-whorl, subsutural ramp broad, concave, shoulder well developed. Suture impressed, undulating. Sculpture of broad, rounded, prosocline axial ribs, slightly narrower than their interspaces, extending between sutures, thinning over subsutural ramp towards adapical suture, nine on second whorl, seven on last whorl, overrun by fine subequal spiral threads. Last whorl 65% total height, broad, concave subsutural ramp, rounded at shoulder, almost straight sided below, weakly constricted at base; axial sculpture extends weakened over base; siphonal fasciole not delimited. Aperture narrow, 43% total height; outer lip tickened; anal sinus narrow, deep U-shaped, apex placed at shoulder; siphonal canal medium length, open. Columella moderately excavated mid-aperture. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – This species is characterised by its biconic shape, very solid shell, poorly constricted base, sculpture consisting of 7-8 broad ribs crossed by much finer, closeset spiral threads, usually of alternating strength, and shallow, wide anal canal that takes up the entire width of

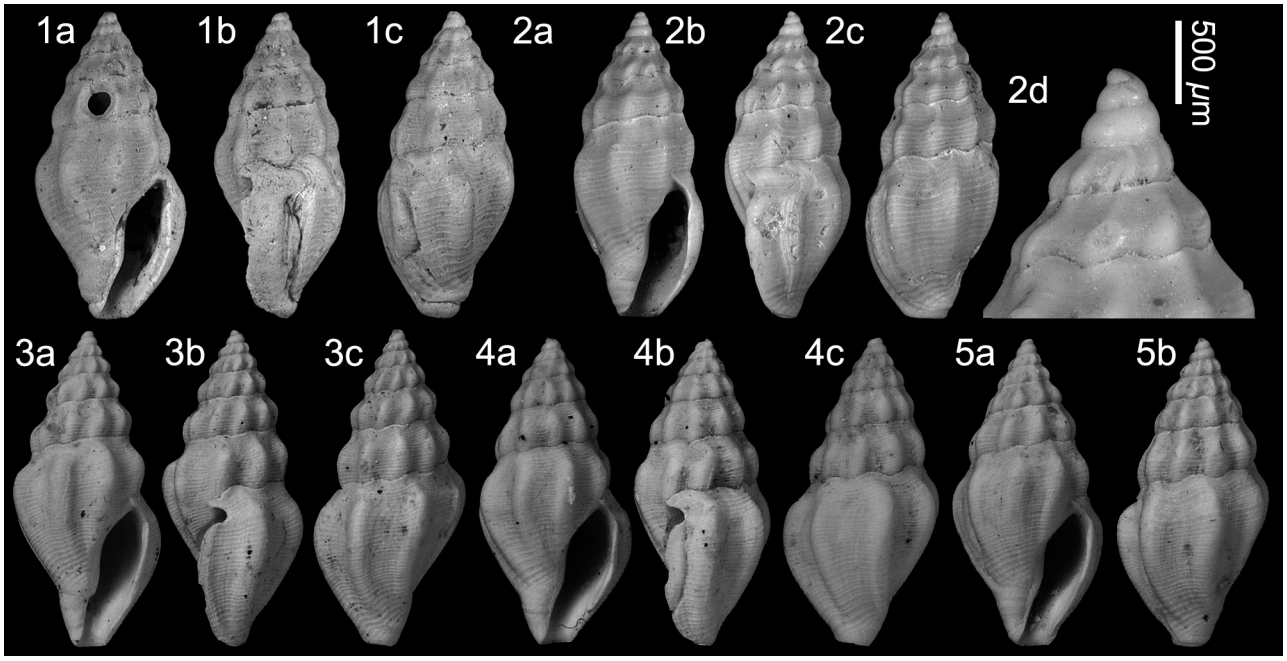

Plate 29. *Bela redoniana* nov. sp.; 1. **Holotype** MNHN.F.A70528, height 7.2 mm, width 3.5 mm; 2. **Paratype 1** MNHN.F.A70529, height 6.1 mm, width 2.6 mm, 2d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 3. **Paratype 2** NHMW 2016/0103/1195, height 9.0 mm, width 4.0 mm; 4. **Paratype 3** NHMW 2016/0103/1196, height 8.0 mm, width 3.9 mm; 5. **Paratype 4** NHMW 2016/0103/1197, height 7.9 mm, width 3.8 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the subsutural ramp. It might represent a European member of the genus *Brachycythara* Woodring, 1928 (type species *Cythara gibba* Guppy, *in* Guppy & Dall, 1896, by original designation, Pliocene, Jamaica), which shares the characters outlined above, although adult shells of *Brachycythara* have lirae within the outer lip (Powell, 1966, p. 117), absent in the French species. As no European fossil or extant species have so far been attributed to *Brachycythara*, we provisionally include it in *Bela*.

If accepted in *Bela*, it is closest to the *Bela menkhorsti* species group of Marriottini *et al*. (2009). The name *Bela menkhorsti* Van Aartsen (1988a) was proposed to replace *Pleurotoma nana* Scacchi, 1836, not of Deshayes, 1835. Members of this species group have often been reported in the literature as *Pleurotoma turgida* Reeve, 1844, which Van Aartsen (1988a, b) considered to be a *nomen dubium*.

The *Bela menkhorsti* group was revised recently by Mariottini *et al*. (2009), who recognised four species. All have very similar teleoconch morphology, but two have paucispiral protoconchs: *B. zenetouae* (Van Aartsen, 1988) and *B. taprurensis* (Pallary, 1904), and two have multispiral protoconchs: *B. menkhorsti* and *B. trinacria*. The difference between the multispiral species was based on protoconch characters, as the protoconch is larger in *B. trinacria* (0.6-0.7 mm *vs.* 0.53-0.54 mm) than in *B. menkhorsti*, with a greater number of whorls in *B. trinacria* (2.7-2.8 vs. 2.0-2.2). Mariottini *et al*. (2009) considered *B. trinacria* to be an extinct species present in the Italian Pliocene, whereas *B. menkhorsti* is the extant species.

Ceulemans *et al*. (2018, p. 101) identified the poorly preserved specimens from the lower Pliocene Assemblage III as *B. trinacria*. The protoconch was not well preserved, but seemed to be multispiral. The more slender forms from Assemblage III were separated by Brébion (1964, p. 584) as var. *pliospiralata* Sacco, 1890, but as illustrated by Mariottini *et al*.
(2009) relatively squatter and more elongate forms of *B. trinacria* occur.

Based on the more plentiful and better preserved material from Assemblage I we do not consider the specimens illustrated here as conspecific with *B. trinacria*. They differ in being squatly biconic in profile, the subsutural ramp is wider, the axial ribs are wider and more nodulose at the shoulder, the siphonal canal is shorter, and the spiral cords are subequal rather than of alternating strength as seen in *B. trinacria* (compare Mariottini *et al*., 2009, figs 17-23). The protoconch in the French species is also taller with half a whorl more than that of *B. trinacria*. The French Assemblage III specimens are still more like *B. trinacria* in being less nodulose at the shoulder, more constricted at the base and having a longer siphonal canal. *Bela redoniana* was probably endemic to the Ligerian Bay in the late Miocene.

Brébion (1964, p. 584, 585) recorded this species from the Assemblage I locality of Thorigné, to which we add St-Clément-de-la-Place, Sceaux-d'Anjou, Renauleau, and Beugnon.

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

***Bela scarponii* nov. sp.**
Plate 30, figs 1-3

Type material – Holotype MNHN.F.A70534, height 4.9 mm, width 2.0 mm; paratype 1 MNHN.F.A70535, height 4.4 mm, width 1.8 mm; paratype 2 NHMW 2016/0103/1190, height 4.8 mm, width 1.8 mm; paratype 3 NHMW 2016/0103/1191, height 4.6 mm, width 1.8 mm; paratype 4 NHMW 2016/0103/1192, height 4.4 mm, width 1.8 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1352523, height 6.9 mm, width 2.7 mm; paratype 6 RGM.1352537, height 7.2 mm, width 3.0 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 7.2 mm, width 3.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1193 (21), RGM.1352671 (3), LC (4), FVD (9). **Sceaux-d'Anjou**: NHMW 2016/0103/1953 (7), RGM.718188 (18), RGM.734986 (10), LC (1), FVD (2).

Etymology – Named after Daniele Scarponi, Italy, in recognition of his valuable work on the genus. *Bela* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Bela* species of small size, fusiform, scalate spire, protoconch of 3.5 convex whorls, last whorl with arcuate riblets, teleoconch whorls strongly shouldered, sculpture of rounded axial ribs, 9-10 on second whorl, 7-8 on last whorl, fine irregularly beaded threads over entire surface, anal sinus of medium depth and width, siphonal canal short to medium length, siphonal fasciole indistinct.

Description – Shell small, fusiform, scalate, of medium thickness. Protoconch multispiral, composed of 3.5 convex whorls with axial riblets on last whorl. Junction with teleoconch sharp. Teleoconch of four shouldered whorls, with periphery just below mid-whorl, subsutural ramp broad, slightly concave, shoulder well developed, rounded. Suture impressed, weakly undulating. Sculpture of broad, rounded, orthocline to slightly opisthocline axial ribs, half width of their interspaces, weakening over subsutural ramp, not reaching adapical suture, 9-10 on second whorl, 7-8 on last whorl, overrun by fine subequal spiral cords, about equal width of their interspaces; four spirals at teleoconch junction, rapidly increasing in number abapically, cords irregularly and finely beaded giving surface a rough appearance. Last whorl 61-63% total height, broad, slightly concave subsutural ramp, roundly angled at shoulder, convex below, weakly to moderately constricted at base; axial sculpture weakens over base; siphonal fasciole indistinct. Aperture ovate, small, 41% total height; outer lip weakly thickened; anal sinus moderately wide and deep, U-shaped, apex placed mid subsutural ramp; siphonal canal short to medium length, relatively wide, open. Columella moderately excavated in upper third. Columellar callus weakly thickened, forming narrow callus rim, slightly expanded over siphonal fasciole.

Discussion – The teleoconch of this small species would suggest placement in the *Bela brachystoma* (Philippi, 1844) group of Della Bella *et al*. (2015), characterised by their small, narrow turreted shells with convex or shouldered whorls separated by a deep suture, and a small aperture. This group is now placed in a separate genus *Sorgenfreispira* Moroni, 1979, a group of small *Bela*-like species characterised by their small shells with slender scalate spires, relatively short aperture and protoconch with granular spiral sculpture on protoconch II (Mariottini *et al*., 2015). In the new French species protoconch II has axials, but no obvious spiral sculpture and the riblets are not granular, therefore we prefer to leave it in the genus *Bela* Leach *in* Gray, 1847.
We cannot separate the teleoconchs of the shells illus-

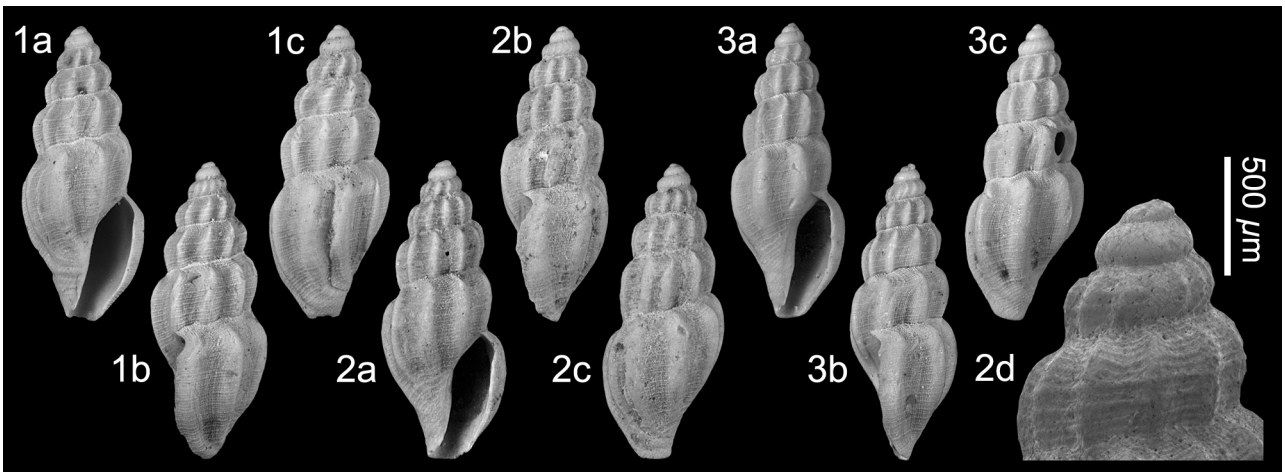

Plate 30. *Bela scarponii* nov. sp.; 1. **Holotype** MNHN.F.A70534, height 4.9 mm, width 2.0 mm; 2. **Paratype 1** MNHN.F.A70535, height 4.4 mm, width 1.8 mm, 2d, detail of protoconch (SEM image); 3. **Paratype 2** NHMW 2016/0103/1190, height 4.8 mm, width 1.8 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

trated here from those described as *Bela pseudoexilis* Della Bella, Naldi & Scarponi, 2015 from the Pliocene of Italy, which should also be transferred to the genus *Sorgenfreispira*. The three specimens illustrated in the original work show some variability in slenderness and in the spiral sculpture, which in the paratype from Altavilla (Della Bella *et al*., 2015, figs 90-92) is more strongly developed. The second teleoconch whorl has 9-11 ribs that decrease abapically to eight on the last whorl and the spiral sculpture is exceedingly fine, with 3-4 primary cords on the second teleoconch whorl (fits within variability of *B. pseudoexilis*; Della Bella *et al*., 2015, p. 77, appendix 3). However, as discussed above the protoconch is axially ribbed, but not granulose, as in *S. pseudoexilis*.
Other small species from the Italian Pliocene with similar teleoconch characters all have granulose protoconchs, and are therefore placed in the genus *Sorgenfreispira*; *S. brachystoma* (Philippi, 1844), *S. nitida* (Pavia, 1975), and *S. scalariforme* (Brugnone, 1862) all differ in having stronger spiral sculpture. *Bela plagiosculpta* Della Bella, Naldi & Scarponi, 2015 does not have granulose sculpture on the teleoconch, which is more like that of *B. scarponii* nov. sp. and is therefore left in the genus *Bela*. That species has a sharper shoulder defined by a stronger spiral cord and a better delimited flattened subsutural ramp. *Bela falbalae* Ceulemans, Van Dingenen & Landau, 2018 from Assemblage I does have strongly granulose protoconch sculpture and should therefore be transferred to *Sorgenfreispira*. It differs from its congeners in being a far taller species, with a more developed subsutural ramp and shoulder and a more constricted base.
We record *B. scarponii* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Bela sceauxensis* nov. sp.**
Plate 31, figs 1-2

1964 *Cythara* (*Mangelia*) *elegans* Brébion, p. 592, pl. 14, figs 23, 24 (*nomen nudum*).

Type material – Holotype MNHN.F.A70536, height 10.8 mm, width 4.3 mm; paratype 1 MNHN.F.A70537, height 8.3 mm, width 3.1 mm; paratype 2 NHMW 2016/0103/1954, height 10.3 mm, width 4.0 mm; paratype 3 NHMW 2016/0103/1955, height 9.8 mm, width 3.7 mm; paratype 4 NHMW 2016/0103/1956, height 11.9 mm, width 4.8 mm; paratype 5 RGM.1352501, height 11.5 mm, width 4.6 mm; paratype 6 RGM.1352502, height 10. 5 mm, width 4.2 mm.

Other material – Maximum height 12.1 mm, width 4.6 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1957 (37), RGM.718157 (50+), RGM.1352503 (40), RGM.1352648 (1), LC (12), FVD (16). **Renauleau**: NHMW 2016/0103/1200 (8), LC (15), FVD (13).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Bela* species medium-sized for genus, biconic fusiform, protoconch of 3.5 whorls, with axial riblets last whorl, teleoconch with weakly shouldered whorls, 15-16 axials extending between sutures, fine spiral sculpture of alternate strength threads, slightly strengthened spiral delimiting shoulder, moderate length siphonal canal, siphonal fasciole indistinct.

Description – Shell medium-sized for genus, biconic fusiform. Protoconch multispiral, composed of 3.5 convex whorls, weak arcuate riblets on last whorl. Junction with teleoconch sharp. Teleoconch of 4.5 weakly shouldered whorls, with periphery just below mid-whorl, subsutural ramp broad, shoulder weakly developed, flat to slightly concave, delimited by slightly strengthened spiral cord. Suture impressed, weakly undulating. Sculpture of sharp prosocline axial ribs, extending between sutures, sinuous over subsutural ramp, 15-16 on last whorl, overrun by extremely fine spiral threads of alternating strength covering entire surface. Last whorl tall, 78% total height, slightly concave subsutural ramp, obtusely angled at shoulder, convex below, weakly to moderately constricted at base;

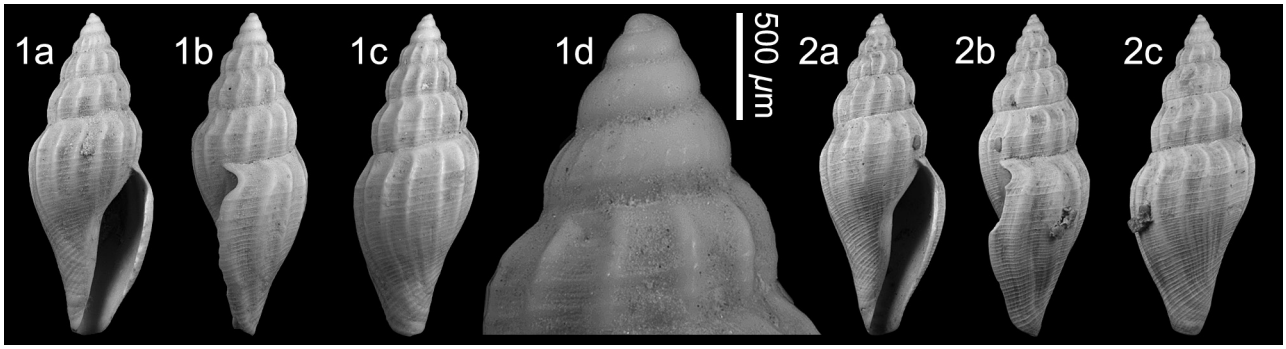

Plate 31. *Bela sceauxensis* nov. sp.; 1. **Holotype** MNHN.F.A70536, height 10.8 mm, width 4.3 mm; 2. **Paratype 1** MNHN.F.A70537, height 8.3 mm, width 3.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

axial sculpture weakens over base; siphonal fasciole not delimited. Aperture elongate, 50% total height; outer lip thin; anal sinus broad, U-shaped, apex placed mid sutural ramp; siphonal canal moderate length, open. Columella excavated upper third. Columellar callus weakly thickened, forming narrow indented callus rim.

Discussion – *Bela sceauxensis* nov. sp. is similar to *B. vulpecula* (Brocchi, 1814) and *B. pseudovulpecula* nov. sp., but differs in being smaller shelled than either of those species, weaker shouldered, more slender biconic in shape. It has more numerous axial ribs (15-16 vs. usually 8-11, exceptionally 12 in *B. pseudovulpecula* and 12-13 in *B. vulpecula*). Like *B. pseudovulpecula* spiral sculpture is composed of narrow spirals separated by wider interspaces, whereas in *B. vulpecula* narrow flattened cords are separated by even narrower grooves. However, in *B. pseudovulpecula* the shoulder is stronger and not delimited by a slightly strengthened cord, as it is *in B. sceauxensis*. *Bela plicatella* (Bellardi, 1847), another member of the *B. hispidula* (Bellardi, 1847) species group (*sensu* Della Bella *et al*., 2015) from Plio-Pleistocene Mediterranean Basin, differs from *B. sceauxensis* again in being larger with strongly shouldered whorls. It differs from all its congeners discussed above in having stronger spiral sculpture. *Bela nevropleura* (Brugnone, 1862), which also occurs in Assemblage I (see above), is similar in having a slender fusiform shape, but has far fewer axial ribs.
Brébion (1964, p. 593) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Thorigné and St-Michel, to which we add Renauleau.

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

Genus *Kyllinia* Garilli & Galletti, 2007

Type species – *Kyllinia parentalis* Garilli & Galletti, 2007, by original designation, present-day, Plio-Pleistocene, central Mediterranean.

2007 *Kyllinia* Garilli & Galletti, p. 747.

***Kyllinia parentalis* Garilli & Galletti, 2007**
Plate 32, figs 1-2

2007 *Kyllinia parentalis* Garilli & Galletti, p. 747, figs 3.1-3.12.
2010 *Kyllinia parentalis* Garilli & Galletti, 2007 – Scarponi & Della Bella, p. 86, figs 241-244.

Material and dimensions – Maximum height 6.5 mm, width 2.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1244 (1 fragment). **Sceaux-d'Anjou**: RGM.719025 (2). **Renauleau**: NHMW 2016/0103/1453 (1), LC (2).

Discussion – As far as we are aware, this is only the second mention of this uncommon species in the European Neogene. It was originally described from the Piacenzian upper Pliocene and Pleistocene of Italy, based on three specimens. Only one complete specimen is available to us from Assemblage I. The protoconch is multispiral, composed of 2.5 convex whorls. No microsculpture is preserved and the crenulations at the adapical protoconch suture, considered by Garilli & Galletti (2007) as a generic character, are not seen. However, the surface is somewhat worn and these features may have been abraded. The teleoconch is very similar to that of the holotype. Fine spiral sculpture covers the entire surface. The only difference we see is the slightly deeper anal sinus in the French fossil shell. The stromboid notch, also considered characteristic for the genus, is also more strongly developed in the French shell. In the absence of further comparative material we consider them conspecific. The genus now occurs off West Africa, from French Guinea to Angola (Rolán *et al*., 1998), represented by *Kyllinia marchadi* (Knudsen, 1956). That species differs in having axial sculpture on the first teleoconch whorl. We note that the species from the Lower Pliocene Zanclean Arenas de Huelva Formation of the Guadalquivir Basin, southern Spain identified as *Diaugasma* sp. by Landau *et al*. (2011, p. 35, pl. 18, fig. 6) probably also belongs in *Kyllinia*. A shallow stromboid notch is also present abapically at the edge of the outer lip. It differs from its congeners in being larger, more robust, with the spiral sculpture subobsolete. The specimen is worn, so

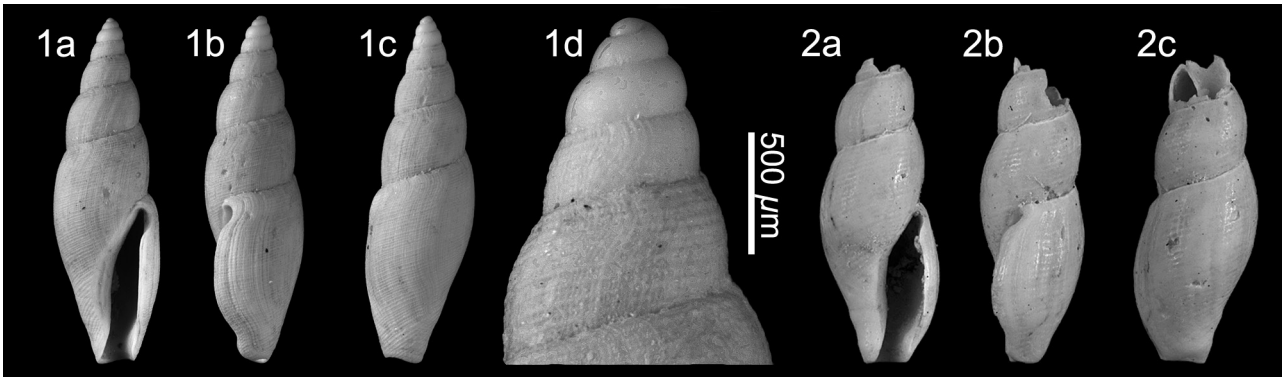

Plate 32. *Kyllinia parentalis* Garilli & Galletti, 2007; 1. NHMW 2016/0103/1453, height 6.5 mm, width 2.0 mm, 1d, detail of protoconch. Renauleau. 2. NHMW 2016/0103/1244, height 2.9 mm, width 1.1 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

the sculpture may have been more prominent, and the protoconch is not preserved.
Kyllinia, therefore, seems to be yet another example of a genus that in the tropical Miocene extended its range to the NW coast of France, but following the cooling that occurred since Miocene times suffered a southward range contraction to the Mediterranean in the Plio-Pleistocene and are now restricted to tropical West Africa.
Kyllinia parentalis is extremely uncommon in Assemblage I, but seems widespread. We record it from St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Scarponi & Della Bella, 2010). Upper Pliocene: central Mediterranean, Italy (Garilli & Galletti, 2007; Scarponi & Della Bella, 2010). Pleistocene (indeterminate), central Mediterranean, Vounargon Formation, Greece (Garilli & Galletti, 2007).

Genus *Mangelia* Risso, 1826

Type species – Mangelia striolata Risso, 1826, by subsequent designation (Gray, 1847b), present-day, Mediterranean.

1826 *Mangelia* Risso, p. 219.

For discussion on the type species, see Spada & Della Bella (2010). For generic synonymy see Ceulemans *et al*. (2018, p. 102).

***Mangelia attenuata* (Montagu, 1803)**
Plate 33, figs 1-2

*1803 *Murex attenuatus* Montagu, p. 266, pl. 9, fig. 6.
1964 *Cythara* (*Mangelia*) *attenuata* Montagu, 1803 – Brébion, p. 577.
2018 *Mangelia attenuata* (Montagu, 1803) – Ceulemans *et al*., p. 103, pl. 3, fig. 2 (*cum syn*.).

Material and dimensions – Maximum height 9.1 mm, width 3.3 mm (incomplete). **St-Clément-de-la-Place**: NHMW 2016/0103/2156 (2). **Sceaux-d'Anjou**: NHMW 2016/0103/2020 (1), NHMW 2016/0103/2043 (1), RGM. 718156 (11), RGM.1352612 (1), RGM.1352616 (1 fragment).

Discussion – Mangelia attenuata (Montagu, 1803) is characterised by its slender elongated shell. The specimens from Assemblage I have seven or eight elevated, opisthocline narrow rounded axial ribs that extend between the sutures and fine spiral cords separated by narrow grooves. The siphonal canal is long and the outer lip is only slightly thickened by a relatively weak labial varix. The multispiral protoconch is very tall, with sinuous axial riblets on the last half whorl. For further discussion see Ceulemans *et al*. (2018, p. 103).
It was suggested to us during the review process that the second specimen figured (Pl. 33, fig. 2) represented Pliocene to present-day Mediterranean *M. tenuicosta* (Brugnone, 1862). Brugnone's species has seldom been figured, but the two illustrations we have found for the lower Pliocene of Italy (Brunetti & Cresti, 2018, p. 92, fig. 376) and present-day coasts of Turkey (Aslan & Ovalis, 2017, p. 4, fig. 2F) both illustrate shells with more convex whorls that are somewhat angular at the shoulder. During the review process it was also suggested that this species should be placed in the genus *Villiersiella* Monterosato, 1890, which is usually regarded as a synonym of *Mangelia* (see Ceulemans *et al*., 2018, p. 102). As far as we are aware, the only recent authors to consider this genus valid were Brunetti & Cresti (2018), who use it in an iconography without discussion. It is not accepted by WoRMS (MolluscaBase, 2019), and we therefore prefer to consider it a synonym until formally reinstated.
Mangelia attenuata (Montagu, 1803) is uncommon in Assemblage I. Brébion (1964, p. 578) recorded it from Assemblage I (Beaulieu), to which we add Sceaux-d'Anjou, Assemblage III (Le Pigeon Blanc, Palluau), and Assemblage IV (Gourbesville).

Distribution – Middle Miocene: Atlantic, Loire Ba-

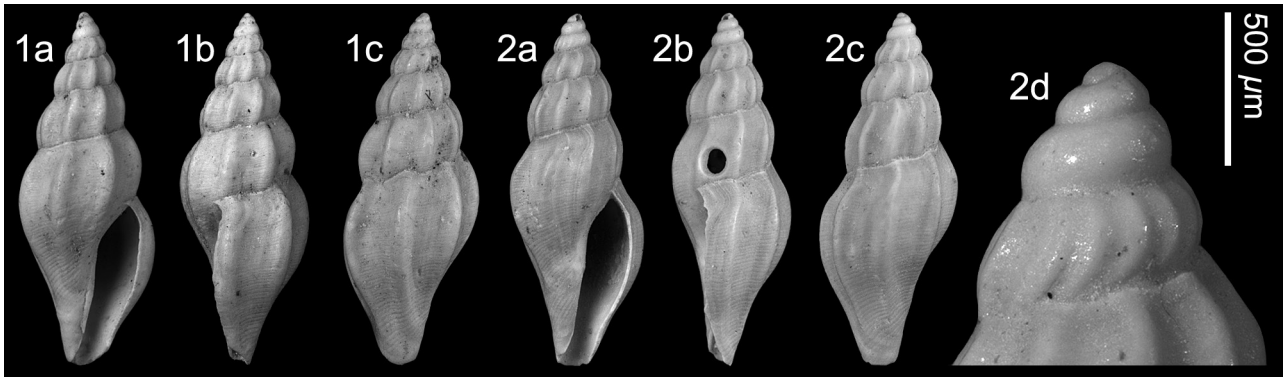

Plate 33. *Mangelia attenuata* (Montagu, 1803); 1. NHMW 2016/0103/2020, height 7.0 mm, width 2.7 mm, 1d, detail of protoconch; 2. RGM.1352612, height 6.2 mm, width 2.3 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

sin (Glibert, 1954). Upper Miocene: Atlantic (Tortonian), NW France (Glibert, 1954; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Glibert, 1954; Brébion, 1964; Ceulemans *et al*., 2018), Guadalquivir Basin, Spain (Landau *et al*., 2011); North Sea Basin, Coralline Crag, England (Harmer, 1915); western Mediterranean, north eastern Spain (Martinell, 1982a); central Mediterranean, Italy (Pavia, 1976; Chirli, 1997). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001); North Sea Basin, Red Crag, England (Harmer, 1915); western Mediterranean, Estepona Basin (Vera Peláez, 2002); central Mediterranean, Italy (Sacco, 1904; Cipolla, 1914; Cavallo & Repetto, 1992). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910). Upper Pleistocene: western Mediterranean, Balearic Islands (Cuerda Barceló, 1987). Pleistocene (indeterminate): Atlantic, Ireland (Harmer, 1915); central Mediterranean, Italy (Malatesta, 1960). Present-day: Mediterranean, north Atlantic Frontage to Norway (Fretter & Graham, 1984).

***Mangelia burgersae* nov. sp.**
Plate 34, figs 1-4

Type material – Holotype NHMW 2016/0103/1937, height 8.0 mm, width 3.1 mm; paratype 1 NHMW 2016/0103/1938, height 7.2 mm, width 2.8 mm; **Renauleau**. Paratype 2 NHMW 2016/0103/1934, height 7.8 mm, width 2.7 mm; paratype 3 NHMW 2016/0103/1935, height 7.9 mm, width 2.8 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 10.0 mm, width 3.3 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1936 (5), RGM.718186 (11), RGM.1352512 (3), RGM.1352668 (1). **Renauleau**: NHMW 2016/0103/1942 (4), LC (2).

Etymology – Named after Hanneke Burgers, collection assistant at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Mangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Mangelia* species of medium size, paucispiral protoconch, teleoconch sculpture of 13-14 flexuous rounded ribs, fine spiral sculpture, weak anal denticle adapically on outer lip.

Description – Shell, slender fusiform. Protoconch paucispiral, composed of 1.5 smooth whorls, with large nucleus. Junction sharply delimited by beginning of adult sculpture. Teleoconch of five whorls with narrow subsutural ramp, roundly angled at high-placed shoulder, weakly convex below. Suture impressed, undulating. Sculpture of 13-15 flexuous rounded axial ribs, roughly equal in width to their interspaces, overrun by narrow spiral threads of secondary and tertiary strength. Last whorl with narrow subsutural ramp, roundly angled at shoulder, broadly convex below, weakly-moderately constricted at base; base and siphonal fasciole not sharply delimited. Aperture elongate; outer lip thickened by narrow varix, with deep U-shaped anal sinus in area of entire subsutural ramp, small tooth developed on inner edge of outer lip at sinus edge. Siphonal canal medium length, open. Columella weakly excavated in upper third. Columellar and parietal callus slightly thickened forming narrow callus rim.

Discussion – *Mangelia burgersae* nov. sp. is very similar to *M. jerbaensis* Della Bella & Spada *in* Chirli, 1997 from the lower Pliocene of Italy (Chirli, 1997; Scarponi & Della Bella, 2010) and still living in the Mediterranean off the coasts of Tunisia (Repetto *et al*., 2005), which also has a paucispiral protoconch of 1.5 smooth whorls with a large nucleus. However, the French species has more numerous axial ribs than stated in the original description [13-15 vs. 9-12 *fide* Della Bella & Spada *in* Chirli (1997, p. 69)]. Another small difference is that the outer lip and the labial denticle delimiting the anal canal abapically are not as thickened in the Assemblage I species as they are in *M. jerbaensis*. Scarponi & Della Bella (2010, p. 36) noted that the Italian fossil specimens had more strongly developed spiral sculpture than the extant specimens. The Assemblage I species, like the Italian

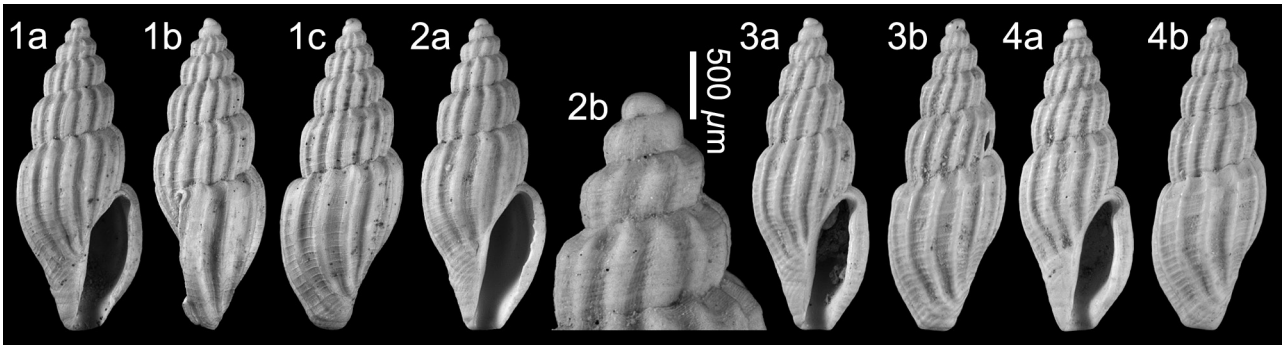

Plate 34. *Mangelia burgersae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1937, height 8.0 mm, width 3.1 mm; 2. **Paratype 1** NHMW 2016/0103/1938, height 7.2 mm, width 2.8 mm, 2b, detail of protoconch. Renauleau. 3. **Paratype 2** NHMW 2016/0103/1934, height 7.8 mm, width 2.7 mm; 4. **Paratype 3** NHMW 2016/0103/1935, height 7.9 mm, width 2.8 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Pliocene form of *M. jerbaensis*, have strongly developed spiral sculpture.
Several Pliocene to extant Mediterranean *Mangelia* species also have a paucispiral protoconch of about 1.5 whorls: *M. striolata* Risso, 1826 has evenly convex whorls with no shoulder developed, and has fewer and broader axial ribs. *Mangelia ovata* Scarponi & Della Bella, 2010 is stockier, broader, with a stronger shoulder and fewer ribs. *Mangelia spadiana* Della Bella *in* Scarponi & Della Bella, 2010 also has fewer and more widely separated ribs and weaker spiral sculpture composed of only a few very widely spaced threads.
We record *M. burgersae* from the Assemblage I localities of Sceaux-d'Anjou and Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (this paper). Lower Pliocene: central Mediterranean, Italy (Chirli, 1997; Scarponi & Della Bella, 2010). Present-day: Mediterranean, Tunisia (Repetto *et al*., 2005).

***Mangelia scabriuscula* (Brugnone, 1862)**
Plate 35, figs 1-2

1862 *Pleurotoma scabriusculum* Brugnone, p. 39, pl. 1, fig. 30.
1904 *Mangilia scabriuscula* (Brugn.) – Sacco, p. 55, pl. 14, figs 18-19.
1910 *Mangilia scabriuscula* Brugn. – Cerulli-Irelli, p. 247, pl. 36, fig. 18.
1914 *Mangilia scabriuscula* Brugnone – Cipolla, p. 138, pl. 13, fig. 6.
?1937 *Mangelia scabriuscula* (Brugn.) – Montanaro, p. 173, pl. 8, figs 10, 11.
1964 *Cythara* (*Mangelia*) *scabriuscula* Brugnone, 1862 – Brébion, p. 583, pl. 14, fig. 13 [*non Mangelia scabriuscula* (Brugnone, 1862)].
1974 *Cytharella scabriuscula* (Brugnone, 1862) – Malatesta, p. 434, pl. 32, fig. 12.
1976 *Cythara* (*Cytharella*) *scabriuscula* (Brugnone) – Pavia, p. 148, pl. 8, figs 6, 7.
1992 *Mangelia scabriuscula* (Brugnone, 1862) – Cavallo & Repetto, p. 142, fig. 390.
2010 *Mangelia scabriuscula* (Brugnone, 1862) – Scarponi & Della Bella, p. 49, figs 133-140).
2018 *Mangelia scabriuscula* (Brugnone, 1862) – Brunetti & Cresti, p. 92, fig. 378.

Material and dimensions – Maximum height 6.1 mm, width 2.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/2010-2012 (3), NHMW 2016/0103/2013 (27), RGM.1352652 (7), RGM.1352676 (10), LC (8), FVD (12). **Sceaux-d'Anjou**: NHMW 2016/0103/2014 (26), RGM.734994 (50+), RGM.1352654 (20), LC (10), FVD (15).

Discussion – We consider these Assemblage I specimens to be conspecific with *Mangelia scabriuscula* (Brugnone, 1862). Some of the specimens are more elongated than those illustrated here (Pl. 35, figs 1, 2). The species is characterised by its sharply angled shouldered whorls, and sculpture of narrow, elevated, sinuous axial ribs and fine spiral sculpture of crowded threads of primary and secondary strength, the primaries separated by 6-9 secondaries. The protoconch is multispiral and typical for the genus. *Mangelia ceddaensis* Della Bella *in* Scarponi & Della Bella 2010 is also closely similar in shape and sculpture, but is smaller (maximum height 4.5 mm). In Assemblage I *M. scabriuscula* is found together with the more abundant *M. turonensis* Peyrot, 1938, but differs in being smaller, less slender, with a more angular shoulder and the primary spiral threads are more strongly developed. *Mangelia scabriuscula* is also similar to the upper Miocene to present-day Mediterranean and adjacent Atlantic *M. unifasciata* (Deshayes, 1835), but that species is larger, the spire is more slender and the shoulder is not as sharp.

Distribution – Upper Miocene: Atlantic (Tortonian): NW France (this paper); ?central Proto-Mediterranean, Italy (Montanaro, 1937). Lower Pliocene: central Mediterranean, Italy (Pavia, 1976; Scarponi & Della Bella, 2010). Upper Pliocene: central Mediterranean, Italy (Brugnone, 1862; Sacco, 1904; Malatesta, 1974; Cavallo & Repetto, 1992; Scarponi & Della Bella, 2010; Brunetti & Cresti, 2018). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1910).

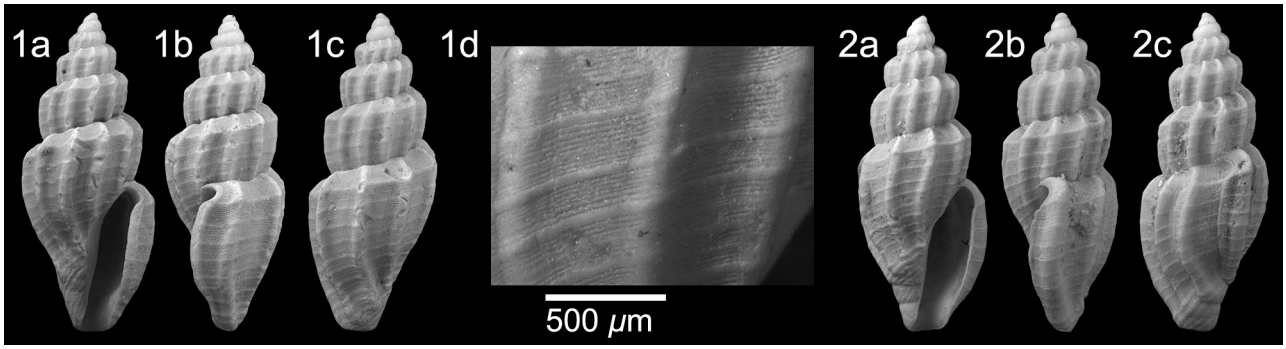

Plate 35. *Mangelia scabriuscula* (Brugnone, 1862); 1. NHMW 2016/0103/2010, height 5.3 mm, width 2.2 mm, 1d, detail of teleoconch sculpture; 2. NHMW 2016/0103/2011, height 5.3 mm, width 2.1 mm, Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

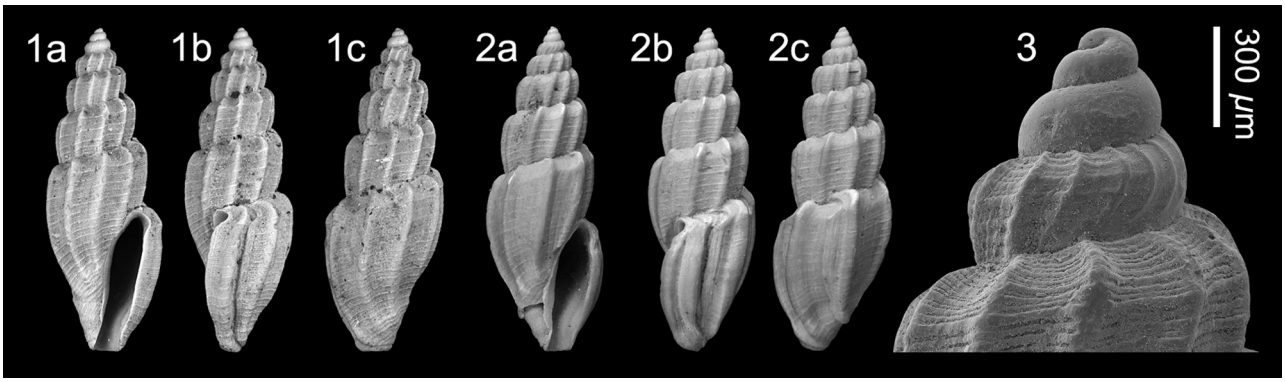

Plate 36. *Mangelia turonensis* Peyrot, 1938; 1. NHMW 2016/0103/1054, height 7.5 mm, width 2.6 mm; 2. NHMW 2016/0103/1055, height 8.2 mm, width 2.8 mm; 3. NHMW 2016/0103/1056, height 5.3 mm, width 2.1 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Mangelia turonensis* Peyrot, 1938**
Plate 36, figs 1-3

1938 *Mangelia turonensis* Peyrot, p. 283, pl. 5, figs 2, 64 (not 51-54 = *Mangelia* (*Clathurella*) *turonensis* Peyrot, p. 292, pl. 5, fig. 51 = *Bela peyroti* Glibert, 1960).
1938 *Mangelia turonensis* var *simplicior* Peyrot, p. 284, pl. 5, figs 10, 16.
1954 *Mangelia turonensis* Peyrot, 1938 – Glibert, p. 50, pl. 6, fig. 10a.
1954 *Mangelia turonensis* forme *decemcostata* Glibert, p. 51, pl. 6, fig. 10b.
1954 *Mangelia turonensis* forme *simplicior* Peyrot, 1938 – Glibert, p. 51, pl. 6, fig. 10b.
1964 *Cythara* (*Mangelia*) *turonensis* Peyrot, 1938 – Brébion, p. 580.

Material and dimensions – Maximum height 8.5 mm, width 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1054-1056 (3), NHMW 2016/0103/1057 (50+), RGM.1352653 (50+), RGM.1352675 (50+), RGM.1352687 (33), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1058 (25), RGM.718159 (50+), RGM.734985 (12), RGM.1352335 (19); RGM.1352513 (50+), LC (12), FVD (14). **Renauleau**: NHMW 2016/0103/1059 (6), LC (7), FVD (4). **Beugnon**: RGM.1352524 (6).

Discussion – *Mangelia turonensis* Peyrot, 1938 is a highly variable species. Peyrot (1938) and Glibert (1954) separated forms based on the number of axial ribs, however, specimens from Assemblage I have anything from 5-11 ribs. Most specimens have 9-10 ribs. The width of the subsutural ramp is also variable, as is the strength of the fine spiral sculpture. The adult size is also highly variable with fully mature specimens with a thickened outer lip measuring from 4.4-8.5 mm in height. The protoconch is typical for the genus; multispiral with axial riblets on the last quarter whorl. This species is very similar to present-day eastern Atlantic *M. costata* (Pennant, 1777), and the protoconch is indistinguishable, but that species is more solid, it constantly has fewer ribs that are more rounded, so that the shoulder is less sharp, and the subsutural platform is broader. In Assemblage I it is most similar to *Mangelia scabriuscula* (Brugnone, 1862), but differs in being larger, more slender, the shoulder is not as sharp and the primary spiral threads are weaker. Due to the great variability seen in *M. turonica*, some of the smaller specimens are not easy to separate from *M. scabriuscula*. *Mangelia burgersae* nov. sp., with which it co-occurs has a similar teleoconch, but is separated by its paucispiral protoconch.
Brébion (1964, p. 581) recorded *M. turonensis* from the Assemblage I localities of Renauleau, Sceaux-d'Anjou, St-Clément-de-la-Place, Thorigné and St-Michel, to which we add Beugnon.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Peyrot, 1938; Glibert, 1954). Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Glibert, 1954; Brébion, 1964).

Family Raphitomidae Bellardi, 1875
Genus *Andonia* Harris & Burrows, 1891

Type species – *Fusus bonellii* Bellardi & Michelotti, 1840, by typification of replacement name, Pliocene, Italy.

1873 *Genea* Bellardi, p. 205. Type species (by monotypy): *Fusus bonellii* Bellardi & Michelotti, 1840, Pliocene, Italy. Junior homonym of *Genea* Rondani, 1850 [Diptera].
1891 *Andonia* Harris & Burrows, p. 112. *Nom. nov. pro Genea* Bellardi, 1873, *non* Rondani, 1850 [Diptera].

***Andonia* cf. *bonellii* (Bellardi & Michelotti, 1840)**
Plate 37, figs 1-3

cf. *1840 *Fusus Bonellii* Bellardi & Michelotti, p. 20, pl. 2, fig. 5.

cf. 1976 *Parvisipho* (*Andonia*) *bonellii* (Bellardi & Michelotti, 1840) – Pavia, p. 141, pl. 6, figs 11, 12, 14, 16.
cf. 1981 *Parvisipho* (*Andonia*) *bonellii* (Bellardi & Michelotti) – Moroni & Ruggieri, p. 99, fig. 1.
cf. 2002 *Andonia bonellii* (Bellardi & Michelotti, 1840) – Vera-Peláez, p. 237, pl. 8, figs N, Ñ, pl. 16, L, M.

Material and dimensions – Maximum height 5.8 mm, width 1.8 mm (incomplete). **Sceaux-d'Anjou**: NHMW 2016/0103/1994-1995 (2), NHMW 2016/0103/2033 (1), RGM.718192 (2 fragments).

Discussion – As discussed by Moroni & Ruggieri (1981, p. 105) and Landau *et al*. (2013, p. 274) there are probably several species of *Andonia* Harris & Burrows, 1891 in the European Neogene that have not been described formally. We add to this the shell illustrated by Chirli (1997, pl. 10, figs 11, 12) as *Andonia bonellii* (Bellardi & Michelotti, 1840) that seems to have a non-planktotrophic type protoconch of about two whorls with a large first whorl, and is therefore not that species, which has a multispiral protoconch of a typically planktotrophic type (Vera-Peláez, 2002, pl. 16, L, M).
The material from Assemblage I is all from Sceaux-d'Anjou and all specimens are incomplete, missing their protoconch. *Andonia bonellii* shows important changes in whorl shape and sculpture with ontogeny and in large adult specimens the axial sculpture becomes obsolete on the last two whorls. Therefore specimens in a similar stage of growth must be compared. Based on material from the lower Upper Pliocene of the Estepona Basin, S. Spain, the French specimens are slightly less slender, they have fewer spiral cords on the subsutural ramp and there is no secondary spiral sculpture, which in the Estepona specimens is present between the mid-whorl primary spirals in most, but not all, specimens. Having said this, the number and disposition of the primary and secondary spirals and the extent and strength of the axial ribs is highly variable within the Estepona populations. Therefore, based on the scant material available, we cannot identify these specimens with certainty.

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

***Andonia delgadoi* nov. sp.**
Plate 38, figs 1-5

Type material – Holotype NHMW 2016/0103/0990, height 4.8 mm, width 1.9 mm; paratype 1 NHMW 2016/0103/1234, height 5.3 mm, width 1.7 mm; paratype 2 NHMW 2016/0103/1242, height 4.9 mm, width 2.1 mm, **St-Clément-de-la-Place**. Paratype 3 NHMW 2016/0103/1790, height 5.3 mm, width 1.8 mm; paratype 4 NHMW 2016/0103/1988, height 6.0 mm, width 2.1 mm; paratype 5 RGM.1352607, height 5.2 mm, width 1.8 mm, **Sceaux-d'Anjou**.

Other material – **St-Clément-de-la-Place**: LC (1). **Sceaux-d'Anjou**: RGM.718191 (6 juveniles).

Etymology – Named after Joaquim Filipe Nery da Encarnação Delgado ('Nery Delgado') (1835-1908), geologist in the Serviços Geológicos de Portugal, and pioneer in Portuguese trilobite palaeontology. *Andonia* gender feminine.

Diagnosis – *Andonia* species of small size, fusiform, solid, paucispiral protoconch of two whorls with spiral microsculpture, teleoconch with convex whorls, shoulder not developed, axials weak or absent, narrow equal spirals predominant, outer lip smooth within.

Description – Shell small, fusiform, solid. Protoconch paucispiral, tall dome-shaped, composed of two convex whorls, bearing fine, close-set spiral sculpture. Junction with teleoconch delimited by beginning of adult sculpture. Teleoconch of 3.5-4 tall convex whorls, separated by impressed suture. Narrow, slightly concave, subsutural area, bearing close-set comma-shaped riblets, ramp and shoulder not developed. Axial sculpture weak or entirely absent, when present consisting of nine low, broad, rounded ribs most strongly developed mid-whorl. Spiral sculpture of narrow equal cords overrun

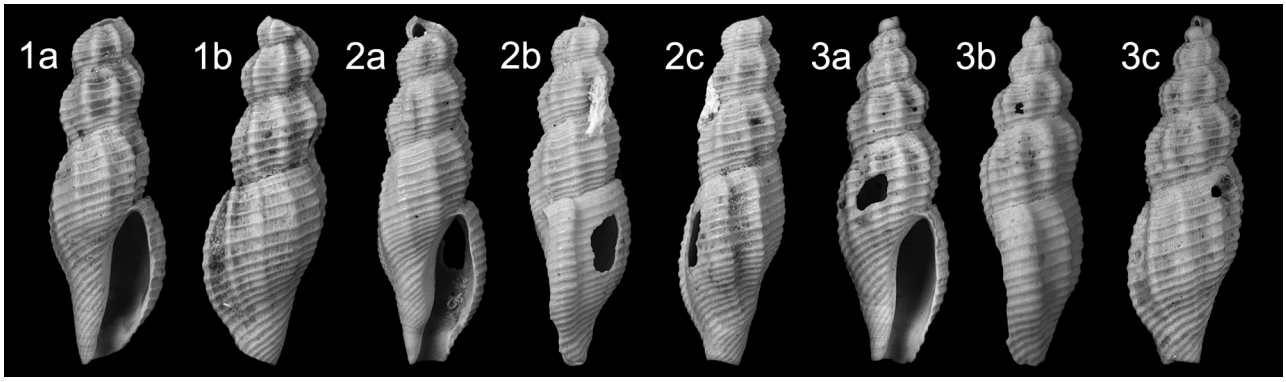

Plate 37. *Andonia* cf. *bonellii* (Bellardi & Michelotti, 1840); 1. NHMW 2016/0103/1994, height 5.2 mm, width 1.8 mm; 2. NHMW 2016/0103/1995, height 5.8 mm, width 1.8 mm; 3. NHMW 2016/0103/2033, height 5.3 mm, width 1.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

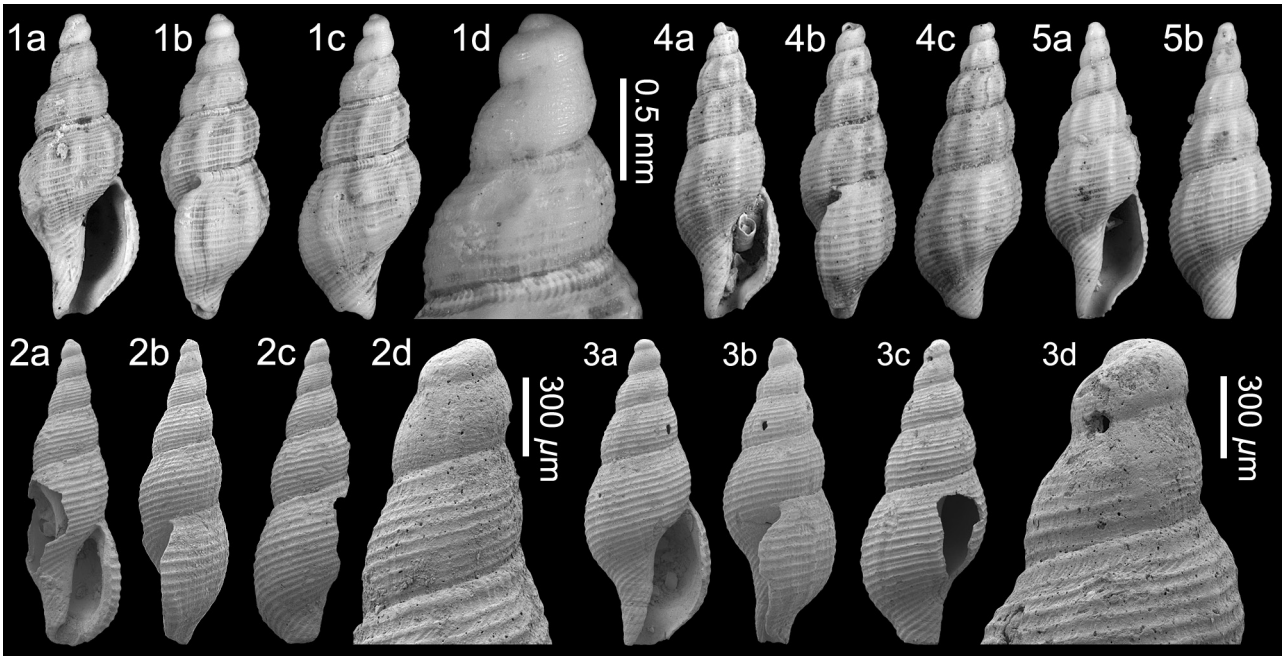

Plate 38. *Andonia delgadoi* nov. sp.; 1. **Holotype** NHMW 2016/0103/0990, height 4.8 mm, width 1.9 mm, 1d, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1234, height 5.3 mm, width 1.7 mm, 1d, detail of protoconch; 3. **Paratype 2** NHMW 2016/0103/1242, height 4.9 mm, width 2.1 mm, 2d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place. 4. **Paratype 3** NHMW 2016/0103/1790, height 5.3 mm, width 1.8 mm; 5. **Paratype 4** NHMW 2016/0103/1988, height 6.0 mm, width 2.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ribs. Fine, close-set axial growth lines give interspaces finely reticulate appearance. Last whorl weakly to moderately inflated, subsutural portion narrow, slightly concave, convex below, moderately constricted at base; axials, if present, do not continue over base, about 26 spirals on last whorl and siphonal fasciole, spiral immediately below suture somewhat thickened forming narrow subsutural collar. Aperture ovate; outer lip moderately thickened, smooth within; anal sinus relatively deep U-shaped; siphonal canal short to medium length, twisted, open. Columella moderately excavated in upper third. Columellar callus poorly developed, forming narrow edge; parietal callus not thickened. Siphonal fasciole indistinct.

Discussion – We have placed this species in the genus *Andonia* although this would be the first record of a paucispiral *Andonia* species. The teleoconch sculpture is not unlike that of *A. bonellii* (Bellardi & Michelotti, 1840) and *A. transsylvanica* (Hoernes & Auinger, 1890) although the shell shape is less slender than either of these two species and the axial sculpture weaker. *Andonia delgadoi* nov. sp. is somewhat variable in teleoconch characters, some specimens broader than others, but mosts importantly the development of ribs is variable; some specimens have broad weak ribs developed mid-whorl (Pl. 38, figs 1, 4), whereas others lack ribs (Pl. 38, figs 2, 3). We are confident they represent extremes of a single species as the protoconch in all these forms is identical (Pl. 38, figs 1c, 2d, 3d). Bałuk (2003) illustrated a shell under the name of *Philbertia raynevali* (Bellardi, 1877) that is similar to the axially costate specimens illustrated here (Pl. 38, figs 1, 4), but the protoconch is tall and multispiral.

Andonia delgadoi is recorded from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou, but is extremely uncommon at both.

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

Genus *Buccinaria* Kittl, 1887

Type species – *Fusus hoheneggeri* Kittl [ex M. Hörnes, MS], 1887, by subsequent designation, Cossmann, 1901, Miocene, Austria.

1887 *Buccinaria* Kittl, p. 250.

1931 *Ootoma* Koperberg, 1931, type species (by original designation): *Ootoma jonkeri* Koperberg, 1931, Miocene, Indonesia. Not available: no type species designation. Junior homonym of *Ootoma* Dejean, 1833 [Coleoptera].

1933 *Ootomella* Bartsch, 1933. *Nom. nov. pro Ootoma* Koperberg, 1931, *non* Dejean, 1833 [Coleoptera].

1952 *Pionotoma* Kuroda, p. 66, type species (by original designation): *Pionotoma pyrum* Kuroda, 1952, present-day, Japan.

***Buccinaria minuscula* nov. sp.**
Plate 39, figs 1-3

Type material – Holotype NHMW 2016/0103/2034, height 6.2 mm, width 3.2 mm; paratype 1 NHMW 2016/0103/2035, height 5.4 mm, width 2.6 mm; paratype 2 NHMW 2016/0103/2036, height 2.8 mm (juvenile); paratype 3 RGM.1352644, height 6.3 mm, width 3.2 mm; paratype 4 RGM.1352645, height 5.3 mm, width 2.7 mm.

Other material – Maximum height 6.3 mm, width 3.2 mm. **Sceaux-d'Anjou**: RGM.718195 (8).

Etymology – Latin '*minusculus, -a, -um*' adjective meaning less important, minor, smaller, refecting small size for genus. *Buccinaria* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Buccinaria* species of small size, stocky biconic shell, protoconch of two whorls, teleoconch of four shouldered whorls with axially dominant reticulate sculpture, last whorl inflated, cords somewhat nodular over ribs mid-whorl.

Description – Shell small, biconic-fusiform. Protoconch of two convex whorls (surface abraded). Teleoconch of four shouldered whorls with slightly concave subsutural ramp, convex below shoulder, separated by impressed, weakly undulating suture. Sculpture predominantly axial, composed of 11 rounded weakly prosocline ribs most strongly developed below shoulder, slightly narrower than interspaces, crossed by cords roughly equal in width to their interspaces, two on subsutural ramp, three below shoulder on first and second whorls, four on penultimate whorl, cords slightly swollen over ribs. Last whorl 70% total height, broad, narrow concave subsutural ramp, shoulder placed high, roundly angled, convex below, weakly constricted at base, axials broaden mid-whorl, weaken and disappear over base, cords somewhat nodular over ribs mid-whorl. Aperture 48% total height, relatively broad, outer lip simple, smooth within, anal canal not developed, siphonal canal short, broad, open, weakly recurved. Columella excavated in upper third, straight below, smooth. Columella callus forming narrow callus rim, thickened abapically; parietal callus not developed.

Discussion – Although represented by scant and somewhat worn specimens, this species warrants description as it is the only representative of the genus in Assemblage I. We provisionally ascribe it to *Buccinaria* Kittl, 1887 based on the broadly biconic shell shape, shouldered whorls, somewhat nodular periphery and short, open siphonal canal, although it is smaller than most of its congeners. Powell (1966, p. 133) described the protoconch as consisting of 2-2.5 whorls, with a sharp apex and diagonally reticulate sculpture. Unfortunately the surface is abraded in all the French specimens available. All extant species ascribed to this species are from Indonesia and Japan, however, the type species is from the middle Miocene Paratethys: *B. hoheneggeri* (Kittl, 1887). That species differs from the *Buccinaria minuscula* nov. sp. in having finer axial ribs that become subobsolete on the last whorl, more numerous spiral cords, a more strongly defined subsutural collar and a more strongly inflated last whorl. *Buccinaria orlaviensis* (Kittl, 1887), also from the Paratethys seems similar to the type species, but with stronger axial sculpture that persists onto the last whorl.

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

Genus *Clathromangelia* Monterosato, 1884

Type species – *Pleurotoma granum* Philippi, 1844, by monotypy, present-day, Mediterranean.

1884 *Clathromangelia* Monterosato, p. 131.

For generic synonymy see Ceulemans *et al*. (2018, p. 106).

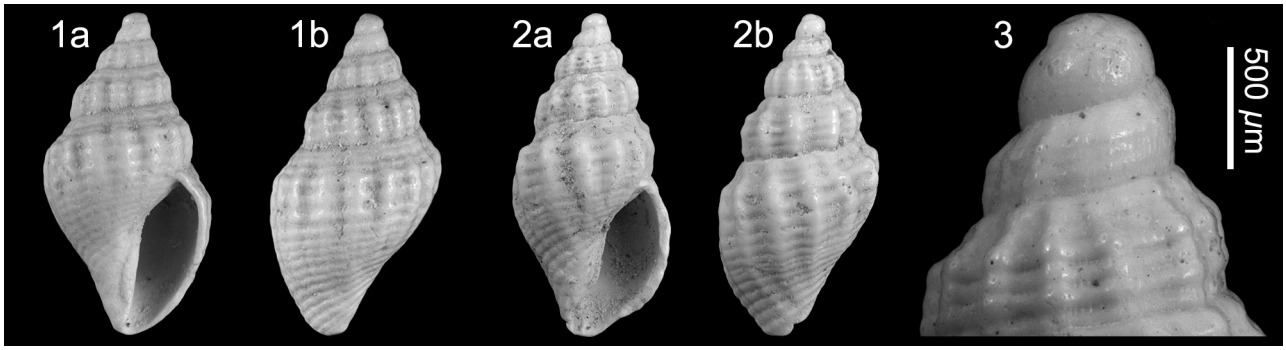

Plate 39. *Buccinaria minuscula* nov. sp.; 1. **Holotype** NHMW 2016/0103/2034, height 6.2 mm, width 3.2 mm; 2. **Paratype 1** NHMW 2016/0103/2035, height 5.4 mm, width 2.6 mm; 3. **Paratype 2** paratype 2 NHMW 2016/0103/2036, height 2.8 mm (juvenile), detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Note – Oliverio (1995) placed the genus in the Daphnellinae Casey, 1904 (= Raphitomidae Bellardi, 1875) rather than the traditional placement in the Mangeliidae/Mangeliinae Fischer, 1883b (i.e. Glibert, 1954; Powell, 1966). Certainly the protoconchs of the species here placed in *Clathromangelia* are similar to those placed in *Raphitoma*. Bouchet *et al.* (2011) suggested placement in the Clathurellidae H. & A. Adams, 1858, but no *Clathromangelia* species were included in their molecular work. Its placement in the Raphitomidae was confirmed based on molecular data by Fassio *et al*. (2019). The genus is extremely speciose in Assemblage I, where it is represented by ten species, showing enormous diversity in protoconch and teleoconch shape and sculpture.

***Clathromangelia daisyae* nov. sp.**
Plate 40, figs 1-3

Type material – Holotype NHMW 2016/0103/1918, height 5.4 mm, width 2.4 mm; paratype 1 NHMW 2016/0103/1919, height 5.7 mm, width 2.6 mm; paratype 2 NHMW 2016/0103/1920, height 6.2 mm, width 2.9 mm.

Other material – Maximum height 6.2 mm, width 2.9 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1758 (2). **Renauleau**: NHMW 2016/0103/1921 (9), LC (3), FVD (7).

Etymology – Named after Daisy Louise Landau, daughter of the first author. *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, scalate spire, paucispiral protoconch of two whorls, with reticulate microsculpture, teleoconch with narrow ramp, bearing 13-15 axial ribs and raised cords, no secondary spirals developed, six labial denticles, D1 strongest developed to variable degree, deep, narrow anal sinus moderately short siphonal canal.

Description – Shell small, subpupoid, robust, weakly scalate spire. Protoconch paucispiral, composed of two convex whorls, bearing axial ribs and spiral cords forming fine reticulated microsculpture. Junction with teleoconch sharply delimited. Teleoconch of 4.5 whorls with narrow subsutural ramp, broadly angular shoulder placed high, convex below, separated by superficial undulating suture. Axial sculpture of elevated, rounded, orthocline ribs, 13-15 on last whorl, equal in width to their interspaces. Spiral sculpture of narrow cords, two on first whorl, three on second, four on fourth whorl, overrun ribs forming rectangular cancellation with axial element strongly dominant, slightly beaded at intersections; no secondary spiral sculpture developed. Last whorl moderately inflated, subsutural ramp narrow, shoulder rounded, evenly convex below, moderately to strongly constricted at base; axials continue over base, 6-7 spirals on last whorl plus further three over siphonal fasciole. Aperture ovate; outer lip thick, convex in profile, bearing up to five tubercular denticles within, D1 strongest; lower denticles not developed in some specimens; anal sinus narrow, deep, symetrically U-shaped, with apex mid-subsutural ramp, delimited laterally by D1 within outer lip; siphonal canal moderately short, twisted, open. Columella excavated in upper third. Columellar callus poorly developed, forming narrow indented edge. Siphonal fasciole not sharply delimited.

Discussion – *Clathromangelia daisyae* nov. sp. is characterised by its small size, strong reticulate sculpture, the axial element predominant and tubercular labial dentition that is not always strongly developed, but D1 is usually present and dominant, with a protoconch of about two whorls suggesting non-planktotrophic development. An-

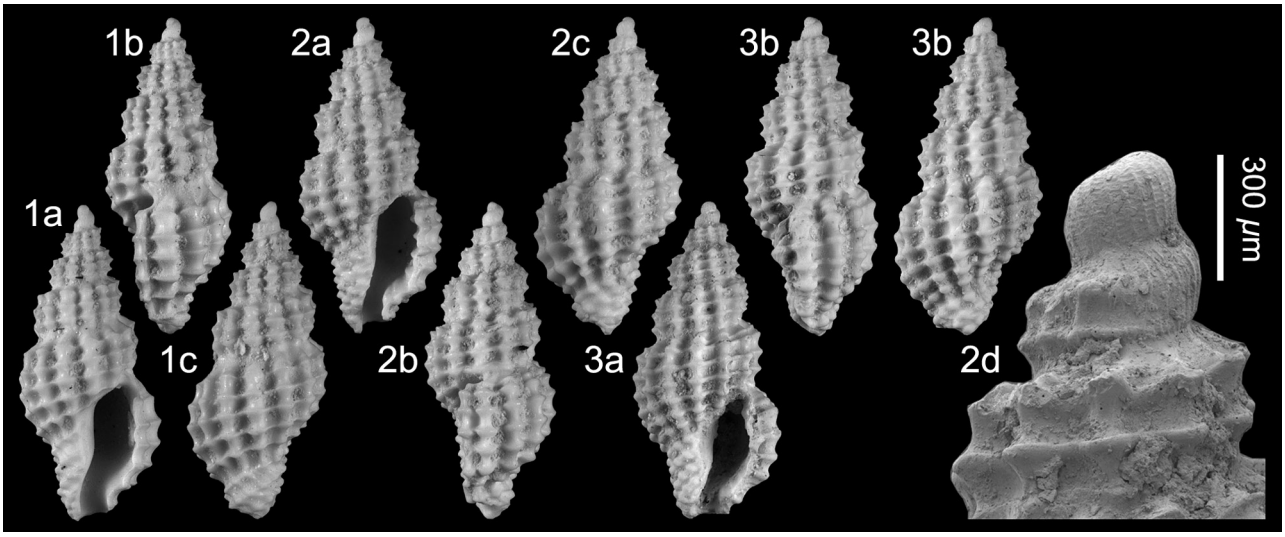

Plate 40. *Clathromangelia daisyae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1918, height 5.4 mm, width 2.4 mm; 2. **Paratype 1** NHMW 2016/0103/1919, height 5.7 mm, width 2.6 mm, 2d, detail of protoconch (SEM image); 3. **Paratype 2** NHMW 2016/0103/1920, height 6.2 mm, width 2.9 mm. Renauleau, NW France, Tortonian, upper Miocene.

other similar species, but without labial denticles, is *C. helwerdae* nov. sp., but it differs in having a well-defined subsutural ramp that is concave and smooth, and fewer, broader axial ribs. Bałuk (2003, pl. 29, figs 5-8) illustrated a two similar species from the middle Miocene of Poland; *Philbertia adelgundae* (Boettger, 1906) and *Peratotoma hildae* Boettger, 1902. Although incomplete in Bałuk's material, both of these species seem to have a multispiral protoconch.
Clathromangelia daisyae has only been at Renauleau and Sceaux-d'Anjou.

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

***Clathromangelia densecostata* nov. sp.**
Plate 41, figs 1-4

Type material – Holotype MNHN.F.A57920, height 6.3 mm, width 2.8 mm; paratype 1 MNHN.F.A57921, height 5.4 mm, width 2.4 mm; paratype 2 NHMW 2016/0103/0956, height 5.5 mm, width 2.5 mm; paratype 5 RGM.1352490, height 5.7 mm, width 2.5 mm; ; paratype 6 RGM.1352611, height 5.6 mm, width 2.3 mm, **Sceaux-d'Anjou**. Paratype 3 NHMW 2016/0103/0957, height 4.4 mm, width 2.1 mm; paratype 4 NHMW 2016/0103/0958 (juvenile), **St-Clément-de-la-Place**.

Other material – Maximum height 5.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0901 (14), RGM.1352314 (2), LC (5), FVD (6). **Sceaux-d'Anjou**: NHMW 2016/0103/0959 (13), RGM.718165 (22), LC (1), FVD (3).

Etymology – Name reflecting the relatively dense sculpture of ribs and cords for the genus. *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Clathromangelia species of small size, paucispiral protoconch with carinate last half whorl, convex teleoconch whorls bearing dense sculpture of ribs and cords, deep pits in interspaces, relatively wide aperture.

Description – Shell small, fusiform. Protoconch paucispiral, composed of 1.5 whorls; postnuclear whorl bears strong carina apically, forming a crater-like depression, in which lie the nucleus and adapical portion of the postnuclear whorl, second broader carina placed mid-whorl, third develops above suture on last quarter whorl. Junction with teleoconch sharply delimited. Teleoconch of three convex whorls with moderately wide subsutural ramp, convex below. Suture superficial. Sculpture of three raised primary cords and 14 orthocline axial ribs, forming regular reticulate pattern with small tubercles formed at intersections, deep pits in interspaces. Last whorl 69% total height, regularly convex, strongly constricted at base, with four primary spirals; abapical spiral delimiting slightly concave base, 3-4 further spirals over base and siphonal fasciole. Aperture 46% total height, ovate, relatively wide, with edge crenulated by spirals, smooth within; anal sinus very shallow U-shaped; siphonal canal wide, open, moderate length. Columella

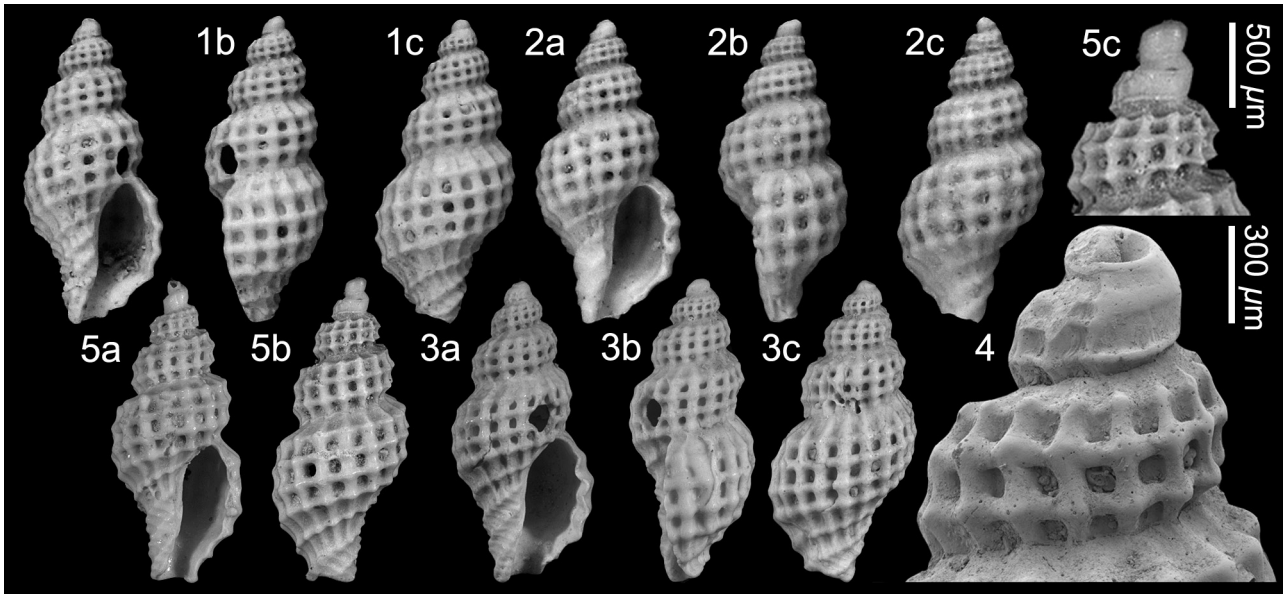

Plate 41. *Clathromangelia densecostata* nov. sp.; 1. **Holotype** MNHN.F.A57920, height 6.3 mm, width 2.8 mm; 2. **Paratype 1** MNHN.F.A57921, height 5.4 mm, width 2.4 mm. La Presselière, Sceaux-d'Anjou. 3. **Paratype 3** NHMW 2016/0103/0957, height 4.4 mm, width 2.1 mm; 4. **Paratype 4** NHMW 2016/0103/0958, detail of protoconch (juvenile; SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene. *Clathromangelia* aff. *densecostata* nov. sp.; 5. NHMW 2016/0103/1901, height 6.6 mm, width 3.1 mm, 5c, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

weakly excavated in upper third. Columellar callus not thickened, forming smooth, narrow indented rim edging medial side of aperture.

Discussion – As discussed by Oliverio (1995) and Ceulemans *et al*. (2018) the genus *Clathromangelia* in the European Neogene is more speciose than previously thought, and the Assemblage I fauna is a perfect example containing several species endemic to the Mio-Pliocene of northwestern France. *Clathromangelia densecostata* nov. sp. differs from all its congeners in having dense reticulate sculpture, in which the axials and spirals are of equal strength, with deep pits in the interspaces. Powell (1966, p. 100) described paucispiral protoconch as a generic character, however some species have multispiral planktotrophic type protoconchs (Oliverio, 1995). Having said this, all the Assemblage I *Clathromangelia* species have protoconchs of a non-planktotrophic type. The protoconch in *C. densecostata*, with its deep crater-like pit placed apically and the nucleus lying within the crater is quite unlike any we have seen before in European turrids. Two specimens have the protoconch well preserved, several others show the same type of protoconch, but abraded. A single specimen has a different type of paucispiral protoconch and is discussed below (see *Clathromangelia* aff. *densecostata* nov. sp.). We record *C. densecostata* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Clathromangelia* aff. *densecostata* nov. sp.**
Plate 41, fig. 5

Material and dimensions – Height 6.6 mm, width 3.1 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1901 (1).

Discussion – One specimen from Sceaux-d'Anjou has a teleoconch that is almost indistinguishable from that of *Clathromangelia densecostata* nov. sp., but differs in the character of its paucispiral protoconch (Pl. 41, fig. 5c). The protoconch is incomplete and the nucleus is missing, but the 1.5 rather disjunct postnuclear whorls preserved are much taller than in *C. densecostata*, there is a suggestion of axially-elongated shoulder nodes and two sharp carinae on the last quarter whorl; one delimiting the shoulder, the lower between mid-whorl and suture. Intraspecific differences in the shape of paucispiral protoconchs has been observed several occasions by us (BL) whilst working with these highly endemic Assemblage I faunas in which most of the protoconchs are non-planktotrophic, but this example is quite extreme and we do not believe that it represents the same species. One possible further difference is that the shoulder on the teleoconch whorls seems to be placed higher and is sharper than in *C. densecostata*. We await further material to clarify the relationship between these two forms.

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

***Clathromangelia fenestrata* (Millet, 1865)**
Plate 42, figs 1-5

1854	*Defrancia Fenestrata* Millet, p. 161 (*nomen nudum*).
*1865	*Defrancia fenestrata* Millet, p. 589.
1964	*Clathromangelia quadrillum* var. *fenestrata* Millet, 1854 [sic] – Brébion, p. 594, pl. 14, fig. 25.
2018	*Clathromangelia fenestrata* (Millet, 1865) – Ceulemans *et al*., p. 106, pl. 3, figs 10-12.

Type material – Cotypes: Sceaux-d'Anjou; musée d'Angers (*fide* Brébion, 1964, p. 595).

Material and dimensions – Maximum height 8.2 mm, width 3.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0960-0961 (2), NHMW 2016/0103/0962 (50+), RGM.1352663 (20), RGM.1352681 (33), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0964 (50+), RGM.718163 (50+), RGM.719024 (3 juveniles), RGM.1352483 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0963 (50+), NHMW 2016/0103/1902-1904 (3), RGM.1349002 (50+), RGM.1352315 (24), LC (50+), FVD (50+). **Beugnon**: RGM.1349150 (8).

Discussion – *Clathromangelia fenestrata* (Millet, 1865) is characterised by its multispiral protoconch composed of 2.5 tall whorls with a micropustular first whorl and large elongated tubercles on subsequent protoconch whorls placed mid-whorl on an elevated carina. Teleoconch whorls bear a regularly reticulated surface sculpture consisting of two spiral cords and 10-12 axial ribs on spire whorls and four cords on the last whorl, with 3-4 further cords on the siphonal canal, but not over the base. There is some variability between specimens with and between the populations in Assemblage I. The specimen illustrated here from St-Clément-de-la-Place (Pl. 42, figs 1, 2) we consider the typical form. At Renauleau, together with the typical form, some specimens are somewhat smaller and notably more elongate (Pl. 42, figs 3, 4) and others smaller with a more angular shoulder (Pl. 42, fig. 5). We have taken SEM images of various specimens from different localities representing these different teleoconch morphotypes and the protoconch is basically similar, although there is some variability in the strength of the nodes developed mid whorl (Pl. 42, figs 2a vs. 3d). Despite the differences in teleoconch shape, the number, strength and disposition of the sculptural elements is the same. We therefore consider this one variable species, although we do not exclude the possibility that they represent a species complex. For further discussion and comparison see Ceulemans *et al*. (2018, p. 106).

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

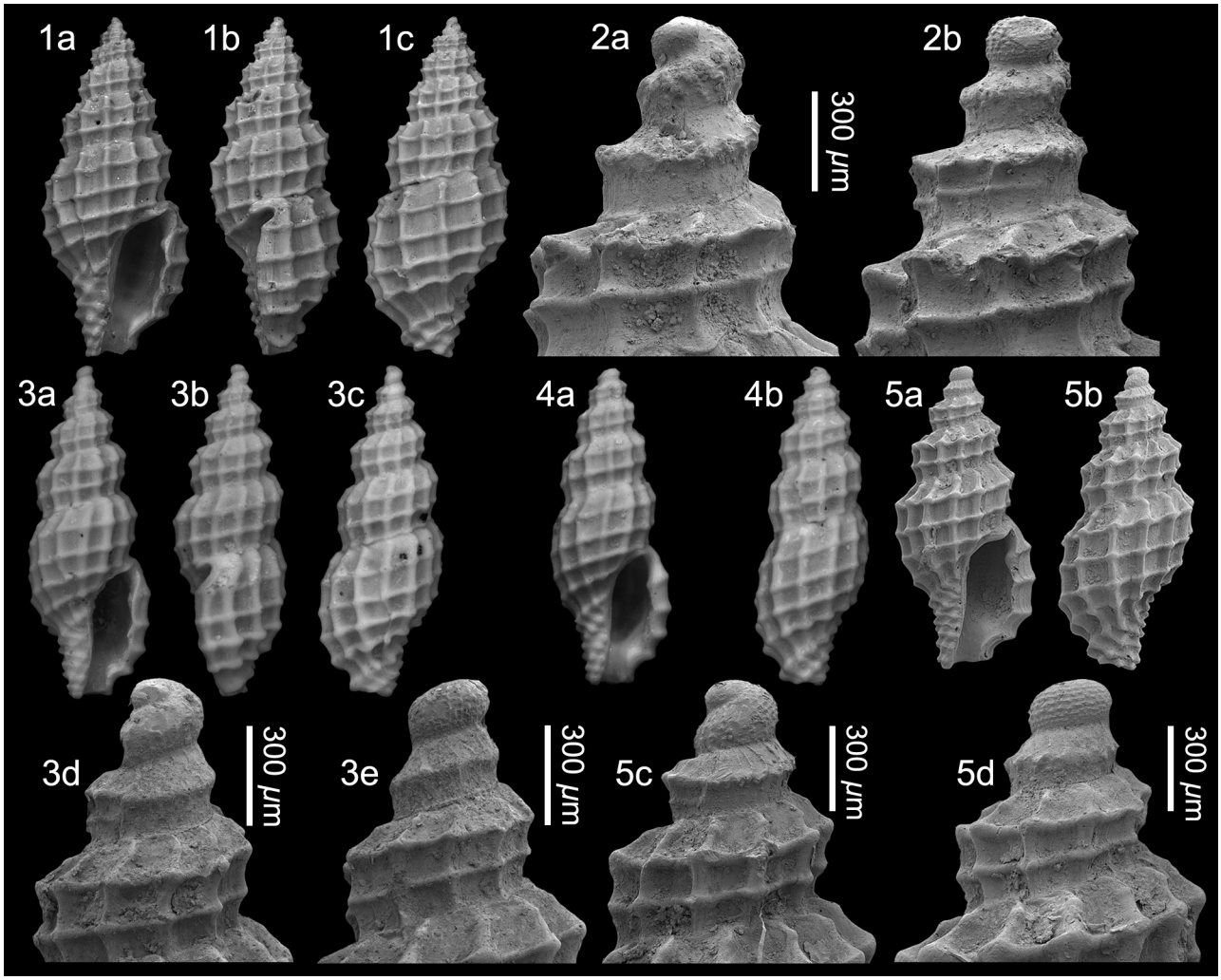

Plate 42. *Clathromangelia fenestrata* (Millet, 1865); 1. NHMW 2016/0103/0960, height 7.6 mm, width 3.5 mm; 2. NHMW 2016/0103/0961 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/1903, height 5.1 mm, width 1.8 mm, 3d, e, detail of protoconch (SEM image); 4. NHMW 2016/0103/1904, height 5.0 mm, width 1.8 mm, 5. NHMW 2016/0103/1902, height 4.4 mm, width 2.0 mm, 5c, d, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

et al., 2018). Upper Pliocene-Pleistocene: NW France (Brébion, 1964).

***Clathromangelia hakkennesi* nov. sp.**
Plate 43, figs 1-2

Type material – Holotype NHMW 2016/0103/1225, height 7.1 mm, width 2.8 mm; paratype 1 NHMW 2016/0103/1906, height 7.9 mm, 2.9 mm, **St-Clément-de-la-Place**. Paratype 2 RGM.1352327, height 6.5 mm, width 2.5 mm; paratype 3 RGM.1352605, height 3.9 mm (subadult); paratype 4 NHMW 2016/0103/1993, 6.8 mm, width 3.1 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 7.1 mm, width 2.8 mm. **St-Clément-de-la-Place**: RGM.1352417 (1 juvenile), LC (3). **Sceaux-d'Anjou**: RGM.1352328 (2), RGM.734995 (5 juveniles).

Etymology – Named after Frits Hakkennes, volunteer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, fusiform, solid, paucispiral protoconch of two whorls, subquadrate post-nuclear whorl, two carinae last half whorl, teleoconch with regularly convex whorls, bearing subquadrate reticulate sculpture, 13-15 raised axial ribs, five narrow spirals on intermediate whorls, anal sinus shallow, siphonal fasciole distinct.

Description – Shell small, fusiform, solid. Protoconch paucispiral, composed of two whorls, no microsculp-

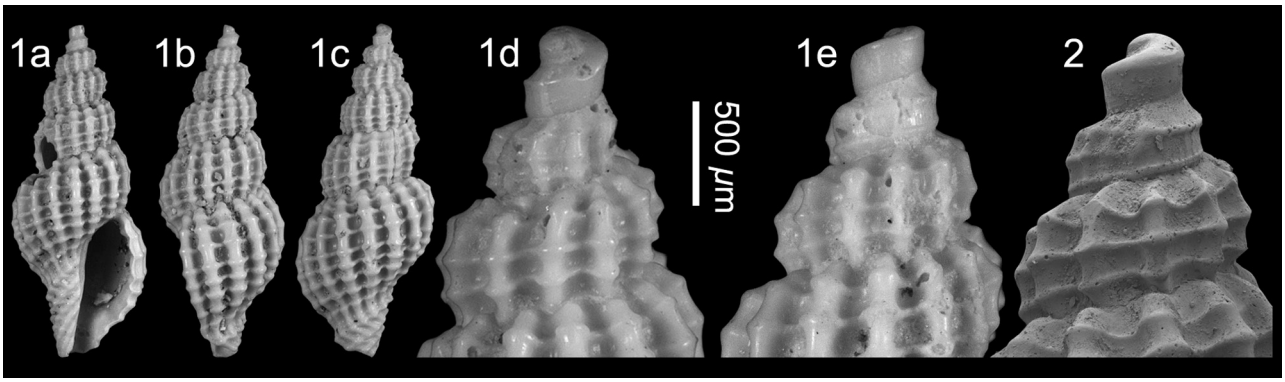

Plate 43. *Clathromangelia hakkennesi* nov. sp.; 1. **Holotype** NHMW 2016/0103/1221, height 7.1 mm, width 2.8 mm, 1d, e, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1906, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ture present, post-nuclear whorl subquadrate in profile, straight sided, developing two raised carinae on last half whorl; adapical carina placed at shoulder, abapical one just above suture. Junction with teleoconch sharply delimited. Teleoconch of five regularly convex whorls, subsutural ramp and shoulder hardly developed, separated by impressed, undulating suture. Axial sculpture of close-set, opisthocline raised rounded ribs, 13-15 on last whorl, half the width of interspaces. Spiral sculpture of narrow cords overrun ribs forming subquadrate cancellation, small tubercles developed at intersections. Three cords on first teleoconch whorl; adapical and abapical cords develop from protoconch carinae; mid-whorl third primary develops immediately equal in strength to other spirals. Number of spirals increases abapically, five on penultimate whorl. Surface smooth, without microsculpture. Last whorl moderately inflated, evenly convex, strongly constricted at base; axials continue over base, eight spirals on last whorl, further five on siphonal fasciole. Aperture ovate; outer lip weakly thickened, weakly denticulate within; anal sinus small, shallow U-shaped, delimited laterally by poorly developed, subobsoletely bifid labial tooth; siphonal canal medium to long, slightly twisted, open. Columella moderately excavated in upper third. Columellar callus poorly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – We are uncertain of the correct systematic position of this species, but we have placed it provisionally in *Clathromangelia* Monterosato, 1884, although the teleoconch shape and sculpture are reminiscent of some Assemblage I *Raphitoma* species. The paucispiral protoconch with its subquadrate profile and lack of any microsculpture we have not encountered in European or West African *Clathromangelia* or *Raphitoma* species. The teleoconch is characterised by its subquadrate reticulate sculpture in which the axials are strongly raised and rounded. *Clathromangelia densecostata* nov. sp. from Assemblage I differs in having dense regular reticulate sculpture in which the axials and spirals are of similar strength, with deep, narrow pits in the interspaces. In *Clathromangelia hakkennesi* nov. sp. the axials are strongly predominant. *Clathromangelia pereirae* nov. sp., also from Assemblage I, is smaller, with fewer axial ribs and spiral cords and a different protoconch (compare Pl. 46, fig. 4).

We record *C. hakkennesi* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou, but it is very uncommon at both localities.

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

***Clathromangelia helwerdae* nov. sp.**
Plate 44, figs 1-3

Type material – Holotype MNHN.F.A57926, height 6.2 mm, width 2.9 mm; paratype 1 MNHN.F.A57927, height 5.7 mm, 2.5 mm; paratype 2 NHMW 2016/0103/0982, height 12.8 mm, width 4.3 mm (juvenile); paratype 3 NHMW 2016/0103/0983, height 6.4 mm, width 2.7 mm; paratype 4 NHMW 2016/0103/0984, height 6.6 mm, width 2.6 mm; paratype 6 RGM.1352367, height 5.3 mm, width 1.9 mm; **St-Clément-de-la-Place**. Paratype 5 RGM.1352329, height 6.2 mm, width 2.8 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 6.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0985 (21), RGM.1352368 (1), LC (18), FVD (10). **Sceaux-d'Anjou**: NHMW 2016/0103/1350 (3), RGM.1352330 (3), RGM.1352515 (4), RGM.718193 (2), LC (1), FVD (1). **Renauleau**: NHMW 2016/0103/1460 (43), LC (30), FVD (28). **Beugnon**: RGM.1352396 (2).

Etymology – Named after Marian Helwerda, volunteer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

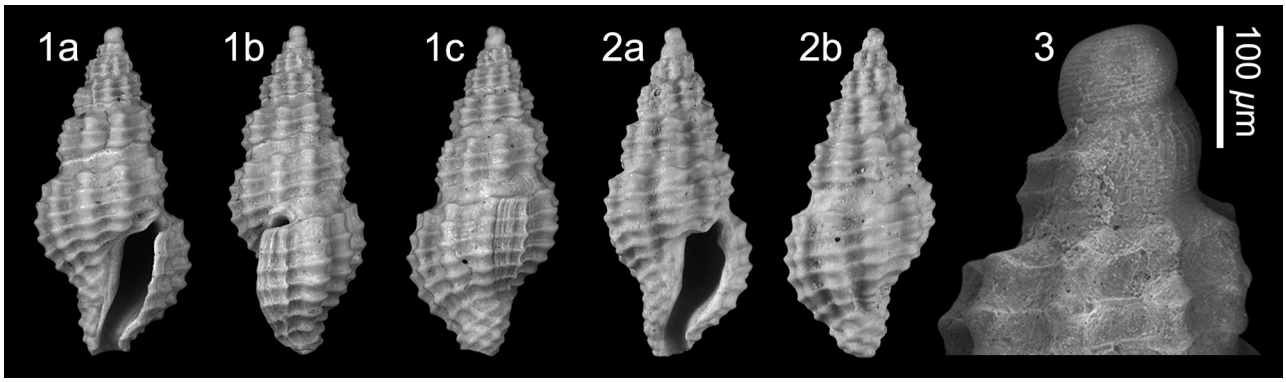

Plate 44. *Clathromangelia helwerdae* nov. sp.; 1. **Holotype** MNHN.F.A57926, height 6.2 mm, width 2.9 mm; 2. **Paratype 1** MNHN.F.A57927, height 5.7 mm, 2.5 mm; 3. **Paratype 2** NHMW 2016/0103/0982 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, paucispiral protoconch of two whorls, with fine reticulate microsculpture, riblets last half whorl, teleoconch with smooth concave subsutural ramp, bearing about 8-10 axial ribs and three spirals on intermediate whorls, hardly swollen over intersection with axials, narrow aperture, deep, narrow anal sinus delimited by labial and parietal tooth, moderately short siphonal canal.

Description – Shell small, cirtopupoid, robust. Protoconch paucispiral, composed of two convex whorls, bearing fine reticulate microsculpture over entire protoconch surface, axial riblets on last half whorl. Junction with teleoconch marked by beginning of adult sculpture. Teleoconch of five whorls with smooth, wide, concave subsutural ramp, angular shoulder placed high, convex below, separated by impressed weakly undulating suture. Axial sculpture of rounded, weakly prosocline ribs, 8-10 on last whorl, slightly narrower than their interspaces. Spiral sculpture of narrow cords overrun ribs forming rectangular cancellation, small tubercles developed at intersections, two on first teleoconch whorl, three on second to penultimate whorl. Surface smooth, without microsculpture. Last whorl moderately inflated, subsutural ramp narrow, strongly concave, shoulder poorly developed, evenly convex below, strongly constricted at base; axials continue over base, seven spirals on last whorl plus further three over siphonal fasciole. Aperture narrow; outer lip thick, smooth within, convex in profile; anal sinus narrow, deep U-shaped, with apex mid-subsutural ramp, delimited laterally by moderate to stout tooth within outer lip; siphonal canal medium length, twisted, open. Columella deeply excavated in upper third. Columellar callus poorly developed, forming narrow edge; parietal callus slightly thickened, with stout tubercle delimiting medial border anal canal. Siphonal fasciole well delimited.

Discussion – At first glance *Clathromangelia helwerdae* nov. sp. is similar to *Cyrillia georgesi* (Ceulemans, Van Dingenen & Landau, 2018) from the younger Assemblage III deposits, but that species has a multispiral protoconch, more numerous axial ribs and more numerous spirals that form large horizontally-elongated tubercles over the ribs. In *C. helwerdae* the spirals are weakly swollen over the intersections. For comparison with other Assemblage I raphitomids, see under *C. daisyae* nov. sp. The teleoconch shape, sculpture and especially the shape of the aperture are similar to those of *C. vandervoorti* (Landau, Harzhauser, İslamoğlu and Silva, 2013) from the middle Miocene eastern Mediterranean Karaman Basin, but that species has a multispiral protoconch.
Raphitoma kharybdis Pusateri & Giannuzzi-Savelli, *in* Giannuzzi-Savelli *et al*., 2018 from the present-day central Mediterranean is somewhat similar in having a paucispiral protoconch, but in that species the last quarter whorl is carinate, the teleoconch has denser sculpture, with short spines produced at intersections, the subsutural ramp is narrower, and the outer lip is denticulate within.
We record *C. helwerdae* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou, Renauleau and Beugnon.

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

***Clathromangelia karinneae* nov. sp.**
Plate 45, figs 1-2

Type material – Holotype MNHN.F.A57916, height 6.5 mm, width 2.5 mm; paratype 1 MNHN.F.A57917, height 6.2 mm, width 2.3 mm; paratype 2 NHMW 2016/0103/0945, height 7.2 mm, width 2.5 mm; paratype 3 NHMW 2016/0103/0946, height 6.5 mm, width 2.3 mm, **St-Clément-de-la-Place**. Paratype 4 RGM.1352484, height 6.9 mm, width 2.7 mm; paratype 5 RGM.1352485, height 5.6 mm, width 2.3 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 7.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0948 (29), RGM.1352664 (2), RGM.1352678 (2), LC (28), FVD (11). **Sceaux-d'Anjou**: NHMW 2016/0103/0950 (20), RGM.718166 (50+), RGM.1352316 (6), RGM.1352486 (17), LC (5),

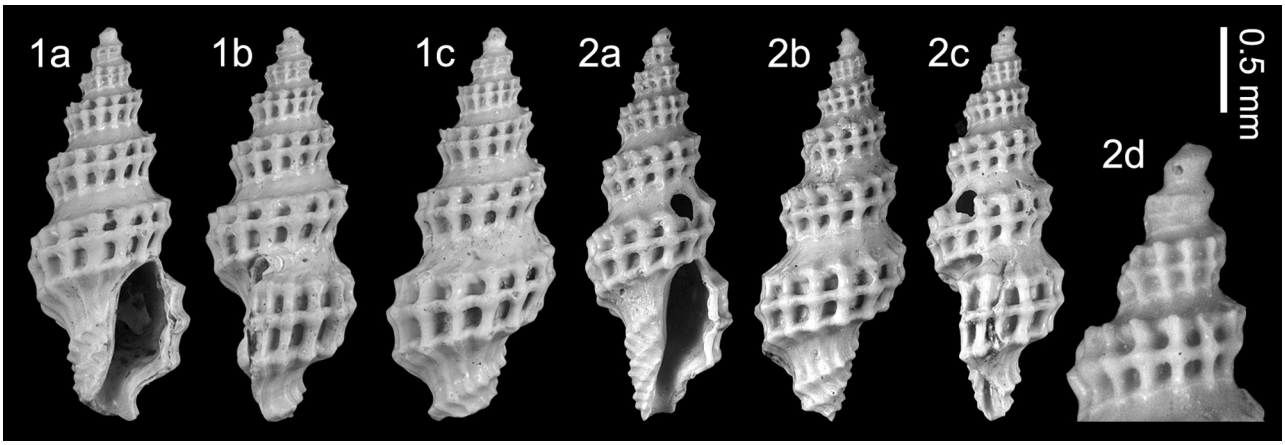

Plate 45. *Clathromangelia karinneae* nov. sp.; 1. Holotype MNHN.F.A57916, height 6.5 mm, width 2.5 mm; 2. paratype 3 NHMW 2016/0103/0946, height 6.5 mm, width 2.3 mm, 2d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

FVD (8). **Renauleau**: NHMW 2016/0103/0949 (2), LC (23).

Etymology – Named after Karinne Vangoethem, partner of one of the authors (LC). *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, slender fusiform shape, paucispiral protoconch of two whorls, first whorl tuberculate mid-whorl, last half bicarinate, teleoconch whorls with smooth convex subsutural ramp, convex below, bearing sculpture of 14 ribs and two cords, deep pits in interspaces, relatively small aperture.

Description – Shell small, slender fusiform. Protoconch paucispiral, composed of two tall decollate whorls, postnuclear whorl bearing tubercular carina mid-whorl, on last half whorl tubercles disappear from carina that migrates adapically to become shoulder cord, second carina develops abapically forming abapical cord. Junction with teleoconch sharply delimited. Teleoconch of five whorls with smooth wide concave subsutural ramp, convex below. Suture superficial. Sculpture of two raised primary cords and 14 orthocline axial ribs developed only below shoulder, forming reticulate pattern with small sharp tubercles formed at intersections, deep pits in interspaces. Last whorl 59% total height, with smooth concave subsutural ramp, strongly constricted at base, with three primary spirals; abapical spiral delimiting strongly concave base, three further spirals over siphonal fasciole. Aperture 40% total height, ovate, with edge strongly crenulated by spirals, broad poorly developed denticles within in some specimens; anal sinus shallow U-shaped; siphonal canal wide, open, moderately long. Columella weakly excavated in upper third. Columellar callus not thickened, forming smooth, narrow indented rim edging medial side of aperture.

Discussion – *Clathromangelia karinneae* nov. sp. is a strange looking shell with its completely smooth convex subsutural ramp and sculpture that is limited to below the shoulder. Sharp tubercles develop at the sculptural intersections and the interspaces form deep pits. Although we have described some denticle-like tubercles within the outer lip they are thickenings of the inner lip coinciding with the interspaces between the primary ribs and cords on the shell surface and extend in rows into the aperture. They are not true labial denticles and are not present in all shells, but seem to be related to shell ontogeny. It is most like *Clathromangelia densecostata* nov. sp., with which it co-occurs in Assemblage I, but that species has a less elongated shell and denser sculpture.
We record *C. karinneae* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

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

***Clathromangelia pereirae* nov. sp.**
Plate 46, figs 1-4

Type material – Holotype NHMW 2016/0103/1972, height 5.1 mm, width 2.3 mm; paratype 1 NHMW 2016/0103/1973, height 5.3 mm, width 2.3 mm; paratype 2 NHMW 2016/0103/1974, height 5.0 mm, width 2.3 mm; paratype 3 NHMW 2016/0103/1975, height 4.8 mm, width 2.1 mm; paratype 4 RGM.1352588, height 5.2 mm, width 2.2 mm; paratype 5 RGM.1352589, height 5.4 mm, width 2.3 mm.

Other material – Maximum height 5.2 mm, width 2.2 mm. **St-Clément-de-la-Place**: RGM.1352680 (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1976 (8), RGM.718167

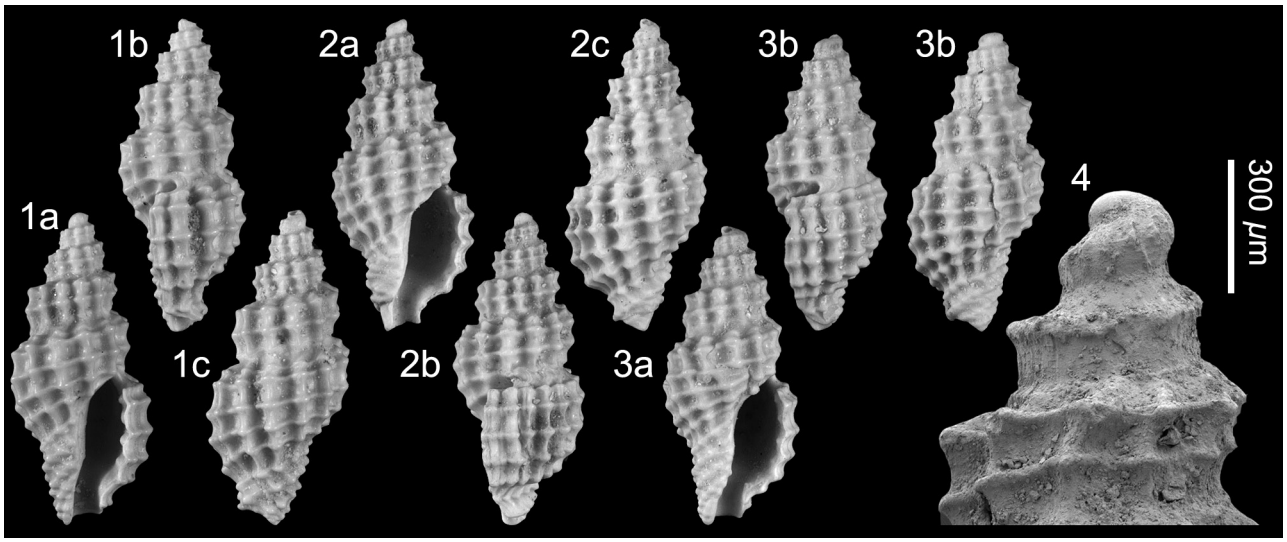

Plate 46. *Clathromangelia pereirae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1972, height 5.1 mm, width 2.3 mm; 2. **Paratype 1** NHMW 2016/0103/1973, height 5.3 mm, width 2.3 mm; 3. **Paratype 2** NHMW 2016/0103/1974, height 5.0 mm, width 2.3 mm; 4. **Paratype 4** NHMW 2016/0103/1975, height 4.8 mm, width 2.1 mm, detail of protoconch (SEM image). La Presselière, Sceaux'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(50+), RGM.1352590 (10), LC (2), FVD (7). **Renauleau**: NHMW 2016/0103/1989 (15), LC (3), FVD (12).

Etymology – Named after Sofia Pereira, Lisbon, Portuguese Ordovician trilobite palaeontologist. *Raphitoma* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, scalate spire, paucispiral protoconch of two whorls, with axial riblets, last whorl carinate, teleoconch with narrow subhorizontal ramp, bearing about 10-13 axial ribs and two spirals on spire whorls, slightly swollen over intersection, outer lip denticulation variable, D1 almost always developed, up to four further teeth below, deep, narrow anal sinus moderately short siphonal canal.

Description – Shell small, subpupoid, robust, scalate spire. Protoconch paucispiral, composed of two convex whorls, bearing widely spaced axial riblets on postnuclear whorls, prominent central carina on last whorl. Junction with teleoconch sharply delimited. Teleoconch of 4-4.5 whorls with narrow, subhorizontal subsutural ramp, angular shoulder placed high, convex below, separated by superficial undulating suture. Axial sculpture of elevated, rounded, weakly opisthocline ribs, 10-13 on last whorl, slightly narrower than their interspaces. Spiral sculpture of narrow cords, two on spire whorls, overrun ribs forming rectangular cancellation, slightly swollen at intersections. Last whorl moderately inflated, subsutural ramp narrow, shoulder rounded, evenly convex below, moderately constricted at base; axials continue over base, six spirals on last whorl plus further four over siphonal fasciole. Aperture ovate; outer lip thick, convex in profile, bearing up to five tubercular denticles within, D1 strongest; lower denticles not developed in most specimens; anal sinus narrow, deep, symetrically U-shaped, with apex mid-subsutural ramp, delimited laterally by D1 within outer lip; siphonal canal moderately short, twisted, open. Columella excavated in upper third. Columellar callus poorly developed, forming narrow indented edge. Siphonal fasciole not sharply delimited.

Discussion – *Clathromangelia pereirae* nov. sp. is similar to *Clathromangelia fenestrata* (Millet, 1865), from which it differs in being smaller, and having less regularly reticulate teleoconch sculpture in which the axial ribs are broader than the cords and not equal in strength, as in *C. fenestrata*. The protoconch in the two species is similar. *Clathromangelia densecostata* nov. sp., also from Assemblage I has denser reticulate sculpture, the interspaces reduced to small, deep pits between the axials and spirals, and the the protoconch is quite different (see Pl. 41, fig. 4). In Assemblage I *C. pereirae* is found at the localities of Sceaux'Anjou and Renauleau.

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

***Clathromangelia vannieulandei* nov. sp.**
Plate 47, figs 1-3

1964 *Clathromangelia couffoni* Brébion, p. 596, pl. 14, fig. 26 (*nomen nudum*).

Type material – Holotype MNHN.F.A57918, height 6.5 mm, width 2.6 mm; paratype 1 MNHN.F.A57919, height

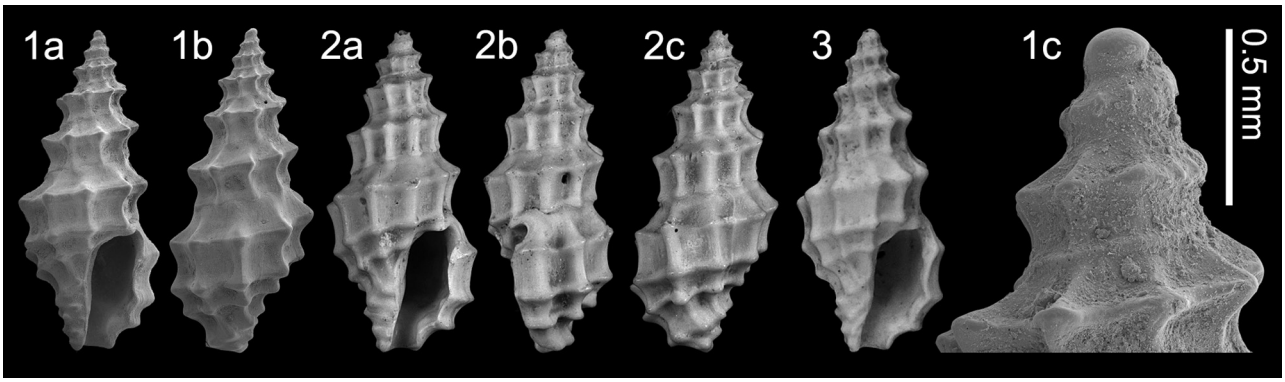

Plate 47. *Clathromangelia vannieulandei* nov. sp.; 1. Holotype MNHN.F.A57918, height 6.5 mm; width 2.6 mm, 1c. detail of protoconch (SEM image); 2. Paratype 1 MNHN.F.A57919, height 6.0 mm, width 2.5 mm; Le Grand Chauvereau, St-Clément-de-la-Place. 3. Paratype 2 NHMW 2016/0103/0951, height 7.6 mm, width 3.1 mm; La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

6.0 mm, width 2.5 mm; **St-Clément-de-la-Place**. paratype 2 NHMW 2016/0103/0951, height 7.6 mm, width 3.1 mm; paratype 3 NHMW 2016/0103/0952, height 7.5 mm, width 2.4 mm; paratype 4, RGM.1352317, height 5.5 mm, width 2.4 mm; paratype 5, RGM.1352573, height 7.5 mm, width 2.9 mm; paratype 6, RGM.1352574, height 7.5 mm, width 3.1 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 7.9 mm, width 3.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0953 (4), LC (4). **Sceaux-d'Anjou**: NHMW 2016/0103/0950 (20), RGM.718164 (50+), RGM.1352318 (3), RGM.1352487 (24), LC (3), FVD (6). **Renauleau**: NHMW 2016/0103/0954 (7), LC (10), FVD (2).

Etymology – Named after Freddy van Nieulande of Nieuw- en St. Joosland, The Netherlands, research associate of the Naturalis Biodiversity Center, Leiden, The Netherlands, who kindly donated his collection to Naturalis, which was used in this work. *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, fusiform shape, protoconch of just over two whorls, strongly tuberculate mid-whorl, last half carinate, teleoconch whorls angular, biconcave, bearing sculpture of 8-9 ribs and one cord, square concave interspaces, small aperture.

Description – Shell small, fusiform, solid. Protoconch paucispiral, composed of just over two tall whorls, postnuclear whorl bearing carina mid-whorl with strong axially elongated tubercles, on last half whorl tubercles weaken, carina becomes shoulder cord. Junction with teleoconch sharply delimited. Teleoconch of five biconcave angular whorls with wide subsutural ramp. Suture superficial. Sculpture of one prominent primary cord forming shoulder, and 8-9 orthocline axial ribs extending between sutures, forming wide reticulate pattern with sharp tubercles formed at shoulder, interspaces large concave squares. Last whorl 57-60% total height, with smooth concave subsutural ramp, strongly constricted at base, with two primary spirals; abapical spiral delimiting concave base, one further spiral developed over base, two over siphonal fasciole. Aperture 38% total height, small, ovate, with edge strongly crenulated by spirals, smooth within; anal sinus deep U-shaped; siphonal canal wide, open, moderately short. Columella weakly excavated in upper third. Columellar callus not thickened, forming smooth, narrow indented rim edging medial side of aperture.

Discussion – It is interesting to note that all the Pliocene to present-day *Clathromangelia* species reviewed by Oliverio (1995) differ in details, but conform to a pattern, whereas the teleoconch of the Assemblage I species are all wildly different from their Mediterranean congeners and from each other. On the other hand, the protoconch of all the Assemblage I species is more or less similar (bearing in mind comment made under *C. densecostata* nov. sp.; see above), and quite different to any of the protoconchs illustrated by Oliverio (1995). We further note that many of the species here included under *Raphitoma* have protoconchs similar to those illustrated by Oliverio for the Mediterranean Pliocene *Clathromangelia* species, again suggesting a close relationship between the two genera (see under *C. karinneae* nov. sp. for further comment).
Clathromangelia vannieulandei nov. sp. is the only species within the genus with only one spiral cord on spire whorls. The only species it could possibly be confused with is *C. fenestrata* (Millet, 1865), with which it co-occurs, but that species has two primary spirals on the spire whorls, more numerous axials and hence a denser reticulate sculpture.
We record *C. vannieulandei* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Clathromangelia wopkeae* nov. sp.**
Plate 48, figs 1-3

Type material – Holotype NHMW 2016/0103/1210, height 8.6 mm, width 3.6 mm; paratype 1 NHMW 2016/0103/1211, height 5.4 mm, width 2.2 mm; paratype 2 MNHN.F.A57924, height 6.9 mm, width 2.6 mm; paratype 3 MNHN.F.A57925, height 6.2 mm, width 2.5 mm; **St-Clément-de-la-Place**. Paratype 4 NHMW 2016/0103/1212 (juvenile), height 3.0 mm, width 1.5 mm; **Renauleau**. Paratype 5 RGM.1352319, height 7.1 mm, width 2.7 mm; paratype 6 RGM.1352320, height 5.8 mm, width 2.2 mm; paratype 7 RGM.1352492, height 7.4 mm, width 3.0 mm, paratype 8 RGM.1352493, height 6.0 mm, width 2.5 mm**, Sceaux-d'Anjou**.

Other material – Maximum height 8.6 mm, width 3.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1212 (19), LC (15), FVD (12). **Sceaux-d'Anjou**: NHMW 2016/0103/1769 (50+), RGM.718155 (50+), RGM.1352321 (14), RGM.1352494 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1802 (39), LC (50+), FVD (50+).

Etymology – Named after Wopke van Akkeren, Amsterdam, The Netherlands, a friend of the first author (BL). *Clathromangelia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clathromangelia* species of small size, elongated-fusiform, solid, paucispiral protoconch of two subquadrate whorls, first whorl with axial ribs, second with two strong carinae, shoulder carina tuberculate, teleoconch whorls with broad subsutural ramp, bearing coarse rectangular reticulate sculpture, 9-11 ribs crossed by wide-spaced primary and secondary cords, aperture small, distinct siphonal fasciole.

Description – Shell small, elongate-fusiform, solid. Protoconch paucispiral, composed of two subquadrate strongly shouldered whorls; first post-nuclear whorl bearing elevated axial ribs; second whorl with two strong rounded carinae, abapical one placed at shoulder, abapical just above suture, axials weaken forming tubercles on shoulder carina; sparce axially elongated linear micropustules scattered on surface. Junction with teleoconch sharply delimited. Teleoconch of five angular whorls, subsutural ramp wide, shoulder roundly angled, whorl convex below, separated by impressed, undulating suture. Axial sculpture of narrow orthocline ribs, 9-11 on last whorl, one quarter width of interspaces. Spiral sculpture of narrow cords overrun ribs forming rectangular cancellation, small tubercles developed at intersections. Three cords on first teleoconch whorl; adapical and abapical cords develop from protoconch carinae; mid-whorl third primary develops immediately equal in strength to other spirals, two weaker spirals appear on subsutural ramp. Single secondary intercalated in interspaces on second half penultimate whorl. Surface covered in fine, crowded growth lines giving surface scabrous appearance. Last whorl moderately inflated, evenly convex, strongly constricted at base; axials weaken over base; two weak spirals on subsutural platform, five primaries with single thread intercalated over last whorl and base, further three on siphonal fasciole. Aperture small, ovate; outer not thickened, not denticulate; anal sinus deep U-shaped; siphonal canal short, open. Columella weakly to moderately excavated in upper third. Columellar callus poorly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – *Clathromangelia wopkeae* nov. sp. is yet another strange *Clathromangelia* that occurs in Assemblage I. Both the protoconch and teleoconch shape and sculpture are quite unlike that of any of its European congeners.
During the review process it was suggested to us that this species might represent the antipodean *Liracraea* Odhner, 1924 (Type species *Clathurella epentroma* Murdoch,

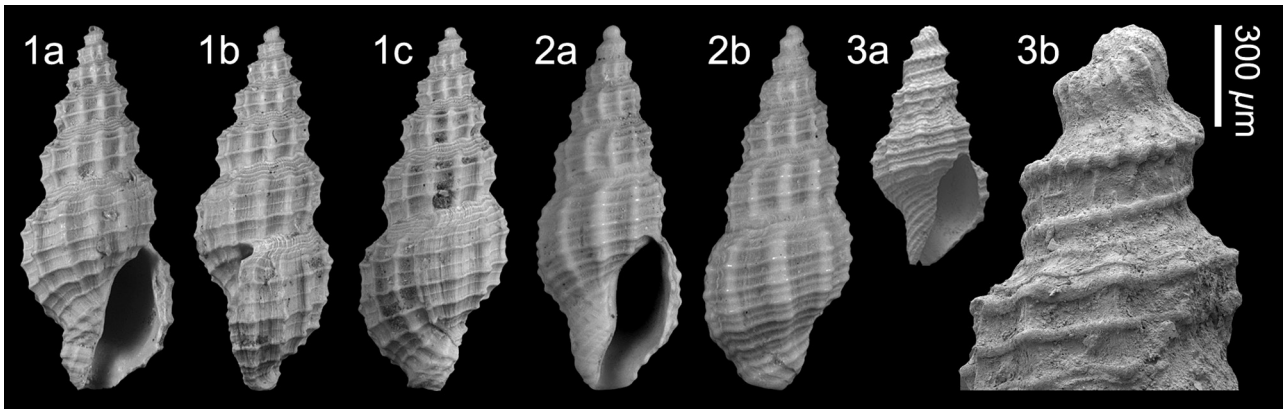

Plate 48. *Clathromangelia wopkeae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1210, height 8.6 mm, width 3.6 mm; 2. **Paratype 1** NHMW 2016/0103/1211, height 5.4 mm, width 2.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 3. **Paratype 4** NHMW 2016/0103/1212 (juvenile), height 3.0 mm, width 1.5 mm, 3b, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1905, by original designation, present-day, New Zealand), based on its small size, narrowly fusiform shape, tall attenuated spire, truncated last whorl with a short anterior canal, and spirally keeled protoconch. The teleoconch shape and sculpture is similar to that of *L. odhneri* Powell, 1942 and the type species *L. epentroma* (Murdoch, 1905). However, the anal canal in *Liracraea* is very shallow (Powell, 1966, p. 107), whereas in the French species it is deep (Pl. 48, fig. 1b). There is little intraspecific variability, mainly concerning the inflation of the whorls; the holotype is slightly more inflated than most specimens, and the strength of the secondary cords varies.
We record *C. wopkeae* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

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

Genus *Cyrillia* Kobelt, 1905

Type species – *Murex linearis* Montagu, 1803, by typification of replacement name, present-day, British-Isles.

1884 *Cirillia* Monterosato, p. 133. Type species (by subsequent designation; Crosse, 1885): *Murex linearis* Montagu, 1803, present-day, British Isles. Junior homonym of *Cirillia* Rondani, 1856 [Diptera].

1905 *Cyrillia* Kobelt, p. 367. Type species (by typification of the replaced name): *Murex linearis* Montagu, 1803, present-day, British Isles. Emendation of *Cirillia* Monterosato, 1884, which is a junior homonym of *Cirillia* Rondani, 1856 [Diptera].

1967 *Cenodagreutes* E.H. Smith, p. 1. Type species (by original designation): *Cenodagreutes aethus* E.H. Smith, 1967, present-day, British Isles.

1977 *Lineotoma* Nordsieck, p. 59. Type species (by typification of replaced name): *Murex linearis* Montagu, 1803, present-day, British Isles. *Nom. nov. pro Cirillia* Monterosato, 1884, *non* Rondani, 1856 [Diptera].

Note – Based on molecular evidence, Fassio *et al*. (2019) recognised three major lineages within species traditionally placed in the genus *Raphitoma* Bellardi, 1847; *Raphitoma*, *Cyrillia* Kobelt, 1905 and *Leufroyia* Monterosato, 1884.
According to those authors the genus *Cyrillia* includes biconic, small shelled species, with a slender spire composed of convex whorls, bearing reticulate sculpture, axially predominant, microsculpture of granules or pustules, a thickened outer lip, denticulate within, the two anteriormost denticles stronger. In their generic description they characterise the protoconch as multispiral, although in this work we include paucispiral species, a species without labial denticles, and microsculpture is only clearly evident in *Cyrillia michalidesi* nov. sp., thus widening the generic concept.
We draw attention to the revision of the extant Mediterranean Raphitomidae recently published (Giannuzzi-Savelli *et al*., 2018), and adopt some of the nomenclature suggested in that paper for shell characteristics; shell outline and aspect (see Giannuzzi-Savelli *et al*., 2018, figs 1, 2, 5-15). For protoconch whorl count we do count the nucleus as first half whorl. Therefore all the species herein have half whorl more than using the Verduin (1977) system adopted by Giannuzzi-Savelli *et al*. (2018).
Ceulemans *et al*. (2018, p. 107) discussed the abundance of '*Raphitoma*' species in the lower Pliocene Assemblage III deposits of northwestern France, where they recorded eight species [*Raphitoma bertrandiana* (Millet, 1865) and *Raphitoma pseudoconcinna* Ceulemans, Van Dingenen & Landau, 2018, are here removed from *Raphitoma* and placed in the genus *Daphnella*, leaving six '*Raphitoma*' species in Assemblage III]. Assemblage I is more than twice as speciose, with 14 species recorded (*Cyrillia*, *Leufroyia* and *Raphitoma*), almost all endemic to the upper Miocene-Pliocene of NW France.
They also commented on the predominance of non-planktotrophic forms within Assemblage III, in which seven of the eight species had protoconchs suggesting of non-planktotrophic development. This is also true of Assemblage I, where 14 of the 16 species have non-planktotrophic protoconchs (direct development of lecithotrophic types). This contrasts strongly with Atlantic faunas today. Høisæter (2016) reviewed the present-day species in the northern European waters off Norway and recorded six species, all of which have planktotrophic-type protoconchs. All nine raphitomid species reviewed by Rolán *et al*. (1998) from the tropical West African coasts also have multispiral protoconchs typical for planktotrophic development. In contrast, Giannuzzi-Savelli *et al*. (2018, p. 67), estimated about 30 species to occur in the Mediterranean, of which 25% have non-planktotrophic development, whilst the approximately 10 exclusively (or nearly exclusively) Atlantic species all have planktotrophic development.

***Cyrillia michalidesi* nov. sp.**
Plate 49, figs 1-3

Type material – Holotype MNHN.F.A70538, height 6.1 mm, width 2.7 mm; paratype 1 MNHN.F.A70539, height 5.1 mm, width 2.5 mm; paratype 2 NHMW 2016/0103/1218, height 7.3 mm, width 3.1 mm; paratype 3 NHMW 2016/0103/1219, height 6.6 mm, width 2.9 mm; paratype 4 RGM.1352383, height 5.2 mm, width 2.5 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1352395, height 5.2 mm, width 2.3 mm; paratype 6 RGM.1352529, height 5.5 mm, width 2.5 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 7.3 mm, width 3.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1220 (23), RGM.1352366 (2), LC (2), FVD (14). **Sceaux-d'Anjou**: NHMW 2016/0103/1801 (17), RGM.739230 (40), RGM.718182 (50+), RGM.1352530 (5), RGM.1352606 (29), RGM.1352614 (9), LC (3), FVD (7). **Renauleau**: NHMW 2016/0103/1762 (26), LC (16), FVD (18). **Beugnon**: RGM.1352349 (1).

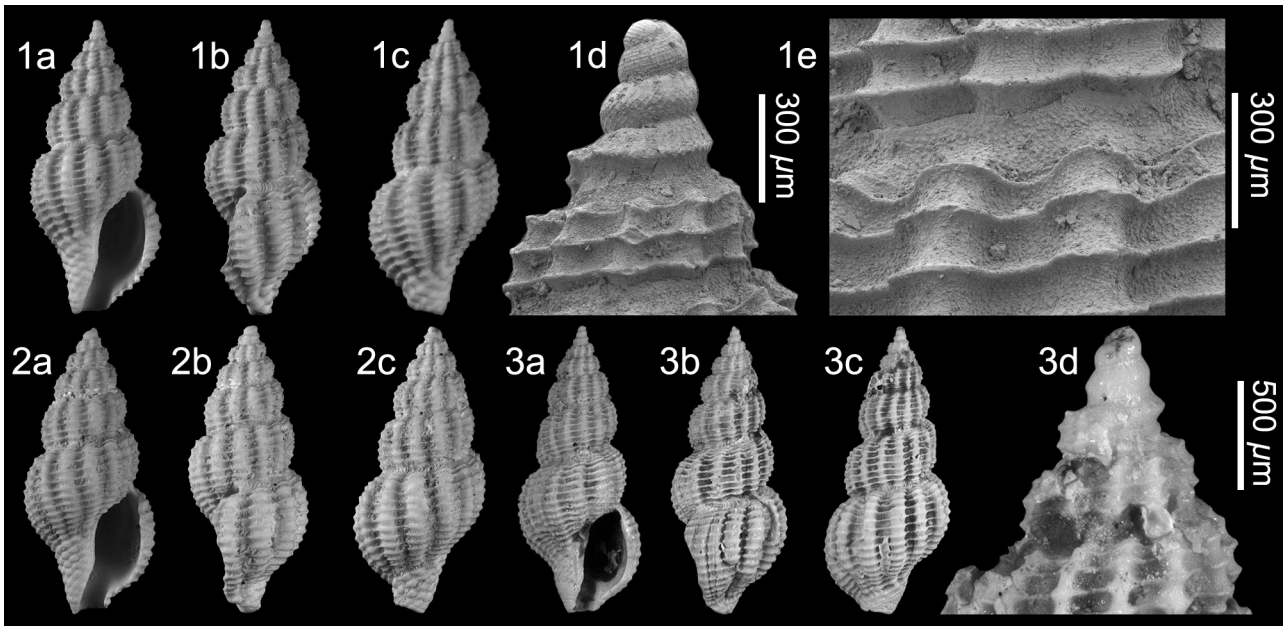

Plate 49. *Cyrillia michalidesi* nov. sp.; 1. **Holotype** MNHN.F.A70538, height 6.1 mm, width 2.7 mm, 1d, detail of protoconch, 1e, detail of teleoconch microsculpture (SEM image); 2. **Paratype 1** MNHN.F.A70539, height 5.1 mm, width 2.5 mm; 3. **Paratype 3** NHMW 2016/0103/1219, height 6.6 mm, width 2.9 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Etymology – Named after Wieke Michalides, volunteer photographer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Cyrillia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Cyrillia* species of small size, cyrtopupoid, robust, multispiral protoconch with early whorls spirally sculptured, later diagonally reticulated, carinate last half whorl, teleoconch with strongly convex whorls, bearing 13-17 rounded axials overrun by numerous equal spirals, spirals beaded over siphonal fasciole, outer lip smooth within, anal sinus moderately deep U-shaped, siphonal canal medium length, siphonal fasciole indistinct.

Description – Shell small, cyrtopupoid, robust. Protoconch tall multispiral, compose of 3.25-3.5 convex whorls; first 1.5 whorls bearing spiral threads, last 1.5-2 whorls diagonally reticulated below mid-whorl, last half whorl strongly carinate mid-whorl. Junction with teleoconch sharply delimited. Teleoconch of 4-4.5 convex whorls, separated by superficial undulating suture, with narrow, concave subsutural ramp bearing comma-shaped axial riblets, convex below. Axial sculpture of rounded, orthocline ribs, 13-17 on last whorl, equal in width to their interspaces. Spiral sculpture of close-set, narrow, equal cords, two on first, seven on penultimate whorl, overrun ribs, not swollen at intersections. Teleoconch with pustular microsculpture. Last whorl moderately inflated, subsutural ramp narrow, evenly convex below, moderately constricted at base; axials continue over base, 10-12 spirals on last whorl plus further 4-6 beaded spirals over siphonal fasciole. Aperture ovate; outer lip thin, convex in profile, smooth within; anal sinus moderately deep, symetrically U-shaped, with apex mid-subsutural ramp; siphonal canal medium length, recurved, open. Columella excavated in upper third. Columellar callus poorly developed, forming narrow indented edge, parietal callus not developed. Siphonal fasciole not sharply delimited.

Discussion – *Cyrillia michalidesi* nov. sp. is the only raphitomid species in Assemblage I with a multispiral protoconch of a typically planktotrophic type. We have placed it in the genus *Cyrillia* Kobelt, 1905 despite the absence of labial teeth, which are a generic character (Fassio *et al*., 2019).
It is very similar to the present-day *Cyrillia aequalis* (Jeffreys, 1867) from the European Atlantic frontage and Mediterranean, but that species has smooth spirals on the siphonal fasciole, whereas *C. michalidesi* has beaded spirals. We note that *C. aequalis* also has micropustular teleoconch sculpture (Høisæter, 2016, fig. 8). Another extant species with a similar distribution is *C. linearis* (Montagu, 1803), which can be difficult to separate from *C. aequalis*, but *C. linearis* does not have pustular microsculpture like *R. aequalis* (Høisæter, 2016, p. 23) and *C. michalidesi*. Both *C. aequalis* and *C. linearis* have tubercles developed at the sculptural intersections, more strongly so in the latter, but in *C. michalidesi* the spirals are not swollen as they cross the axials.
Cyrillia michalidesi is widespread in Assemblage I and

not uncommon. We record it from St-Clément-de-la-Place, Sceaux-d'Anjou, Renauleau and Beugnon.

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

Genus and subgenus *Daphnella* Hinds, 1844

Type species – *Pleurotoma limneiformis* Kiener, 1840, by subsequent designation, Herrmannsen, 1847, present-day, Mauritius.

1844 *Daphnella* Hinds, p. 25.

***Daphnella* (*Daphnella*) *bertrandiana* (Millet, 1865)**
Plate 50, figs 1-3

1854 *Buccinum Bertrandianum* Millet, p. 165.
*1865 *Buccinum bertrandianum* Millet, p. 595.
1964 *Raphitoma ligustica* var. *bertrandiana* Millet, 1854 [*sic*] – Brébion, p. 601, pl. 14, figs 29-31.
2018 *Raphitoma bertrandiana* (Millet, 1865) – Ceulemans *et al*., p. 107, pl. 4, figs 1, 2.

Type material – Syntypes: Sceaux-d'Anjou, Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 602).

Material and dimensions – Maximum height 19.7 mm, width 7.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0974-0976 (3), NHMW 2016/0103/0977 (18), RGM.1352407 (1), LC (21), FVD (20). **Sceaux-d'Anjou**: NHMW 2016/0103/0978 (2), RGM.718194 (21), RGM.718198 (4 fragments), RGM.1352326 (3), RGM.1352584 (3), LC (1). **Renauleau**: NHMW 2016/0103/1496 (16), LC (50+), FVD (22).

Discussion – During the review process it was suggested to us that although the separation between the raphitomid genera *Leufroyia* Monterosato, 1884 and *Daphnella* Hinds, 1844 may not always be clear, this species was better placed in *Daphnella*. The teleoconch sculpture of dense spirals reticulated by equally dense and fine axials is more typical of that genus. The protoconch is not typical of *Daphnella*, which usually has a tall multispiral diagonally reticulate protoconch (Powell, 1966, p. 123).
Daphnella (*Daphnella*) *bertrandiana* (Millet, 1865) was discussed by Ceulemans *et al*. (2018) based on material from Assemblage III. It is the largest raphitomid species present in Assemblage I and quite distinctive. The protoconch in the Assemblage I material is beautifully preserved and consists of 2-2.5 whorls with finely reticulate sculpture covering the entire protoconch (Pl. 50, fig. 3). The teleoconch is fusiform, rather inflated, although in some specimens more than others. The axial ribs that extend between the sutures on early whorls can persist, albeit weakened, onto the adapical portion of the first half of the last whorl (Pl. 50, fig. 1) or become obsolete by the second half of the penultimate whorl (Pl. 50, fig. 2). For comparison with similar species see Ceulemans *et al*. (2018, p. 108). In Assemblage I it most similar to *Leufroyia aldrovandi* (Millet, 1865), which has a similar shell shape and protoconch sculpture, but that species has coarser axial and spiral sculpture. In *D.* (*D.*) *bertrandiana* the axial sculpture becomes obsolete on the second half of the penultimate whorl, whereas in *L. aldrovandi* it persists to the lip edge. For further comparison, see *Leufroyia seani* nov. sp.
Millet (1854, 1865) described the species from the Assemblage I localities of Sceaux-d'Anjou and Thorigné, to which Brébion (1964, p. 603) added Saint-Clément-de-la-Place and St-Michel and we add Renauleau, and the Assemblage III locality of Le Pigeon Blanc.

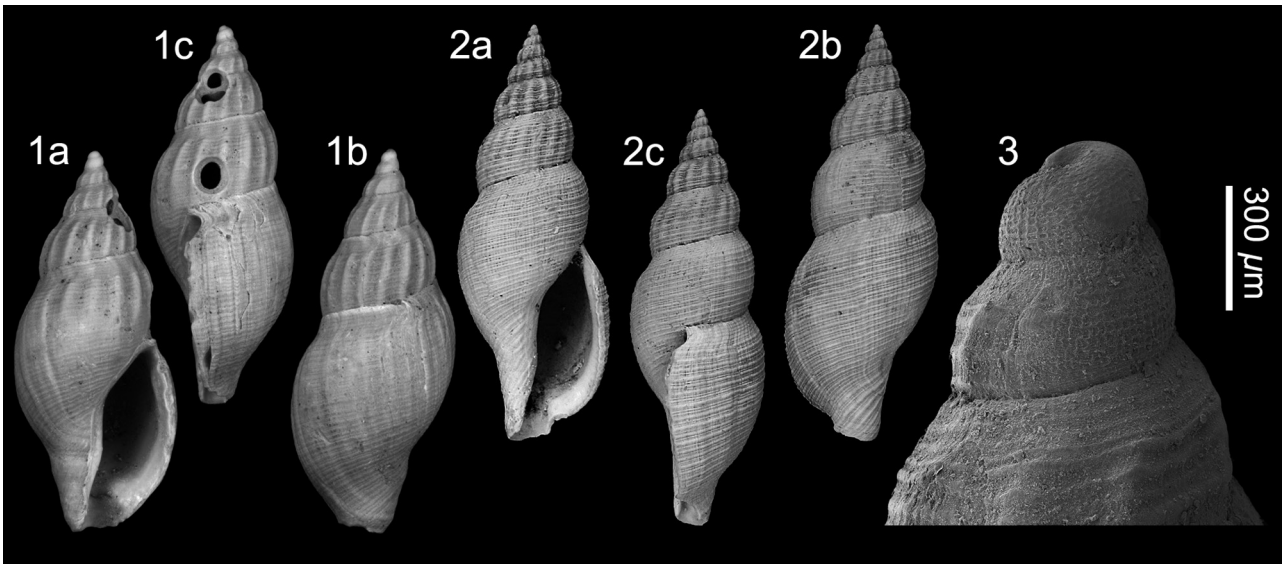

Plate 50. *Daphnella* (*Daphnella*) *bertrandiana* (Millet, 1865); 1. NHMW 2016/0103/0974, height 10.2 mm, width 4.3 mm; 2. NHMW 2016/0103/0975, height 19.7 mm, width 7.0 mm; 3. NHMW 2016/0103/0976 (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018).

***Daphnella* (*Daphnella*) *pseudoconcinna* (Ceulemans, Van Dingenen & Landau, 2018)**
Plate 51, figs 1-2

*2018 *Raphitoma pseudoconcinna* Ceulemans, Van Dingenen & Landau, p. 113, pl. 5, fig. 7.

Material and dimensions – Maximum height 16.0 mm, width 5.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1239-1240 (2), RGM.1352448 (5), RGM.1352693 (2), LC (?1).

Discussion – As with the previous species, reviewers suggested that this species was better placed in *Daphnella*. Again, the protoconch is not typical of *Daphnella*, which usually has a tall multispiral diagonally reticulate protoconch (Powell, 1966, p. 123).
Daphnella (*Daphnella*) *pseudoconcinna* (Ceulemans, Van Dingenen & Landau, 2018) and *Daphnella* (*Daphnella*) *bertrandiana* (Millet, 1865) are the only two relatively large raphitomid species in Assemblage I, of which *D.* (*D.*) *pseudoconcinna* is by far the more uncommon. Only a few specimens are at hand and none is in perfect condition. The protoconch is paucispiral and consists of two convex whorls covered in fine reticulate microsculpture. This microsculpture was abraded in the holotype from Assemblage III. Apart from the relatively large size, *D.* (*D.*) *pseudoconcinna* is characterised by its fusiform shape, thin shell, and sculpture composed of prosocline axials that weaken abapically and disappear on the penultimate whorl and very fine spirals of alternate strength, that together with numerous prominent axial growth lines, give the surface a finely reticulated pattern [hence placement in genus *Daphnella*; see under *D.* (*D.*) *bertrandiana*]. The last whorl is moderately inflated, with a weakly delimited subsutural ramp, regularly convex below, and moderately constricted at the base. The siphonal fasciole is not separated. The aperture is large, the outer lip thin and the siphonal canal long and twisted. It is superficially similar to *L. concinna* (Scacchi, 1836), but that species has a multispiral protoconch (see Høisæter, 2016, figs A, C). For further discussion see Ceulemans *et al*. (2018, p. 113). In Assemblage I we have found *D.* (*D.*) *pseudoconcinna* only at St-Clément-de-la-Place, where it is uncommon.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Ceulemans *et al*., 2018).

Subgenus *Paradaphne* Laseron, 1954

Type species – *Daphnella botanica* Hedley, 1918, by original designation, present-day, New South Wales, Australia.

1954 *Paradaphne* Laseron, p. 44.

Note – Fassio *et al*. (2019) suggested that the West African '*Daphnella*-like' species, *Raphitoma corimbensis* Rolán, Otero-Schmitt & Fernandes, 1998 and *Raphitoma bedoyai* Rolán, Otero-Schmitt & Fernandes, 1998 should be placed in the Antipodean subgenus *Paradaphne* Laseron, 1954. They suggested that *Daphnella*, as used currently, might be polyphyletic and likened the shell shape and sculpture to the type species *Daphnella botanica* Hedley, 1918. The species herein attributed to the subgenus is indeed closely similar in teleoconch characters to its West African consubgeners, but differs in having a paucispiral protoconch, whereas both extant species have a multispiral protoconch.

***Daphnella* (*Paradaphne*) *groeneveldi* nov. sp.**
Plate 52, figs 1-3

Type material – Holotype NHMW 2016/0103/1759, height 5.0 mm, width 1.8 mm; paratype 1 NHMW 2016/0103/1760, height 5.1 mm, width 1.7 mm; **Re-**

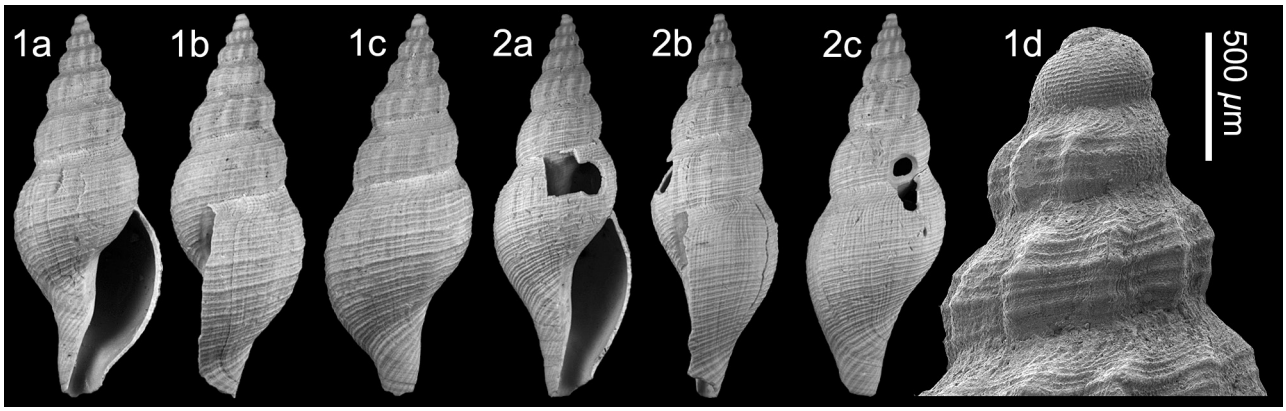

Plate 51. *Daphnella* (*Daphnella*) *pseudoconcinna* (Ceulemans, Van Dingenen & Landau, 2018); 1. NHMW 2016/0103/1239, height 16.0 mm, width 5.5 mm, 1d, detail of protoconch (SEM image); 2. NHMW 2016/0103/1240, height 12.4 mm, width 4.9 mm, Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

nauleau. Paratype 2 RGM.1352434, height 6.5 mm, width 2.3 mm; paratype 3 RGM.1352608, height 5.4 mm, 1.7 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 6.5 mm, width 2.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0991 (1 incomplete), RGM.1352435 (1 juvenile), LC (1). **Sceaux-d'Anjou**: RGM.718197 (9 juveniles and fragments), RGM.1352587 (2 fragments). **Renauleau**: LC (1).

Etymology – Named after the late Wim Groeneveld of Santpoort-Noord, The Netherlands, who kindly donated his collection to the Naturalis Biodiversity Center, Leiden, The Netherlands, which was used in this work. *Daphnella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Daphnella* (*Paradaphne*) species of small size, fusiform, solid, paucispiral protoconch of two whorls, post-nuclear whorls bicarinate crossed by axial riblets, teleoconch with regularly convex whorls without well-developed subsutural ramp or shoulder, bearing very fine subquadrate reticulate sculpture.

Description – Shell small, fusiform, solid. Protoconch paucispiral, composed of two whorls, nucleus bearing fine reticulate microsculpture only on nucleus, post-nuclear whorl develops two broad carinae, making whorl subquadrate in profile, placed at shoulder and between mid-whorl and suture, crossed by narrow, wide-spaced, sinuous axial riblets. Junction with teleoconch sharply delimited. Teleoconch of four regularly convex whorls, subsutural ramp and shoulder hardly developed, separated by impressed suture. Axial sculpture of crowded, orthocline narrow ribs, about 40 on last whorl, half to one-third width of interspaces. Spiral sculpture of narrow cords overrun ribs forming fine subquadrate cancellation, small tubercles developed at intersections. Three cords on first teleoconch whorl; adapical and abapical cords develop from protoconch carinae; mid-whorl third primary develops immediately equal in strength to other spirals. Number of spirals increases abapically, 10-11 on penultimate whorl; third cord below suture slightly reinforced forming very weak shoulder. Surface smooth, without microsculpture. Last whorl weakly inflated, subsutural ramp narrow, poorly developed, evenly convex below, strongly constricted at base; axials continue over base, about 35 spirals on last whorl and siphonal fasciole. Aperture ovate; outer lip weakly thickened, weakly denticulate within; anal sinus narrow, relatively deep U-shaped, with apex placed on adapical half of subsutural ramp, delimited laterally by poorly developed, subobsoletely bifid labial tooth; siphonal canal short to medium length, twisted, open. Columella moderately excavated in upper third. Columellar callus poorly developed, forming narrow edge; parietal callus not thickened. Siphonal fasciole indistinct.

Discussion – *Daphnella* (*Paradaphne*) *groeneveldi* nov. sp. is a very distinctive species, but exceedingly uncommon in all the Assemblage I deposits. The protoconch is unique amongst European raphitomid species. It bears

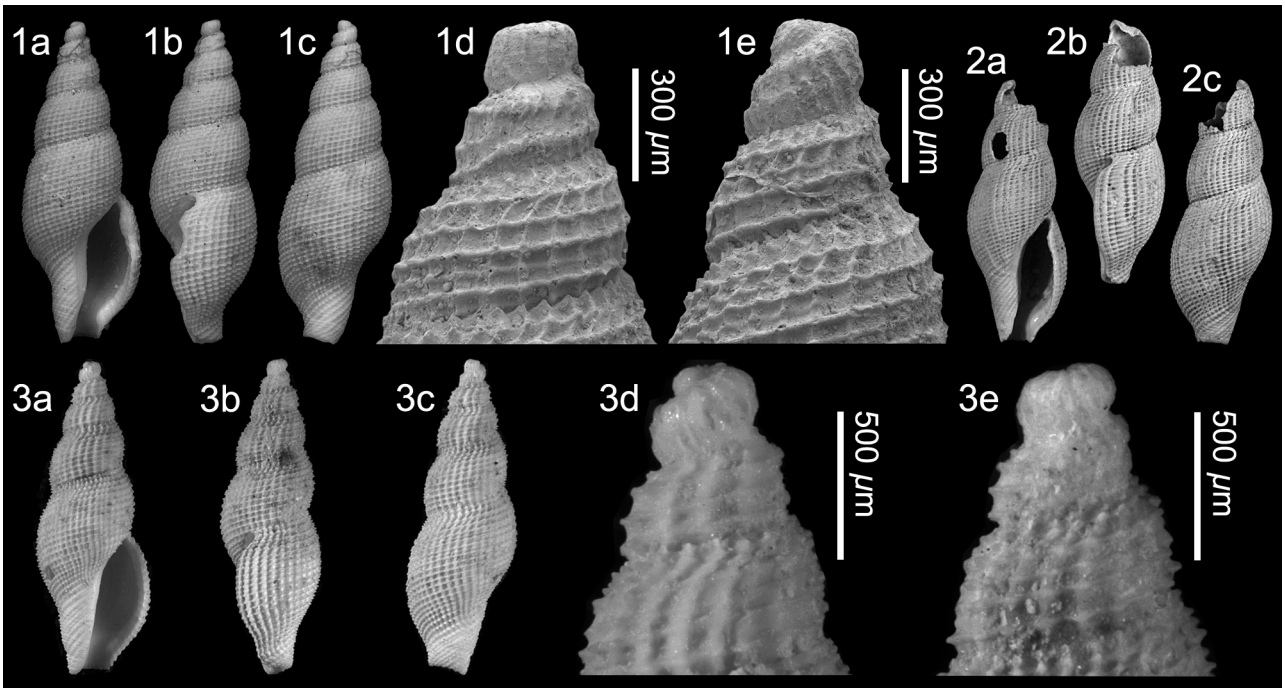

Plate 52. *Daphnella* (*Paradaphne*) *groeneveldi* nov. sp.; 1. **Holotype** NHMW 2016/0103/1759, height 5.0 mm, width 1.8 mm, 1d, e, detail of protoconch (SEM image). Renauleau. 2. NHMW 2016/0103/0991, height 4.3 mm, width 1.8 mm. St-Clément-de-la-Place. 3. **Paratype 1** NHMW 2016/0103/1760, height 5.1 mm, width 1.7 mm, 3d, e, detail of protoconch. Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

two broad carinae that start after the nucleus and give a subquadrate aspect to the protoconch, crossed by sinuous axial spirals. Some of the protoconchs of the Assemblage III raphitomids described by Ceulemans *et al*. (2018) and the extant Mediterranean ones reviewed by Giannuzzi-Savelli *et al*. (2018) are bicarinate, but usually only the last half protoconch whorl, and not as strongly as in this species. The teleoconch is also distinctive with its very fine mesh-like subquadrate reticulate sculpture. This finely reticulate sculpture is similar to that seen in *Daphnella botanica* Hedley, 1922 from Australia, for which Laseron (1954) erected the subgenus *Paradaphe*. That species differs in having a multispiral protoconch (see generic note). It is also closely similar to two West African species from Angola; *Daphnella* (*Paradaphne*) *corimbensis* (Rolán, Otero-Schmitt & Fernandes, 1998), which also has regular fine reticulate sculpture and *D.* (*P.*) *bedoyai* (Rolán, Otero-Schmitt & Fernandes, 1998), which differs somewhat in having broader axials that weaken abapically, but both of these species are immediately separated by their multispiral, diagonally reticulated protoconchs.
In the Caribbean *Daphnella* is represented by numerous species that differ in having broader axial ribs on early teleoconch whorls that weaken abapically and lacking regularly finely reticulated sculpture seen in *D.* (*P.*) *groeneveldi*, and the Caribbean species all have multispiral protoconchs. Espinosa & Fernández-Garcés (1990) also assigned some extant Caribbean species to the subgenus *Paradaphne*.
We record *D. groeneveldi* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, but very uncommon at all localities.

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

Genus *Leufroyia* Monterosato, 1884

Type species – Pleurotoma leufroyi Michaud, 1828, by subsequent designation, Crosse, 1885, present-day, Mediterranean.

1884 *Leufroyia* Monterosato, p. 134.

Note – Fassio *et al*. (2019) characterised species within the genus *Leufroyia* Monterosato, 1884 as being suboval to fusiform, medium to large for the family, with a slender spire composed of regularly convex whorls, undulating axial ribs and numerous finer, low spiral cords, microsculpture of growth lines, but no pustules, a smooth outer lip devoid of denticles and short to long siphonal canal. In their generic description they characterise the protoconch as multispiral, although in this work we include paucispiral species.

***Leufroyia aldrovandi* (Millet, 1865)**
Plate 53, figs 1-6

1854 *Pleurotoma Aldrovandi* Millet, p. 161 (*nomen nudum*).
1854 *Pleurotoma Selecta* Millet, p. 161 (*nomen nudum*).
*1865 *Pleurotoma Aldrovandi* Millet, p. 588.
1865 *Pleurotoma selecta* Millet, p. 588.
1938 *Mangelia* (*Leufroyia*) *Leufroyi* var. *praecedens* Dollfus & Dautzenberg *in* Peyrot, p. 285, pl. 5, figs 40, 56.
1954 *Philbertia* (*Leufroyia*) *leufroyi* f. *praecedens* Dollfus et Dautzenberg *in* Peyrot, 1938 – Glibert, p. 60, pl. 7, figs 8a, b, c.
1964 *Raphitoma* (*Leufroyia*) *leufroyi* Michaud, 1827 – Brébion, p. 611, pl. 15, fig. 5 [*non Raphitoma leufroyi* (Michaud, 1827)].
1964 *Raphitoma* (*Leufroyia*) *leufroyi* var. *praecedens* Dollfus et Dautzenberg in Peyrot, 1938 – Brébion, p. 613.
1964 *Raphitoma* (*Leufroyia*) *leufroyi* var. *selecta* Millet, 1854 – Brébion, p. 614, pl. 15, fig. 6.
1964 *Raphitoma* (*Leufroyia*) *leufroyi* var. *milleti* Brébion, p. 615, pl. 15, fig. 7 (*nomen nudum*).

Type material – Syntypes: Sceaux-d'Anjou or Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 615).

Material and dimensions – Maximum height 7.1 mm, width 2.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1214-1216 (3), 2016/0103/1235-1237 (3), NHMW 2016/0103/1238 (29), RGM.1352665 (3), RGM.1352695 (9), LC (5), FVD (14). **Sceaux-d'Anjou**: NHMW 2016/0103/1910 (37), RGM.718170 (46), RGM.718180 (32), RGM.734989 (32), RGM.1352325 (16), RGM.1352496 (32), RGM.1352609 (40), LC (4), FVD (18). **Renauleau**: NHMW 2016/0103/1911 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1352402 (1).

Original description –'Pleurotoma Aldrovandi, *Millet. Coq. de moyenne grandeur, composée de huit à neuf tours de spire bombés, séparés entre eux par une espèce de gouttière très-étroite; tous ces tours couverts de petites côtes verticales, sont croisés par des stries très-fines. Ouverture très-ample, terminée inférieurement par un canal court et portant au sommet du bord droit un léger sinus. Longueur: 15 millimètres; diamètre: 6-7 millimètres. Sc, Th*.' (Millet, 1865, p. 588).

Discussion – Leufroyia aldrovandi (Millet, 1865) is characterised by its paucispiral protoconch composed of two convex whorls with finely reticulate microsculpture. The teleoconch is fusiform, composed of convex whorls with a broad subsutural ramp bearing prominent comma-shaped marks below the suture. Its sculpture is somewhat variable, which has led to the description of several varieties. The ribs are rounded, low to moderately raised, half to equal the width of their interspaces, overrun by narrow cords of primary to tertiary strength. The last whorl is regularly convex (Pl. 53, figs 4, 5), in larger specimens somewhat elongated (Pl. 53, figs 1, 2), the aperture wide, the anal sinus U-shaped, of moderate depth, and the siphonal canal short to medium length. Millet (1965) described two forms of this spe-

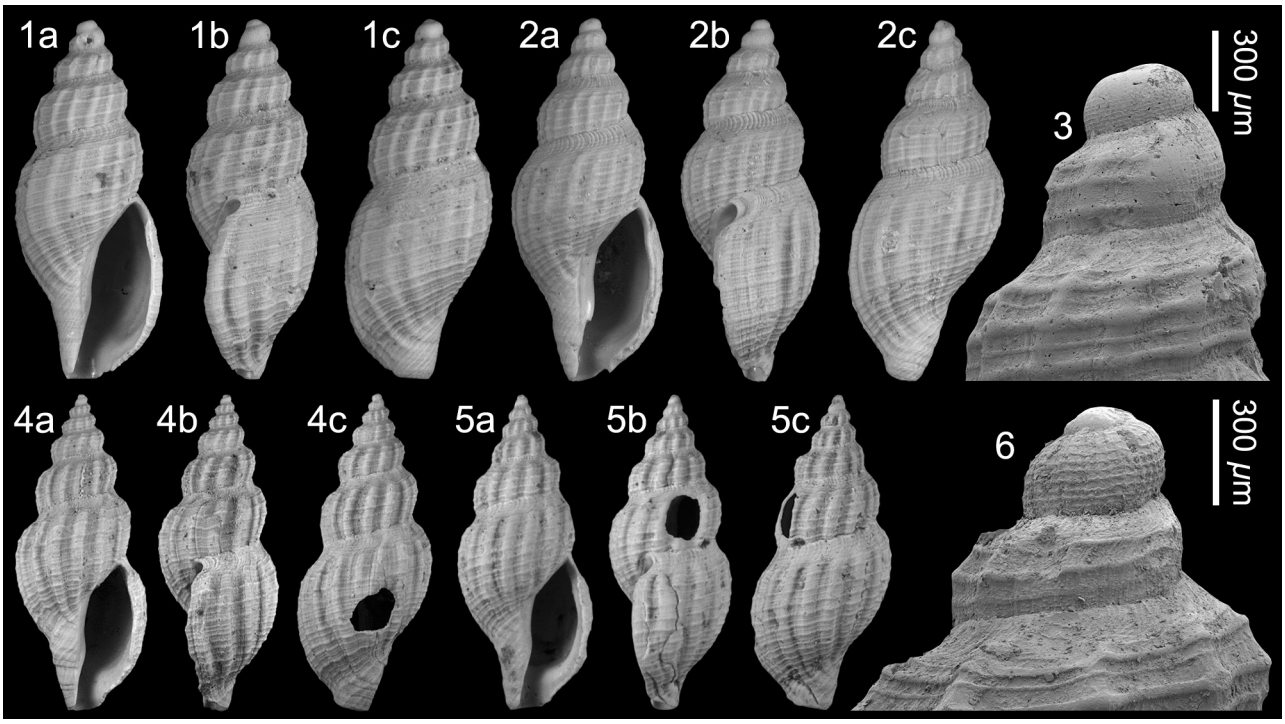

Plate 53. *Leufroyia aldrovandi* (Millet, 1865); 1. NHMW 2016/0103/1235, height 12.2 mm, width 5.0 mm; 2. NHMW 2016/0103/1236, height 10.3 mm, width 4.1 mm; 3. NHMW 2016/0103/1237, height 7.2 mm (juvenile), detail of protoconch (SEM image); 4. NHMW 2016/0103/1214, height 6.7 mm, width 2.8 mm; 5. NHMW 2016/0103/1215, height 7.1 mm, width 2.9 mm; 6. NHMW 2016/0103/1216, height 6.4 mm, width 2.3 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cies, as first revisers we chose *Leufroyia aldrovandi* as name for this species (ICZN, 1999, Art. 24.2.1). Dollfus & Dautzenberg *in* Peyrot (1938, p. 285, pl. 5, figs 40, 56) described what looks like the same species from the middle Miocene of the Loire Basin of France. Luckily the original states '*spire formée de deux tours embryonnaires* lisses….', thus clearly describing a paucispiral protoconch. The microsculpture cannot be seen without SEM imaging. The species was again figured by Glibert (1954, p. 60, pl. 7, figs 8a, b, c) based on Loire Basin material. He compared it with *Leufroyia leufroyi* (Michaud, 1829), but did not notice the difference in protoconch type.

Leufroyia aldrovandi forms part of a group of species in Assemblage I with shape and teleoconch sculpture similar to that of the extant European *L. leufroyi*. This group was recognised by Brébion (1964) in the upper Miocene and Pliocene of NW France and identified as *L. leufroyi* or subspecies thereof. However, they are immediately separated from that species by having paucispiral protoconchs. *Leufroyia leufroyi* has a multispiral protoconch. *Leufroyia ferrierii* Brunetti & Della Bella, 2006 from the Pliocene of Italy has a similarly shaped and sculptured teleoconch, but differs in having a tall multispiral protoconch. For further comparison, see *Leufroyia seani* nov. sp.

Brébion (1964, p. 613) recorded this species (and its various forms) from several Assemblage I localities (Sceaux-d'Anjou, Thorigné, Renauleau), to which we add St-Clément-de-la-Place and Beugnon, and from the Assemblage II locality of Apigné.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Peyrot, 1938; Glibert, 1954). Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1865; Brébion, 1964).

***Leufroyia alternata* (Millet, 1865)**
Plate 54, figs 1-4

1854	*Buccinum Alternatum* Millet, p. 165 (*nomen nudum*).
*1865	*Buccinum alternatum* Millet, p. 597.
1964	*Cythara* (*Mangelia*) *alternata* Millet, 1854 – Brébion, p. 579, pl. 14, figs 10, 11.

Type material – Syntypes: Sceaux-d'Anjou or Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 579).

Material and dimensions – Maximum height 7.0 mm, width 3.0 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1963-1966 (4), NHMW 2016/0103/1967 (6), RGM.1352585 (3), RGM.1352631 (8), LC (1), FVD (2).

Original description – 'Buccinum alternatum. *Millet. Coq. petite, fusiforme, plus ou moins effilée; composée de 6-7 tours de spire, surmontés de petites côtes aiguës,*

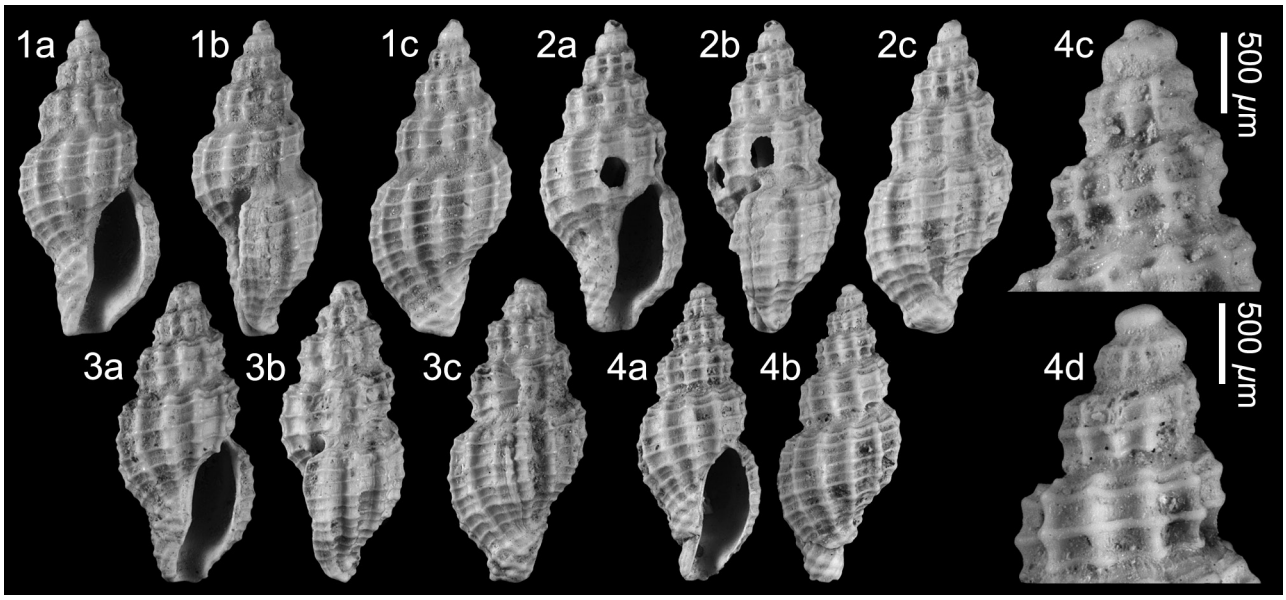

Plate 54. *Leufroyia alternata* (Millet, 1865); 1. NHMW 2016/0103/1963, height 7.0 mm, width 3.0 mm; 2. NHMW 2016/0103/11964, height 6.4 mm, width 2.9 mm; 3. NHMW 2016/0103/11965, height 6.4 mm, width 2.9 mm; 4. NHMW 2016/0103/1966, height 6.0 mm, width 2.7 mm, 4c, d, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

croisées par des stries qui souvent alternent en grosseur. Ouverture petite, terminée inférieurement par un canal court et légèrement oblique. Longueur: 7 millimètres; diamètre: 2 millimètres. Sc., Th.' (Millet, 1865, p. 597).

Discussion – *Leufroyia alternata* (Millet, 1865) has a typical raphitomid shell shape, sculptured by 11-12 prominent orthocline axial ribs, overrun by narrow elevated cords; on the penultimate whorl one cord over the subsutural ramp, three below the shoulder, with secondary cords developed in some of the interspaces on the last whorl. The anal sinus is relatively deep and asymmetrically U-shaped, with the apex placed on the upper half of the subsutural ramp. No denticles are developed within the outer lip. The protoconch is abraded in all specimens, but seems to be of a non-planktotrophic type, of about two whorls with a carinate last half whorl (Pl. 54, figs 4c, d). Brébion (1964, p. 579) placed this species in the Mangeliidae, which is, in our opinion, incorrect and it has little in common with the *Mangelia* species compared by Brébion. *Leufroyia turtaudierei* (Ceulemans, Van Dingenen & Landau, 2018) from the lower Pliocene Assemblage III of NW France is similar in shape and sculpture, but differs in having a broader shell and the secondary spirals appear earlier and are present in all the interspaces. The protoconch in both species is non-planktotrophic, but the sculpture is different, depite the poor preservation in the Assemblage I specimens.
Brébion (1964, p. 580) recorded this species from several Assemblage I localities (Sceaux-d'Anjou, St-Clément-de-la-Place, Thorigné, St-Michel Renauleau).

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

***Leufroyia annegienae* nov. sp.**
Plate 55, figs 1-5

Type material – Holotype MNHN.F.A57928, height 5.2 mm, width 2.6 mm; paratype 1 NHMW 2016/0103/1230, height 5.6 mm, width 2.7 mm; paratype 2 NHMW 2016/0103/1231, 4.6 mm, width 2.2 mm (juvenile); paratype 3 NHMW 2016/0103/1232, height 5.3 mm, width 2.6 mm, **St-Clément-de-la-Place**. Paratype 4 RGM.1352491, height 5.2 mm, width 2.7 mm; paratype 5 RGM.1352514, height 5.2 mm, width 2.5 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 5.6 mm, width 2.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1233 (6), RGM.1352666 (2), LC (1), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/1968-70 (3), NHMW 2016/0103/1971 (11), RGM.718151 (50+), RGM.719021 (11), RGM.734988 (50+), RGM.734990 (1), RGM.734992 (50+), RGM.718173 (50+), RGM.1352586 (21), FVD (3).

Etymology – Named after Annegien Blokpoel, Amsterdam, The Netherlands, friend of the first author (BL). *Leufroyia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Leufroyia* species of small size, biconic, solid, paucispiral dome-shaped protoconch of two whorls, bearing large cruciform micropustules arranged in rows, on second whorl pustules become irregularly coalescent vertically, teleoconch bearing 10-14 axials overrun by

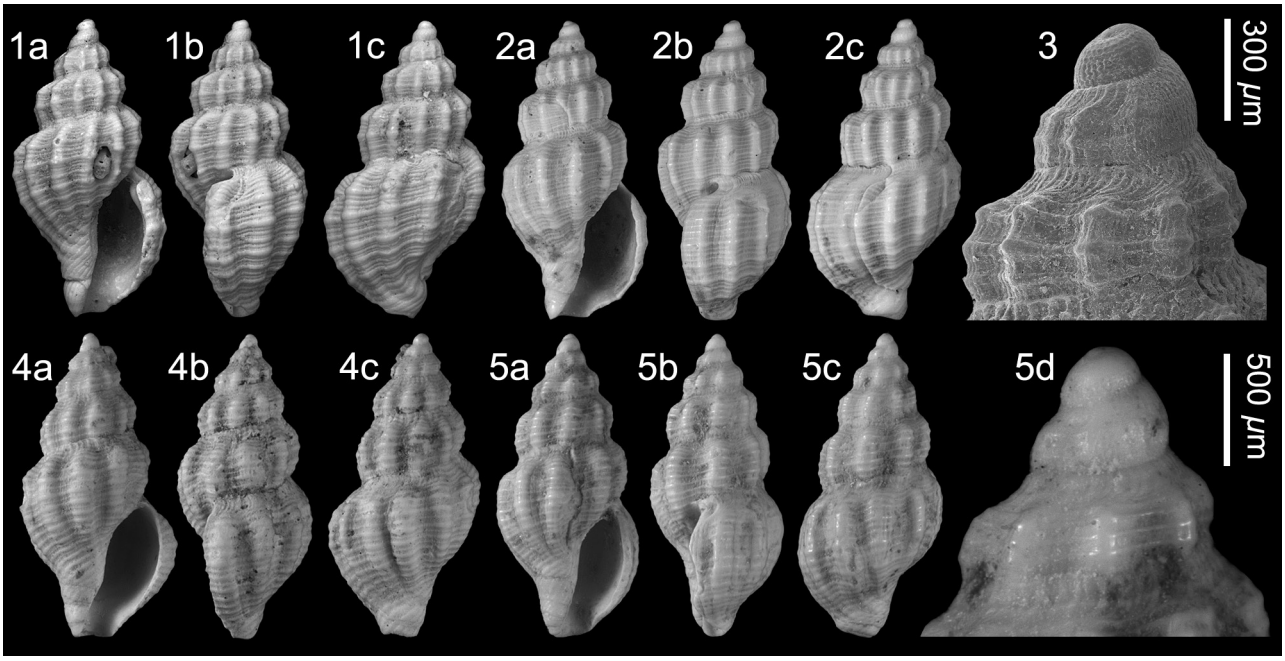

Plate 55. *Leufroyia annegienae* nov. sp.; 1. **Holotype** MNHN.F.A57928, height 5.2 mm, width 2.6 mm; 2. **Paratype 1** NHMW 2016/0103/1230, height 5.6 mm, width 2.7 mm; 3. **Paratype 2** NHMW 2016/0103/1231, height 4.6 mm, width 2.2 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place. 4. NHMW 2016/0103/1968, height 5.6 mm, width 3.0 mm; 5. NHMW 2016/0103/1969, height 5.5 mm, width 2.5 mm, 5d, detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

numerous spirals of primary to tertiary strength, anal sinus narrow, deep U-shaped, siphonal canal short, siphonal fasciole distinct.

Description – Shell small, biconic, solid. Protoconch paucispiral with medium size nucleus, composed of two convex whorls bearing large cruciform micropustules arranged in rows, on second whorl pustules become irregularly coalescent vertically. Junction with teleoconch sharply delimited. Teleoconch of four whorls, broad subsutural ramp with comma-shaped marks just below suture, rounded at high-placed shoulder, convex below, separated by impressed undulating suture. Axial sculpture of 10-14 narrow, rounded, orthocline ribs, half width of their interspaces. Spiral sculpture overruns ribs, three spiral cords on first whorl, abapically secondary and tertiary cords become intercalated, filling interspaces with fine crowded cords of primary to tertiary strength, separated by narrow interspaces. Close-set axial growth lines give surface scabrous appearance, especially immediately below suture. Last whorl with convex subsutural ramp, weakly angled at shoulder, convex below, moderately constricted at base, bearing five primary spiral cords, abapical primary delimits base. Aperture ovate; outer lip weakly thickened, not denticulate within; anal sinus narrow, deep U-shaped, with apex placed on adapical half of subsutural ramp; siphonal canal short, open. Columella moderately excavated just below upper third. Columellar callus poorly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – *Leufroyia annegienae* nov. sp. is characterised by its dense spiral sculpture composed of cords of primary to tertiary strength and its paucispiral protoconch bearing large cruciform pustules that become vertically coalescent on the last half whorl. There is quite some intraspecific variation; the holotype (Pl. 55, fig. 1) is a little squatter than usual with relatively narrow ribs and the primary to tertiary spiral sculpture is well differentiated, whereas some specimens have broader ribs and the spirals are more equal in strength (Pl. 55, figs 4, 5). Numerous intermediates between these two extremes are present and the protoconchs in the two forms are the same, which make us consider this a single variable species. This species is another Assemblage I species similar to that of the extant European *Leufroyia leufroyi* (Michaud, 1828), which is separated by its multispiral protoconch [see under *L. aldrovandi* (Millet, 1865)]. *Leufroyia aldrovandi* (Millet, 1865), with which it co-occurs in Assemblage I is another member of this group that differs from *L. annegienae* in having regularly reticulated microsculpture on its paucispiral protoconch, and a larger, fusiform teleoconch. *Leufroyia landreauensis* (Ceulemans, Van Dingenen & Landau, 2018) is the Assemblage III representative of this group. It differs from *L. annegienae* most notably in its protoconch sculpture. The first whorl is sculptured with irregular threads with very fine tubercles. Coarse tubercles only develop on the last whorl, and only on the abapical half. On the last quarter whorl two tuberculose carinae develop. The teleoconch in *L. landreauensis* is fusiform rather than biconic and the siphonal canal is longer. The sculpture composed of primary to tertiary cords is remarkably

similar in the two species. The specimen from the middle Miocene Paratethys of Poland illustrated by Bałuk (2003, pl. 29, fig. 12) as *Peratotoma leufroyi* (Michaud, 1828) is very similar indeed to some of the shells illustrated here. Unfortunately, in that work Bałuk dedicated to the middle Miocene turrids of Poland, little information was given on protoconch type. The specimen from Poland illustrated does not have its protoconch intact, however, *L. leufroyi* has a tall planktotrophic-type multispiral protoconch that immediately separates it from *L. annegienae*. Bałuk (2003, pl. 29, fig. 4) illustrated another species, *Peratotoma hildae* Boettger, 1902 that also has a similar teleoconch to some of the specimens of *L. annegienae* illustrated here, but in the Polish specimen a tall multispiral protoconch is preserved separating it from the French shell. In the extant Mediterranean fauna *L. erronea* Monterosato, 1884 is very similar to *L. annegienae* in teleoconch shape and sculpture, but differs in having a tall multispiral protoconch.
We record *L. annegienae* from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou.

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

***Leufroyia hesseli* nov. sp.**
Plate 56, figs 1-5

Type material – Holotype MNHN.F.A70541, height 7.8 mm, width 3.3 mm; paratype 1 MNHN.F.A70542, height 6.4 mm, width 3.0 mm; paratype 2 NHMW 2016/0103/1908, height 6.2 mm, width 2.9 mm; paratype 3 NHMW 2016/0103/1226, height 7.5 mm, width 3.4 mm; paratype 4 NHMW 2016/0103/1227, height 7.4 mm, width 3.0 mm; **St-Clément-de-la-Place**. Paratype 5 NHMW 2016/0103/1228, height 6.2 mm, width 3.0 mm; paratype 6 NHMW 2016/0103/1229, height 5.2 mm, width 2.3 mm; **Renauleau**. Paratype 7 RGM.1352322, height 4.7 mm, width 2.5 mm; paratype 8 RGM.1352323, height 5.5 mm, width 2.5 mm; paratype 9 RGM.1352325, height 4.8 mm, width 2.2 mm; **Sceaux-d'Anjou**.

Other material – Maximum height 7.8 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1213 (50+), RGM.1352369 (2), RGM.1352667 (2), RGM.1352694 (2), LC (30), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1799 (34), RGM.718187 (50+), RGM.1352456 (1), RGM.1352495 (4), LC (3), FVD (17). **Renauleau**: NHMW 2016/0103/1909 (50+), LC (50+), FVD (50+).

Etymology – Named after Piet Hessel of Utrecht, The Netherlands, who kindly donated the collection of his *'Stichting Schepsel Schelp*' to the Naturalis Biodiversity Center, Leiden, The Netherlands, which was used in this work. *Leufroyia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

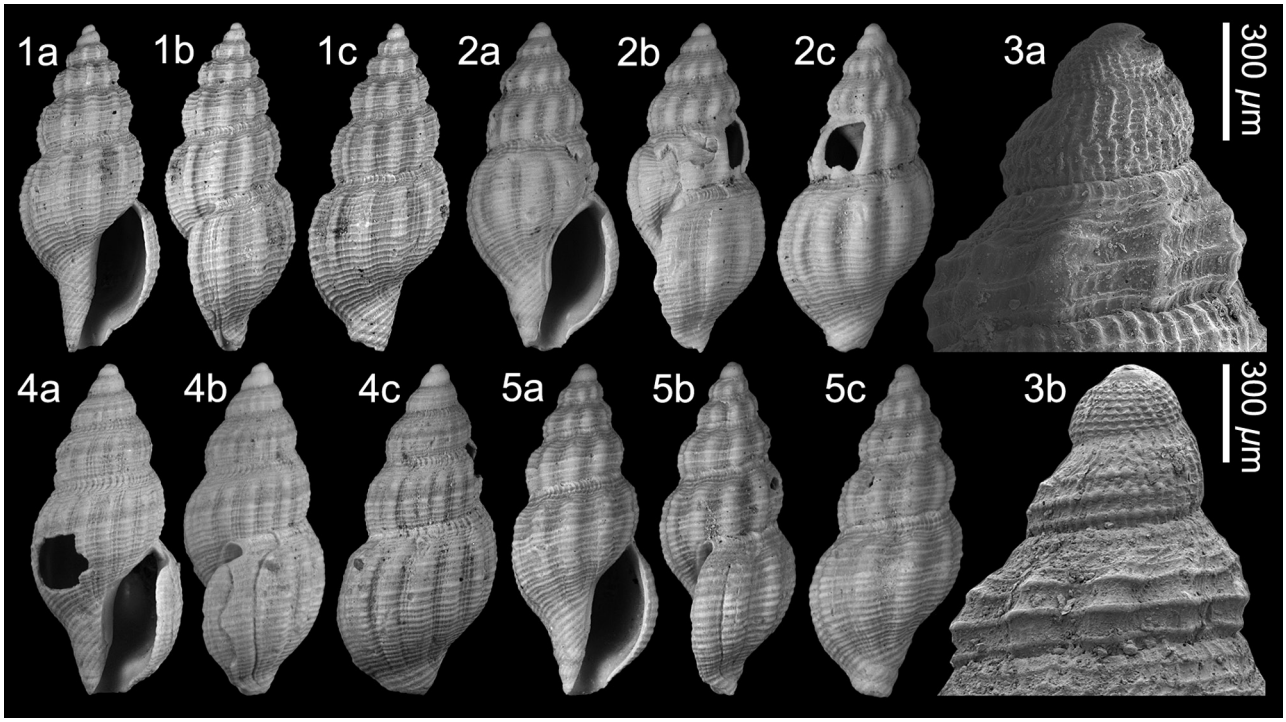

Plate 56. *Leufroyia hesseli* nov. sp.; 1 **Holotype** MNHN.F.A70541, height 7.8 mm, width 3.3 mm; 2. **Paratype 1** MNHN.F.A70542, height 6.4 mm, width 3.0 mm; 3. **Paratype 2** NHMW 2016/0103/1908, height 6.2 mm, width 2.9 mm, 3a, b, detail of protoconch (SEM image); Le Grand Chauvereau, St-Clément-de-la-Place. 4. NHMW 2016/0103/1227, height 6.0 mm, width 2.6 mm; 4. **Paratype 5** NHMW 2016/0103/1228, height 6.2 mm, width 3.0 mm; 5. **Paratype 6** NHMW 2016/0103/1229, height 5.2 mm, width 2.3 mm; Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – Leufroyia species of small size, cyrtopupoid, solid, paucispiral dome-shaped protoconch of just over two whorls, bearing large cruciform micropustules arranged in rows that on second whorl become tuberculose on abapical half of whorl, teleoconch bearing 12-18 broad axials overrun by numerous spirals of subequal strength, anal sinus deep U-shaped, siphonal canal medium to short, siphonal fasciole indistinct.

Description – Shell small, cyrtopupoid, solid. Protoconch paucispiral, composed of just over two convex whorls bearing large cruciform micropustules arranged in rows, on second whorl pustules become tuberculose on abapical half of whorl. Junction with teleoconch sharply delimited. Teleoconch of 4.5 convex whorls, subsutural ramp moderately wide, with comma-shaped marks just below suture, shoulder rounded, poorly developed, convex below, separated by impressed linear suture. Axial sculpture of 12-18 broad, depressed, rounded, orthocline ribs developed only below shoulder, slightly narrower than their interspaces. Spiral sculpture overruns ribs, three spiral cords on first whorl, abapically further cords develop, all subequal and very narrow, about ten on penultimate whorl, about one-third width of their interspaces. Close-set axial growth lines give surface scabrous appearance, especially immediately below suture. Last whorl with moderately wide subsutural ramp, rounded at shoulder, convex below, moderately constricted at base, axials fade over base, covered in fine spiral cords that continue uninterrupted over base and siphonal fasciole. Aperture ovate; outer lip not thickened, not denticulate within; anal sinus narrow, deep U-shaped, with apex placed on abapical half of subsutural ramp; siphonal canal medium to short, open. Columella moderately excavated just below upper third. Columellar callus poorly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole indistinct. Colour pattern of alternating colour bands is preserved in some specimens.

Discussion – Leufroyia hesseli nov. sp. belongs to the group of Assemblage I raphitomids with dome-shaped, strongly sculptured, paucispiral protoconchs, including *L. aldrovandi* (Millet, 1865) and *L. annegienae* nov. sp. The protoconch of *L. aldrovandi* bears finely reticulate microsculpture, as opposed to the coarse pustules seen in *L. hesseli*. That of *L. annegienae* is more similar, as both have large cruciform pustules arranged in rows, but in that species they become irregularly vertically coalescent on the second protoconch whorl, whereas in *L. hesseli* they become tuberculous on the abapical half of the whorl, but not coalescent. The teleoconch of *L. hesseli* can easily be separated from the other two species based on the spiral sculpture. In all three the sculpture consists of numerous fine cords, but in *L. hesseli* they are all of subequal strength, whereas in the other two they are of primary to tertiary strength.
We record this species from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau.

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

***Leufroyia ligeriana* nov sp.**
Plate 57, figs 1-3

Type material – Holotype NHMW 2016/0103/1914, height 11.1 mm, width 5.2 mm; paratype 1 NHMW 2016/0103/1915, height 12.0 mm, width 5.5 mm; paratype 2 NHMW 2016/0103/1916, height 10.4 mm, width 5.2 mm.

Other material – Maximum height 12.0 mm, width 5.5 mm. **Renauleau**: NHMW 2016/0103/1917 (2), LC (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

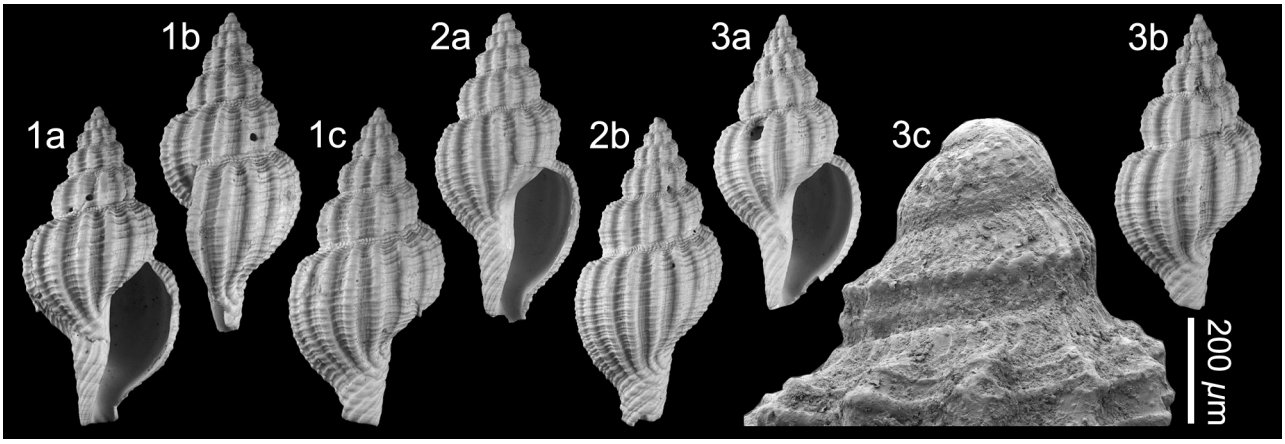

Plate 57. *Leufroyia ligeriana* nov sp.; 1. **Holotype** NHMW 2016/0103/1914, height 11.1 mm, width 5.2 mm; 2. **Paratype 1** NHMW 2016/0103/1915, height 12.0 mm, width 5.5 mm; 3. **Paratype 2** NHMW 2016/0103/1916, height 10.4 mm, width 5.2 mm, 3c, detail of protoconch (SEM image). Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Diagnosis – *Leufroyia* species of medium size, biconic, thin, dome-shaped protoconch of just over two whorls, bear large coalescent micropustules on adapical half, rows of small micropustules on abapical half, axial riblets on last half whorl, stronger central and weaker abapical carinae on last quarter whorl, teleoconch bearing 14-18 axials overrun by numerous spirals of primary to tertiary strength, shallow sinus, siphonal canal long, siphonal fasciole distinct with strong spirals.

Description – Shell medium-sized, biconic, thin. Protoconch dome-shaped, composed of 2-2.25 low convex whorls; postnuclear whorls bear large coalescent micropustules on adapical half, small crowded micropustules arranged in horizontal rows on abapical half, axial riblets on last half whorl, stronger central and weaker abapical carinae on last quarter whorl. Junction with teleoconch sharply delimited. Teleoconch of 5-5.5 strongly convex whorls, subsutural ramp narrow, hardly developed, bearing comma-shaped marks just below suture, shoulder rounded, poorly developed, regularly convex below. Axial sculpture of 14-18 elevated, rounded, weakly prosocline ribs, slightly narrower than their interspaces, overrun by close-set narrow spirals of primary to tertiary strength. Close-set axial growth lines give surface finely reticulate appearance. Last whorl strongly inflated, regularly convex, strongly constricted at base, axials persist over base. Aperture large, ovate; outer lip not thickened, not denticulate within; anal sinus very shallow asymmetrically U-shaped; siphonal canal long, open, straight. Columella strongly excavated in upper third. Columellar callus hardly developed, forming narrow edge; parietal callus not thickened. Siphonal fasciole distinct, bearing strong spiral cords.

Discussion – In Assemblage I *Leufroyia ligeriana* nov sp. is similar to *L. aldrovandi* (Millet, 1865), but that species has a more elongated shell, the last whorl is not as strongly inflated as it is in *L. ligeriana*, the axial sculpture, especially on the last whorl, is weaker, and the protoconch has finely reticulate sculpture without carinae being developed on the last portion (Pl. 53, figs 3, 6) as opposed to the complex protoconch sculpture seen in *L. ligeriana* (Pl. 57, fig. 3c). *Daphnella* (*Daphnella*) *bertrandiana* (Millet, 1865) is more fusiform, with a less inflated last whorl and has subdued sculpture which is finely reticulate on the last whorl, placing it in the genus *Daphnella* rather than *Leufroyia*. The protoconch reticulate microsculpture is similar to that of *L. aldrovandi* and therefore quite different from that seen in *L. ligeriana*. For further comparison see *Leufroyia seani* nov. sp. In the extant Mediterranean fauna the teleoconch of *L. erronea* Monterosato, 1884 shows some similarities to that of *L. ligeriana* in shape and sculpture, but the species differs in having a tall multispiral protoconch.
We have found *L. ligeriana* only at the locality of Renauleau, where it is uncommon.

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

***Leufroyia renauleauensis* nov. sp.**
Plate 58, figs 1-3

Type material – Holotype NHMW 2016/0103/1728, height 4.0 mm, width 1.5 mm; Paratype 1 NHMW 2016/0103/1217, height 3.4 mm, width 1.3 mm; **Renauleau**. Paratype 2 NHMW 2016/0103/1243, height 3.5 mm, width 1.4 mm (incomplete); paratype 3 NHMW 2016/0103/1990, height 3.3 mm, width 1.3 mm; paratype 4 RGM.1352688, height 2.8 mm, width 1.1 mm **St-Clément-de-la-Place**.

Other material – Maximum height 4.0 mm, width 1.5 mm. **St-Clément-de-la-Place**: RGM.1352689 (6 fragments). **Renauleau**: 2016/0103/1927 (4), LC (3).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Leufroyia* species of small size, slender fusiform, thin, paucispiral dome-shaped protoconch of just over two whorls, nucleus raised, post nuclear whorls axially sculptured with numerous spiral threads in interspaces, two strong carinae on last quarter whorl, teleoconch bearing subquadrate reticulate sculpture, 17-19 axial ribs, four narrow spirals on penultimate whorl, secondaries in some interspaces, anal sinus moderately shallow and wide, siphonal fasciole distinct.

Description – Shell small, slender fusiform, thin. Protoconch paucispiral, high dome-shaped, composed of just over two whorls; nucleus raised, rounded; post-nuclear whorls convex, bearing widely spaced axial ribs, with numerous fine spiral threads in interspaces; two raised carinae develop on last half whorl; adapical one placed at shoulder, abapical just above suture. Junction with teleoconch sharply delimited. Teleoconch of three convex whorls, subsutural ramp broad, with strong comma-shaped marks below suture, shoulder rounded, profile convex below, separated by deeply impressed linear suture. Axial sculpture of orthocline to slightly opisthocline narrow rounded ribs, 17-19 on last whorl, half width of their interspaces. Spiral sculpture of narrow cords overrun ribs forming subquadrate cancellation, small tubercles developed at intersections. Three cords on first teleoconch whorl; adapical and abapical cords develop from protoconch carinae; mid-whorl third primary develops immediately equal in strength to other spirals. On penultimate whorl fourth primary develops at abapical suture, single secondary intercalated in interspaces on second half penultimate whorl in some specimens. Last whorl weakly inflated, evenly convex, moderately constricted at base; axials weaken over base, one spiral over subsutural platform, six below shoulder, with variable number of secondary threads intercalated, further 5-6 on siphonal fasciole. Aperture ovate; outer lip weakly thickened,

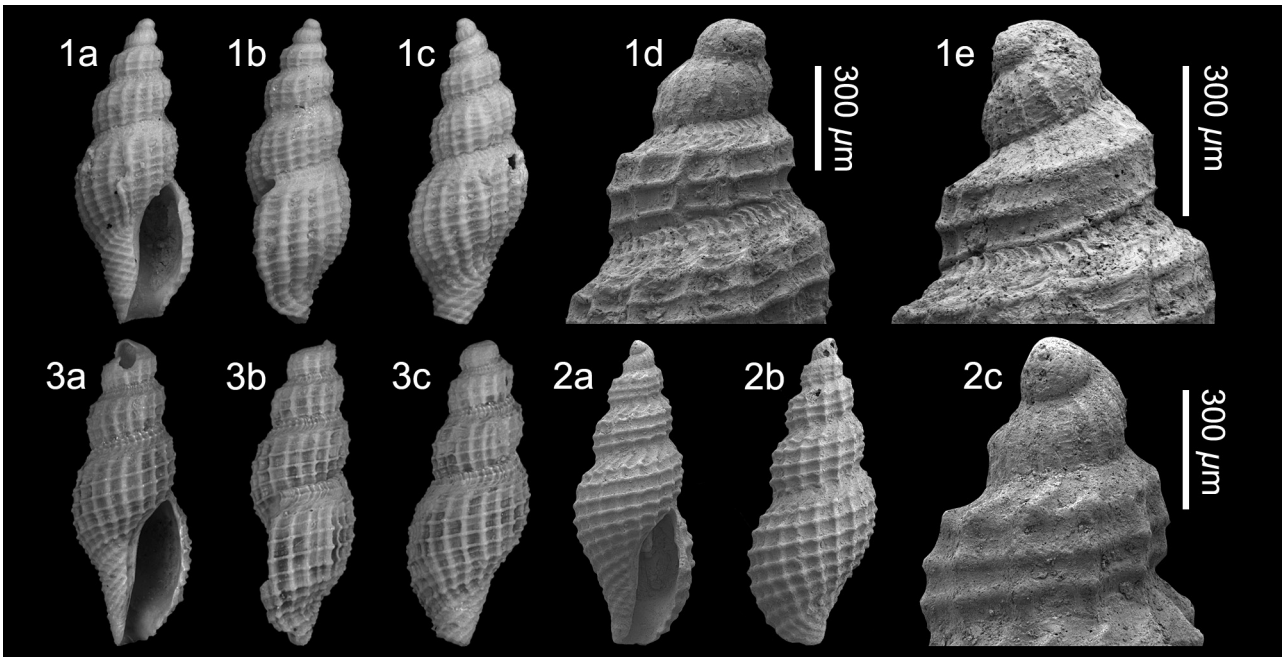

Plate 58. *Leufroyia renauleauensis* nov. sp.; 1. **Holotype** NHMW 2016/0103/1728, height 4.0 mm, width 1.5 mm, 1d, e, detail of protoconch (SEM image); 2. **Paratype 1** NHMW 2016/0103/1217, height 3.4 mm, width 1.3 mm, 2c, detail of protoconch (SEM image). Renauleau. 3. **Paratype 2** NHMW 2016/0103/1243, height 3.5 mm, width 1.4 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

not denticulate; anal sinus moderately shallow and wide, U-shaped; siphonal canal short, wide, open. Columella weakly excavated. Columellar callus poorly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – *Leufroyia renauleauensis* nov. sp. is yet another unusual Assemblage I raphitomid. The dome-shape, paucispiral protoconch, with a high nucleus and convex, axially sculptured post-nuclear whorl with numerous fine threads in the interspaces between the ribs is not a protoconchs type we have encountered in any other European Neogene to present-day raphitomid. The teleoconch sculpture is typical for raphitomids, reticulate with tubercles produced at the intersections, some of the extant European species also have a relatively slender teleoconch. Bałuk (2003, pl. 26, figs 1, 2) illustrated a shell from the middle Miocene Paratethys of Poland with a very similar teleoconch under the name *Clathurella henrichi* Boettger, 1902. However, Bałuk's figure clearly shows that species to have a tall multispiral protoconch.
It seems to be uncommon in Assemblage I, where we have found it only at Renauleau and St-Clément-de-la-Place, but the small number of specimens shows some variability mainly in the development of secondary spiral sculpture. The holotype (Pl. 58, fig. 1) has secondary threads developed in some of the interspaces on the penultimate whorl, whereas Paratype 1 (Pl. 58, fig. 2) has no secondary spiral sculpture.

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

***Leufroyia riccardoi* nov. sp.**
Plate 59, fig. 1

Type material – Holotype NHMW 2016/0103/2056, height 3.5 mm, width 1.5 mm.

Other material – Known only from holotype.

Etymology – Named after Riccardo Giannuzzi-Savelli of Palermo, Italy, in recognition of his enormous contribution to Mediterranean malacology. *Leufroyia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Leufroyia* species of small size, subpupoid, solid, protoconch of almost three whorls with net-like microsculpture, teleoconch of three whorls, bearing ten narrow axials overrun by narrow spirals, anal sinus hardly developed, siphonal canal medium length, siphonal fasciole indistinct.

Description – Shell small, subpupoid, solid. Protoconch of almost three convex whorls, covered in reticulated net-like sculpture, horizontal on first postnuclear whorl, diagonal on last protoconch whorl. Junction with teleoconch sharply delimited by change in sculpture. Teleoconch of three convex whorls, separated by impressed undulating suture. Sculpture of ten narrow, rounded

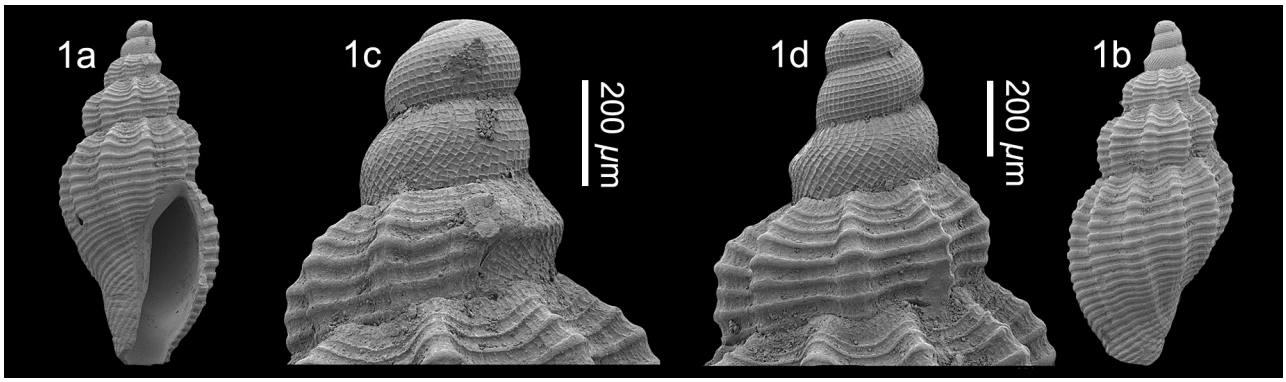

Plate 59. *Leufroyia riccardoi* nov. sp.; 1 **Holotype** NHMW 2016/0103/2056, height 3.5 mm, width 1.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

axial ribs overrun by eight narrower spirals; shoulder spiral slightly strengthened. Micropustules are present in interspaces between spirals. Last whorl evenly convex, moderately constricted at base, axials fade over base, covered in fine spiral cords that continue uninterrupted over base and siphonal fasciole. Aperture ovate-elongate; outer lip not thickened, not denticulate within; anal sinus hardly developed; siphonal canal medium length, open. Columella excavated in upper third. Columellar and parietal callus poorly developed, forming narrow callus rim. Siphonal fasciole indistinct.

Discussion – *Leufroyia riccardoi* nov. sp. differs from all its Assemblage I congeners in having a netted protoconch microsculpture, so typically seen in raphitomids, but absent in all but one of the Assemblage I species. Only *Cyrillia michalidesi* nov. sp. has netted protoconch microsculpture (see above), but that species is immediately separated by having a protoconch with an extra whorl and denser teleoconch sculpture with more crowded ribs and cords. This species is exceedingly uncommon and so far found only at Sceaux-d'Anjou.

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

***Leufroyia seani* nov sp.**
Plate 60, figs 1-3

Type material – Holotype NHMW 2016/0103/1922, height 10.9 mm, width 4.2 mm; paratype 1 NHMW 2016/0103/1923, height 9.1 mm, width 3.4 mm; paratype 2 NHMW 2016/0103/1924, height 9.2 mm, width 4.0 mm.

Other material – Maximum height 12.0 mm, width 5.5 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1926 (5). **Renauleau**: NHMW 2016/0103/1925 (7), LC (10), FVD (8).

Etymology – Named after Sean Michael Landau, son of the first author. *Leufroyia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Leufroyia* species of medium size, fusiform, thin, protoconch of two whorls, postnuclear whorl coronate, strongly angled at shoulder carina, sculptured with prominent axial riblets, tubercular over shoulder carina, teleoconch bearing 14-16 axials overrun by narrow spirals of equal strength, siphonal canal medium-length, siphonal fasciole bearing strong spirals.

Description – Shell medium-sized, fusiform, thin. Protoconch paucispiral, composed of two whorls; nucleus medium-sized, postnuclear whorl strongly angled at broad shoulder, carina placed high, giving whorl coronate appearance, sculptured with prominent strongly prosocline axial riblets, tubercular over shoulder carina. Junction with teleoconch sharply delimited. Teleoconch of 5.5 convex whorls, subsutural ramp narrow, shoulder rounded, poorly developed, regularly convex below. Axial sculpture of 14-16 elevated, rounded, weakly prosocline ribs, slightly narrower than their interspaces, overrun by narrow spirals of equal strength, rarely a secondary cord developed in one or two interspaces on later whorls. Close-set axial growth lines visible in interspaces between spirals. Last whorl moderately inflated, convex, moderately constricted at base, axials persist over base. Aperture ovate; outer lip not thickened, not denticulate within; anal sinus medium-depth, narrow symmetrically U-shaped, with apex mid-subsutural ramp; siphonal canal medium length, open, slightly recurved. Columella weakly excavated in mid-portion. Columellar callus hardly developed, forming narrow indented edge; parietal callus not thickened. Siphonal fasciole distinct, bearing strong spiral cords.

Discussion – Several species with similar teleoconch shape and sculpture to those seen in *Leufroyia seani* nov sp. occur in Assemblage I that are most easily separated by their protoconchs. All have protoconch suggesting non-planktotrophic development, but with quite distinct shape and sculpture. *Leufroyia aldrovandi* (Millet, 1865) differs in having a well-defined subsutural platform with comma-shape riblets and spiral sculpture of primary to

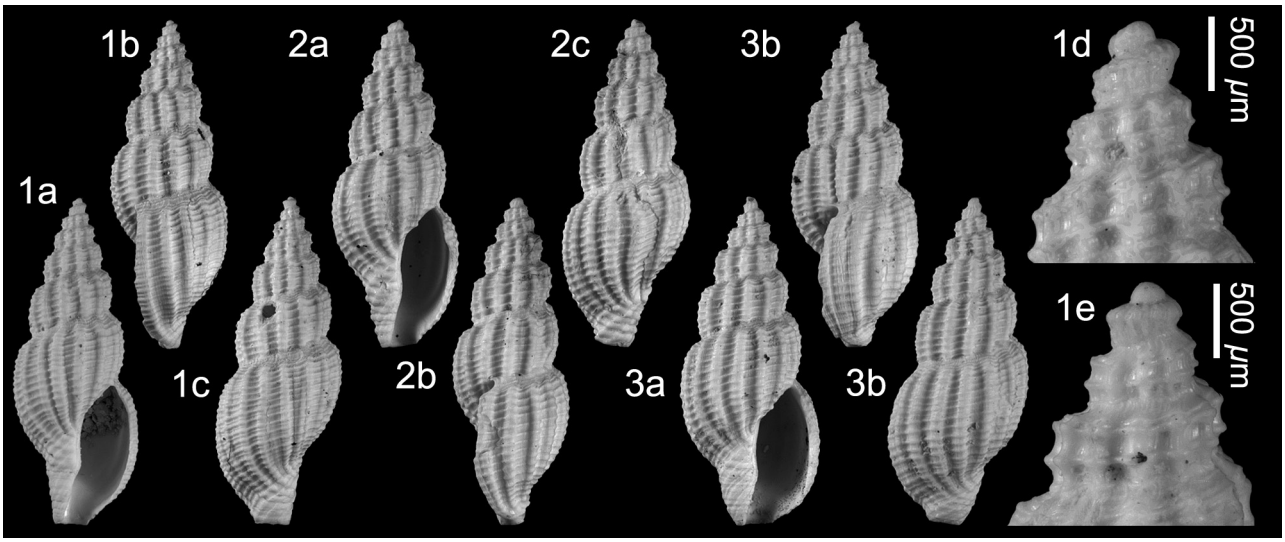

Plate 60. *Leufroyia seani* nov sp.; 1. **Holotype** NHMW 2016/0103/1922, height 10.9 mm, width 4.2 mm, 1d, e, detail of protoconch; 2. **Paratype 1** NHMW 2016/0103/1923, height 9.1 mm, width 3.4 mm; 3. **Paratype 2** NHMW 2016/0103/1924, height 9.2 mm, width 4.0 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

tertiary strength, whereas all the spiral cords in *R. seani* are of equal strength. The protoconch of that species consists of two convex whorls with fine reticulate microsculpture (Pl. 53, figs 3, 6). *Daphnella* (*Daphnella*) *bertrandiana* (Millet, 1865) is larger shelled, with much finer reticulated sculpture on the last whorl, placing it in the genus *Daphnella* rather than *Leufroyia*. It also has a finely reticulate protoconch (Pl. 50, fig. 3). *Leufroyia ligeriana* nov. sp. has a wider, more inflated biconic shell shape and spirals of alternating strength. Its dome-shaped protoconch has a complex tubercular sculpture (Pl. 57, fig 3c). *Leufroyia seani* nov. sp. has so far been found only at the locality of Renauleau.

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

Genus *Raphitoma* Bellardi, 1847

Type species – *Raphitoma histrix* Bellardi, 1847, by subsequent designation, Monterosato, 1872, Pliocene, Italy.

1847 *Raphitoma* Bellardi, p. 16.

1875 *Homotoma* Bellardi, p. 22. Type species (by subsequent designation; Powell, 1966): *Murex reticulatus* Renier, 1804, present-day, Italy. Junior homonym of *Homotoma* Guérin-Méneville, 1844 [Hemiptera].

1884 *Cordieria* Monterosato, p. 131. Type species (by subsequent designation; Crosse, 1885): *Murex reticulatus* Brocchi, 1814, Pliocene, Italy. Junior homonym of *Cordieria* Rouault, 1848.

1884 *Philbertia* Monterosato, p. 132. Type species (by subsequent designation; Crosse, 1885): *Pleurotoma bicolor* Risso, 1826, present-day, Mediterranean.

1891 *Peratotoma* Harris & Burrows, p. 133. Type species (by subsequent designation; Powell, 1966): *Murex reticulatus* Renier, 1804, present-day, Italy. *Nom. nov. pro Homotoma* A. Bellardi, 1875, *non* Guérin-Méneville, 1844 [Hemiptera].

1968 *Cyrtoides* Nordsieck, p. 176. Type species (by original designation): *Pleurotoma rudis* Scacchi, 1836, present-day, Mediterranean.

Note – Fassio *et al*. (2019) characterised species within the genus *Raphitoma* Bellardi, 1847 as being turreted to biconic-pupoid, small to medium sized for the family, with a slender spire composed of regularly convex whorls, bearing reticulate sculpture, with the axials predominant, granular microsculpture present in some species, a thickened denticulate outer lip, and a very short to moderately long siphonal canal. The protoconch was described as multispiral or paucispiral with reticulate sculpture. The species included here are all paucispiral, but some show other types of sculpture; axially ribbed (*R. soniusae* nov. sp. and *R. vercingetorixi* Ceulemans, Van Dingenen & Landau, 2018) or sharply keeled (*Raphitoma vogeli* nov. sp.).
In their taxonomic revision of the lower Pliocene Assemblage III gastropods of northwestern France, Ceulemans *et al*. (2018) placed eight species within the genus *Raphitoma*, at the time used in a wider sense. These are here reassigned to genera, following Fassio *et al*. (2019).

Raphitoma bertrandiana (Millet, 1865) = *Daphnella* (*Daphnella*)
Raphitoma georgesi Ceulemans, Van Dingenen & Landau, 2018 = *Cyrillia*
Raphitoma landreauensis Ceulemans, Van Dingenen & Landau, 2018 = *Leufroyia*
Raphitoma palumbina Ceulemans, Van Dingenen & Landau, 2018 = not reassigned

Raphitoma pseudohystrix (Sykes, 1906) = *Raphitoma dellabellaorum* nov. sp. (see below)
Raphitoma turtaudierei Ceulemans, Van Dingenen & Landau, 2018 = *Leufroyia*
Raphitoma vercingetorixi Ceulemans, Van Dingenen & Landau, 2018 = not reassigned
Raphitoma pseudoconcinna Ceulemans, Van Dingenen & Landau, 2018 = *Daphnella* (*Daphnella*)

***Raphitoma breitenbergeri* nov. sp.**
Plate 61, figs 1-4

Type material – Holotype NHMW 2016/0103/1977, height 5.6 mm, width 2.6 mm, **Renauleau**. Paratype 1 NHMW 2016/0103/1979, height 6.7 mm, width 3.4 mm; paratype 2 NHMW 2016/0103/1980, height 5.7 mm, width 2.5 mm; paratype 3 NHMW 2016/0103/1981, height 4.8 mm (subadult); paratype 4 RGM.1352600, 6.2 mm, width 2.8 mm; paratype 5 RGM.1352601, 5.9 mm, width 2.8 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 6.4 mm, width 3.4 mm. **Sceaux-d'Anjou:** RGM.734996 (5). **Renauleau**: NHMW 2016/0103/1978 (1), LC (2).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Raphitoma* species of small size, ovatopupoid, paucispiral protoconch of 1.5 whorls, with smooth nucleus followed by close-set axial riblets, teleoconch of 3.5 convex whorls, bearing 16-18 axial ribs and raised narrow cords, no secondary spirals developed, 8-9 labial denticles, D1 strongest developed to variable degree, narrow anal sinus, moderate length siphonal canal.

Description – Shell small, ovatopupoid, robust. Protoconch paucispiral, composed of 1.5 whorls; nucleus large, smooth, postnuclear whorl bearing close-set axial riblets. Junction with teleoconch sharply delimited. Teleoconch of 3.5 convex whorls, subsutural ramp and shoulder hardly delimited; suture impressed, undulating. Axial sculpture of narrow, raised, rounded weakly opisthocline ribs, 16-18 on last whorl, about half width of interspaces. Spiral sculpture of narrow elevated equal cords overrun ribs, weakly swollen at intersections, six on penultimate whorl; no secondary spirals developed. Last whorl moderately globose, evenly convex, moderately constricted at base; axials strongly developed and elevated, continuing onto base, about 12 spirals on last whorl plus further 5-6 stronger beaded cords over siphonal fasciole. Aperture ovate, outer lip thickened, convex in profile, bearing 8-9 tubercular denticles within, D1 strongest; lower denticles not developed in some specimens; anal sinus narrow, relatively deep, symetrically U-shaped, with apex mid-subsutural ramp, delimited laterally by D1 within outer lip; siphonal canal moderate length, straight, open. Columella excavated in upper third. Columellar callus poorly developed, forming narrow indented edge. Siphonal fasciole not sharply delimited.

Discussion – *Raphitoma breitenbergeri* nov. sp. is similar to *Raphitoma vercingetorixi* Ceulemans, Van Dingenen & Landau, 2018 (see below) in sculpture and apertural characters, but differs in being smaller, squatter, with

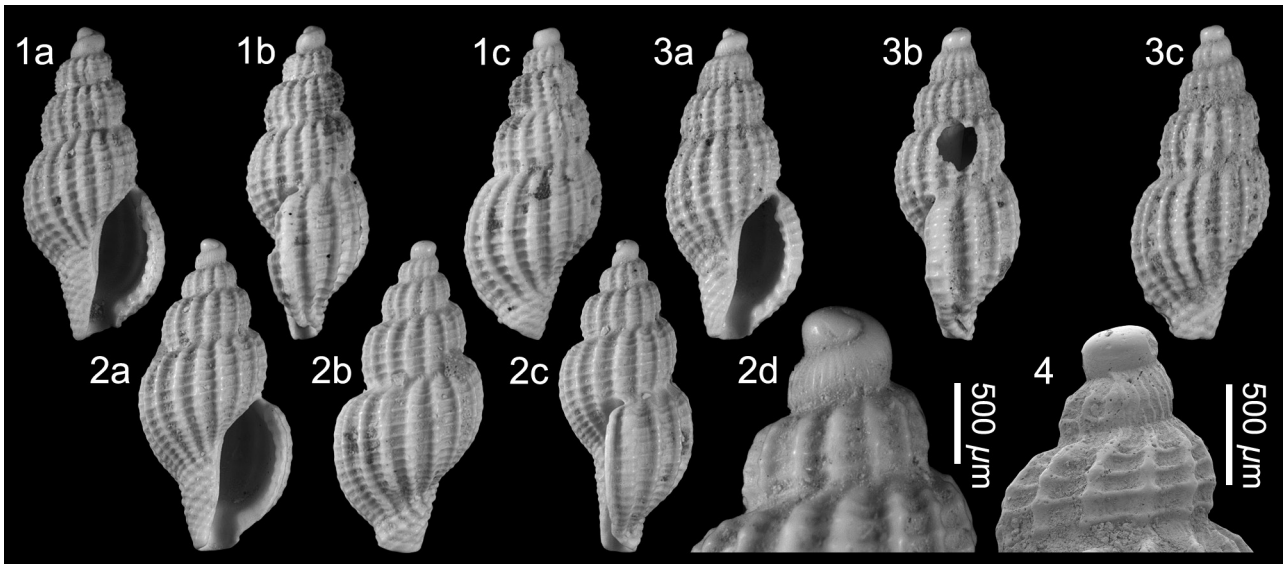

Plate 61. *Raphitoma breitenbergeri* nov. sp.; 1. **Holotype** NHMW 2016/0103/1977, height 5.6 mm, width 2.6 mm. **Renauleau**. 2. **Paratype 1** NHMW 2016/0103/1979, height 6.7 mm, width 3.4 mm, 2d, detail of protoconch; 3. **Paratype 2** NHMW 2016/0103/1980, height 5.7 mm, width 2.5 mm; 4. **Paratype 3** NHMW 2016/0103/1981, height 4.8 mm (subadult), detail of protoconch (SEM image). La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

fewer teleoconch whorls, denser axial sculpture, spiral sculpture composed of only primary cords, whereas the spirals are of alternate strength in *R. vercingetorixi*, and in having a larger, dome-shaped protoconch with denser axial riblets. Moreover, the axial ribs are present over the entire protoconch of *R. vercingetorixi*, whereas in *R. breitenbergeri* the nucleus is smooth.
Raphitoma breitenbergeri is here recorded from the Assemblage I localities of Sceaux-d'Anjou and Renauleau.

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

***Raphitoma dellabellaorum* nov. sp.**
Plate 62, figs 1-2

1964 *Raphitoma hystrix* Jan, 1832 – Brébion, p. 603, pl. 14, figs 32-34 [*non Raphitoma hystrix* (De Cristofori & Jan, 1832)].
2018 *Raphitoma pseudohystrix* (Sykes, 1906) – Ceulemans *et al*., p. 110, pl. 5, figs 1-3 [*non Raphitoma hystrix* (Sykes, 1906)].

Type material – Holotype NHMW 2016/0103/0979, height 8.7 mm, width 3.2 mm; paratype 1 NHMW 2016/0103/0980, height 5.5 mm, 2.2 mm (juvenile), **St-Clément-de-la-Place**. Paratype 2 NHMW 2016/0103/1791, height 8.5 mm, width 3.1 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 13.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0981 (27), RGM.1352382 (4), RGM.1352690 (10), LC (18), FVD (24). **Sceaux-d'Anjou**: RGM.734998 (2), RGM.1352591 (1 fragment), LC (1).

Etymology – Named after Giano Della Bella and his son Enzo Della Bella for their help and advice during this work. *Raphitoma* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Raphitoma* species of medium size, slender fusiform shape, fragile, paucispiral protoconch with fine reticulate microsculpture, teleoconch densely sculptured with 20-30 ribs and close-set subequal cords with small spines developed at intersections.

Description – Shell medium sized, fragile, fusiform, slender. Protoconch paucispiral, comprised of 1.5-2 convex whorls, with large nucleus, covered in fine, irregularly reticulate microsculpture. Junction with teleoconch sharply delimited by change to adult sculpture. Teleoconch of 5-5.5 scalate whorls, with smooth, narrow, concave subsutural ramp, evenly convex below, separated by superficial suture. Axial sculpture of 20-30 narrow, slightly opisthocline axial ribs on last whorl, about one-third width of interspaces. Spiral sculpture of subequal narrow cords, three at protoconch/teleoconch junction, with fourth appearing at abapical suture soon after, five on second whorl, eight on penultimate whorl, 6-10 above aperture on last whorl; short spines developed at intersections. Last whorl evenly convex below narrow subsutural ramp, strongly constricted at base, occasional secondary spiral thread developed in some interspaces, mainly mid-whorl. Aperture narrow, elongate; outer lip not thickened, smooth within, anal canal narrow U-shaped, occupying area of subsutural ramp. Siphonal fasciole long, slightly twisted, bearing 7-9 spinous cords.

Discussion – Ceulemans *et al*. (2018) identified this species in the lower Pliocene Assemblage III of NW France as *Raphitoma pseudohystrix* (Sykes, 1906), and indeed they are very similar, both sharing a paucispiral netted protoconch, slender fusiform teleoconch sculpture consisting of fine axial ribs and cords with small spines produced at the intersections. However, with the additional material now available from Assemblage I, and the advice given to us from Italian specialists (Riccardo Gian-

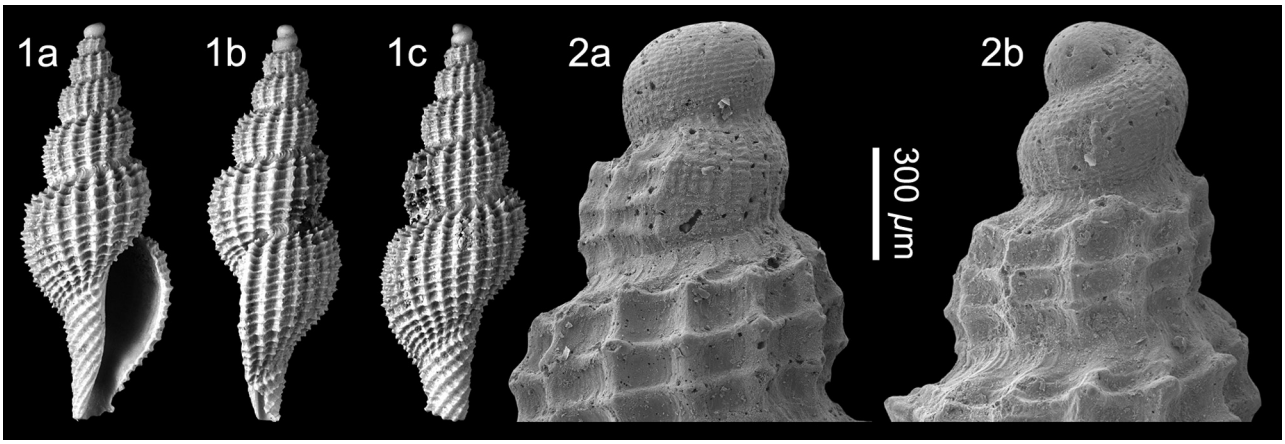

Plate 62. *Raphitoma dellabellaorum* nov. sp.; 1. **Holotype** NHMW 2016/0103/0979, height 8.7 mm, width 3.2 mm; 2. **Paratype 1** NHMW 2016/0103/0980, height 5.5 mm, 2.2 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

nuzzi-Savelli and Giano Della Bella, in review, 2019), we describe it as a separate species; *Raphitoma dellabellaorum* nov. sp. The French species differs from *R. pseudohystrix* most importantly in its spiral sculpture. There are three spirals at the protoconch/teleoconch boundary, with a fourth developing at the abapical suture immediately after the boundary, whereas there are only two spirals at the protoconch/teleoconch boundary and first two teleoconch whorls in *R. pseudohystrix*. On later whorls the spirals are more numerous and subequal in strength in *R. dellabellaorum*, whereas in *R. pseudohystrix* they are less numerous and of alternating strength. Other differences are that on average *R. dellabellaorum* are more numerous axial ribs on last whorl 20-30 (12-29[14] for extant *R. pseudohystrix*), although their ranges overlap, and there are no denticles developed within the outer lip. Both species have 6-10 cordlets above the aperture on the last whorl (up to 9 for extant *R. pseudohystrix*), and 7-9 cords on the siphonal canal.
We record this species from Assemblage I (Sceaux-d'Anjou, St-Clément-de-la-Place). Brébion (1964, p. 604) and Ceulemans *et al*. (2018, p. 110) recorded it from Assemblage III (Le Pigeon Blanc).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018).

***Raphitoma soniusae* nov. sp.**
Plate 63, figs 1-3

Type material – Holotype NHMW 2016/0103/1912, height 5.6 mm, width 2.6 mm; paratype 1 NHMW 2016/0103/1913, height 3.1 mm (juvenile); **Renauleau**. Paratype 2 NHMW 2016/0103/1241, height 5.3 mm, width 2.3 mm; paratype 3 RGM.1352370, height 3.3 mm, width 1.6 mm; paratype 4 RGM.1352371, height 3.2 mm, width 1.5 mm; **St-Clément-de-la-Place**.

Other material – Maximum height 5.6 mm, width 2.6 mm. **Renauleau**: NHMW 2016/0103/1800 (3 juveniles and fragments), LC (2). **Sceaux-d'Anjou**: RGM.1352592 (5).

Etymology – Named after Petra Sonius, volunteer photographer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Raphitoma* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Raphitoma* species of small size, turreted, fragile, paucispiral protoconch of two whorls, post-nuclear whorls subquadrate with riblets most strongly developed in adapical half, teleoconch with angular, convex whorls, subsutural ramp broad, smooth, bearing coarse rectangular reticulate sculpture, ribs and cords very raised and narrow, long siphonal canal, distinct siphonal fasciole.

Description – Shell small, turreted, fragile. Protoconch paucispiral, composed of just over two whorls, post-nuclear whorls strongly angled at shoulder and tapering towards suture just above base, straight sided mid-whorl, producing subquadrate profile; widely spaced axial riblets on post-nuclear whorls, most strongly developed above and over shoulder; no microsculpture present. Junction with teleoconch sharply delimited. Teleoconch of four angular whorls, subsutural ramp broad, shoulder angular; suture superficial, undulating. Axial sculpture of widely spaced, orthocline, narrow, strongly raised, rounded ribs, 12 on last whorl, one sixth width of interspaces. Spiral sculpture of narrow cords overrun ribs forming rectangular cancellation, spinulose tubercles developed at intersections. Two cords on first teleoconch whorl. On second whorl third primary develops mid-whorl between the two primaries always remaining slightly weaker than primaries, further cord develops above shoulder cord. Last whorl moderately inflated, subsutural ramp broad, smooth, concave, roundly angled at shoulder, strongly convex below, very strongly constricted at base; axials

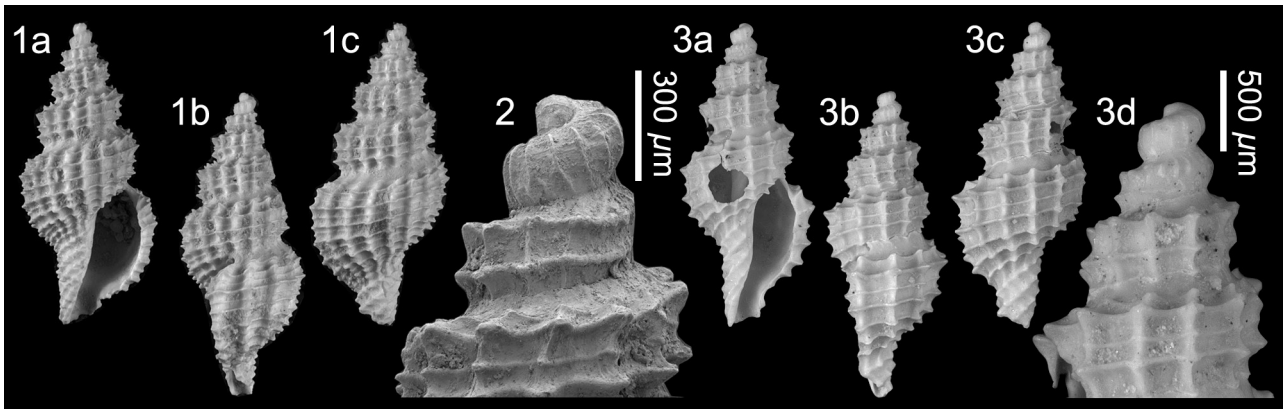

Plate 63. *Raphitoma soniusae* nov. sp.; 1. **Holotype** NHMW 2016/0103/1912, height 5.6 mm, width 2.6 mm; 2. **Paratype 1** NHMW 2016/0103/1913, height 3.1 mm (juvenile), detail of protoconch (SEM image). Renauleau. 3. **Paratype 2** NHMW 2016/0103/1241, height 5.3 mm, width 2.3 mm, 3d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

continue over base, seven spirals on last whorl, further five on siphonal fasciole. Aperture elongate-ovate; outer lip incomplete; anal sinus incomplete, but probably deeply U-shaped; siphonal canal long, twisted, open. Columella moderately excavated in upper third. Columellar callus poorly developed, forming narrow callus edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – The protoconch of *Raphitoma soniusi* nov. sp. is different from any other *Raphitoma* species from Assemblage I and of a type we have not encountered in the European Neogene to extant faunas. The paucispiral protoconch of just over two whorls is strongly shouldered adapically and constricted just above the suture, giving the post-nuclear whorls a subquadrate profile. This species is most similar to *R. vogeli* nov. sp., with which it co-occurs, but that species has a biconic rather than turreted profile and although both have a paucispiral subquadrate protoconch, in *R. vogeli* it is covered in cruciform micropustules rather than riblets. The teleoconch sculpture of the two species is very similar. The shape and teleoconch sculpture is also similar to that of *R. subpurpurea* (Boettger, 1902), from the middle Miocene Paratethys and eastern Mediterranean, but that species has a multispiral protoconch (see Bałuk, 2003, pl. 28, figs 11-13).
We record *R. soniusi* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, uncommon at all localities.

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

***Raphitoma vercingetorixi* Ceulemans, Van Dingenen & Landau, 2018**
Plate 64, figs 1-3

1964 *Raphitoma* (*Philbertia*) *purpurea* var. *gliberti* Brébion, p. 606, pl. 14, figs 36, 37 (*nomen nudum*).
*2018 *Raphitoma vercingetorixi* Ceulemans, Van Dingenen & Landau, p. 112, pl. 5, figs 5, 6.

Material and dimensions – Maximum height 8.3 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0986-0988 (3), NHMW 2016/0103/0989 (50+), RGM.1352381 (22), RGM.1352691 (28), LC (26), FVD (19). **Sceaux-d'Anjou**: NHMW 2016/0103/1798 (8), RGM.718171 (36 juveniles), RGM.1352593 (2), LC (1), FVD (4). **Beugnon**: RGM.717786 (1).

Discussion – *Raphitoma vercingetorixi* Ceulemans, Van Dingenen & Landau, 2018 is characterised by its small, fusiform, robust shell. The protoconch is paucispiral, of about two whorls, of which the first whorl bears fine reticulate microsculpture, the second predominant axial riblets. The teleoconch whorls are strongly convex, with a plain and wide subsutural ramp, finely sculptured by 15 weakly prosocline raised axial ribs overrun by narrow spirals, four on penultimate whorl, forming rectangular reticulate pattern, with elongated tubercles developed at the intersections. The surface is smooth, without microsculpture. The aperture is thickened, denticulate within in fully adult specimens. The anal sinus is small, shallow U-shaped, with its apex just above mid-subsutural ramp, delimited laterally by a double tooth within the outer lip.

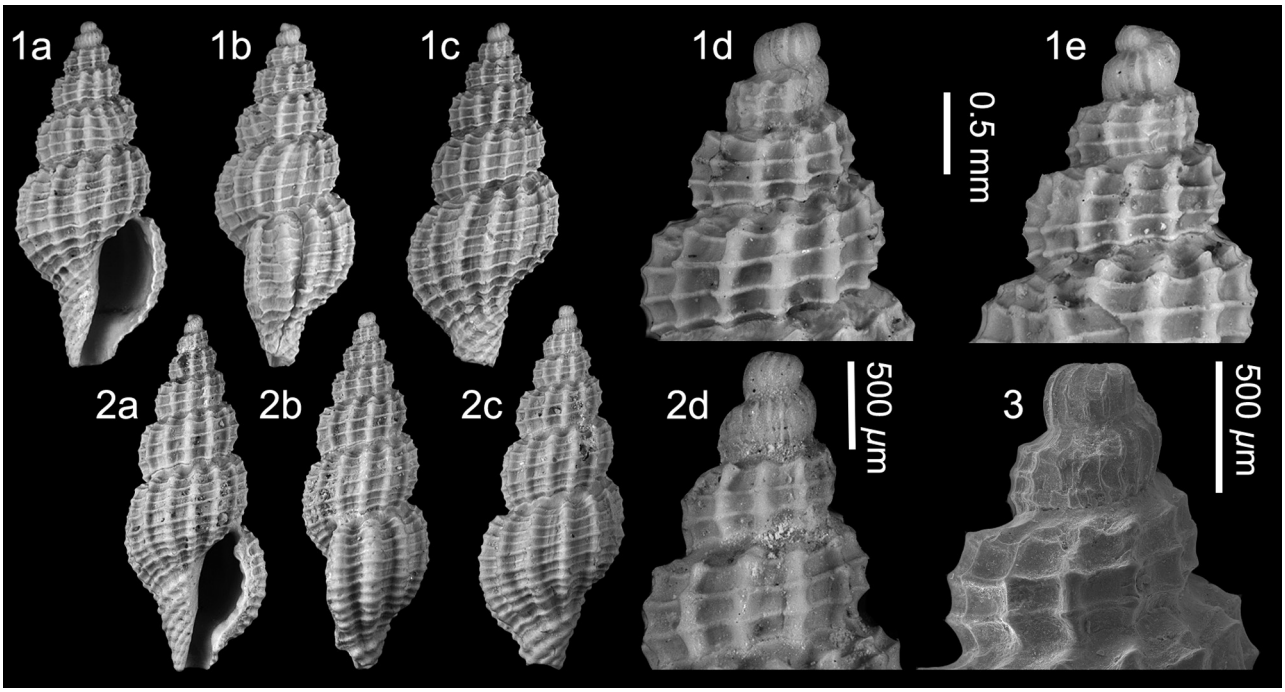

Plate 64. *Raphitoma vercingetorixi* Ceulemans, Van Dingenen & Landau, 2018; 1. NHMW 2016/0103/0986, height 6.5 mm, width 2.6 mm, 1d, e, detail of protoconch; 2. NHMW 2016/0103/0987, height 8.6 mm, 2.9 mm, 2d, detail of protoconch; 3. NHMW 2016/0103/0988, height 6.1 mm, width 2.3 mm (juvenile), detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

The siphonal fasciole is well delimited, and the siphonal canal of medium length. In Assemblage I it most similar to *Raphitoma breitenbergeri* nov. sp.; for comparison see under that species. For comparison with other congeners see Ceulemans *et al*. (2018, p. 112).
We report it for the first time from the Assemblage I localities of St-Clément-de-la-Place and Sceaux-d'Anjou. Brébion (1964, p. 607) recorded it from Assemblage II (Apigné) and Brébion (1964) and Ceulemans *et al*. (2018) from Assemblage III (Le Pigeon Blanc).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Brébion, 1964; this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018).

***Raphitoma vogeli* nov. sp.**
Plate 65, figs 1-2

Type material – Holotype NHMW 2016/0103/1221, height 7.5 mm, width 3.7 mm; paratype 1 NHMW 2016/0103/1222, height 6.5 mm, width 3.5 mm, **St-Clément-de-la-Place**. Paratype 2 RGM.1352607, height 8.6 mm, width 4.1 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 6.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1907 (1 adult + 4 juveniles), LC (1 adult + 1 juvenile). **Sceaux-d'Anjou**: RGM.739228 (3 fragments). **Renauleau**: NHMW 2016/0103/1761 (6), LC (6), FVD (4).

Etymology – Named after Eduard de Vogel, volunteer photographer at the Naturalis Biodiversity Center, Leiden, The Netherlands. *Raphitoma* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Raphitoma* species of small size, biconic, fragile, paucispiral protoconch of two whorls, post-nuclear whorls subquadrate with dense rows of cruciform micropustules, teleoconch with angular, strongly convex whorls subsutural ramp broad, bearing coarse rectangular reticulate sculpture, ribs and cords very raised and narrow, long siphonal canal, distinct siphonal fasciole.

Description – Shell small, biconic, fragile. Protoconch paucispiral, composed of two whorls, post-nuclear whorls strongly shouldered, almost straight sided below, subquadrate in profile, microsculpture of dense cruciform pustules arranged in rows. Junction with teleoconch sharply delimited. Teleoconch of 3.5 angular whorls, subsutural ramp broad, with comma-shaped marks just below suture, shoulder angular; suture superficial, undulating. Axial sculpture of widely spaced, orthocline, narrow, strongly raised, rounded ribs, 12 on last whorl, one fifth width of interspaces. Spiral sculpture of narrow cords overrun ribs forming rectangular cancellation, spinulose tubercles developed at intersections. Two cords on first teleoconch whorl, third primary develops at abapical suture on second whorl, penultimate whorl with one weaker cod on subsutural ramp, three below. Last whorl inflated, broad subsutural ramp weakly concave, roundly angled at shoulder, strongly convex below, very strongly constricted at base; axials continue over base, seven spirals on last whorl, further five on siphonal fasciole. Aperture ovate; outer lip incomplete; anal sinus not preserved; siphonal canal long, strongly twisted, open. Columella moderately excavated in upper third. Columellar callus poorly developed, forming narrow callus edge; parietal callus not thickened. Siphonal fasciole distinct.

Discussion – *Raphitoma vogeli* nov. sp. is another very distinct Assemblage I raphitomid. The protoconch is subquadrate covered in rows of cruciform pustules. Again, this is not a protoconch type we have seen before in European fossil or extant raphitomids. It is the only Assemblage I species with a biconic shell shape (see Giannuzzi-Savelli *et al*., 2018, fig. 5). Several extant Mediterranean species have this shell shape, such as *R. brunneofasciata* Pusateri & Giannuzzi-Savelli, 2013 and *R. syrtensis* Nordsieck, 1977. These two form a species pair (Giannuzzi-Savelli *et al*., 2018), of which *R. syrtensis* is the non-planktotrophic

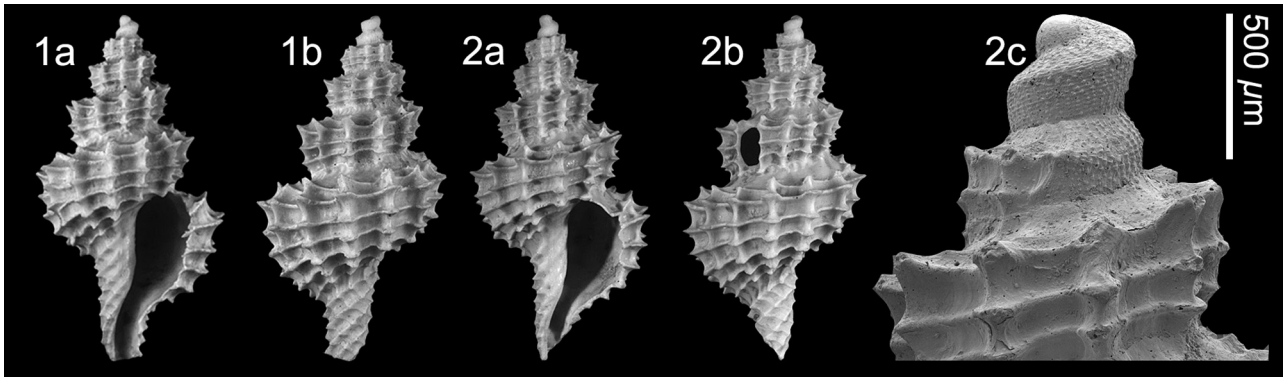

Plate 65. *Raphitoma vogeli* nov. sp.; 1. **Holotype** NHMW 2016/0103/1221, height 7.5 mm, width 3.7 mm; 2. **Paratype 1** NHMW 2016/0103/1222, height 6.5 mm, width 3.5 mm, 2c, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

partner. The protoconch of that species differs from that of *R. vogeli* in having convex whorls and the more usual finely reticulated microsculpture of the genus rather than the cruciform pustules seen in *R. vogeli*. Their teleoconch sculpture is remarkably similar (cf. Giannuzzi-Savelli *et al*., 2018, fig. 64A). Other raphitomids with the same shell shape in the Mediterranean are *R. horrida* (Monterosato, 1884) and *R. bracteata* (Pallary, 1904). Both of these have a paucispiral protoconch, but again with convex rather than shouldered post-nuclear whorls. *Raphitoma hispidella* Pusateri & Giannuzzi-Savelli, in Giannuzzi-Savelli *et al*., 2019 (*nom. nov. pro Cordieria cordieri* var. *hispida* Monterosato, 1890, *non Raphitoma hispida* Bellardi, 1877), from the present-day Mediterranean, has almost identical teleoconch shape and sculpture, but is immediately separated by its tall multispiral protoconch.
We record *R. vogeli* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, where it is extremely uncommon.

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

Genus *Teretia* Norman, 1888

Type species – needs to be fixed, see below.

1883 *Teres* Bucquoy, Dautzenberg & Dollfus, p. 187. Type species (by original designation): '*Pleurotoma anceps* Eichwald, 1830', present-day, Mediterranean. Junior homonym of *Teres* Boettger, 1878 [Clausiliidae].

1888 *Teretia* Norman, p. 8. Type species (by typification of replacement name): *Pleurotoma teres* (Reeve, 1844), present-day, Mediterranean. Proposed as an emendation of *Teres* Bucquoy, Dautzenberg & Dollfus, 1883, and later used as a substitute name for it as *Teres* is preoccupied. Bucquoy, Dautzenberg & Dollfus fixed *Pleurotoma anceps* Eichwald, 1830, as the type species of *Teres*, but they used the name *P. anceps* for a present-day Mediterranean species and listed '*Pleurotoma teres* Forbes (non Reeve)' in its synonymy. However, *Pleurotoma anceps* Eichwald, 1830, is a Miocene-Pliocene species (see Landau *et al*., 2013, p. 275). The name *Pleurotoma teres* Reeve, 1844, was established for the present-day species.

***Teretia horroi* nov. sp.**
Plate 66, figs 1-2

Type material – Holotype NHMW 2016/0103/1730, height 4.4 mm, width 1.7 mm; **Renauleau**. Paratype 1 NHMW 2016/0103/1389, height 1.4 mm, width 0.7 mm; paratype 2 RGM.1352404, height 1.6 mm, width 0.8 mm; paratype 3 RGM.1352405, height 1.7 mm, width 1.0 mm, **St-Clément-de-la-Place**. Paratype 4 RGM.1352602, height 4.2 mm, width 1.6 mm; paratype 5 RGM.1352603, height 3.2 mm, width 1.3 mm, ; paratype 6 RGM.1352604, height 3.3 mm, width 1.4 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 4.4 mm, width 1.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1390 (5 juveniles and fragments), RGM.1352406 (3 juveniles), LC (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1947 (3 fragments), RGM.718175 (50+ fragments and juveniles), LC (1).

Etymology – Named after Juan Horro of Vigo, Spain, in recognition of his work on this genus. *Teretia* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Teretia* species of small size, multispiral protoconch, first two whorls micropustular, last two diagonally reticulated, last half whorl carinate, teleoconch of four whorls, first two carinate, last two convex, sharp spiral cords, two on first whorl, three on second and third whorls, with single secondary delimiting subsutural ramp, interspaces strongly concave, last whorl four primary spirals, three over base, ten on siphonal fasciole, siphonal canal moderately long.

Description – Shell small, fusiform. Protoconch tall multispiral, composed of 3.5 whorls, first 1-2 whorl bearing dense micropustules, later teleoconch whorls diagonally reticulated, last half whorl strongly carinate mid-whorl. Junction with teleoconch marked by beginning adult sculpture. Teleoconch of four whorls, first two whorls angular at carina, last two convex, subsutural ramp wide, strongly concave, bearing crowded prominent comma-shaped riblets. Suture impressed, linear. Sculpture of sharp spiral cords; two at teleoconch boundary, abapical strongest forming carina, third cord appears at abapical suture on second whorl, single secondary cord develops above adapical cord delimiting subsutural ramp, third whorl with mid-cord slightly stronger placed mid-whorl, adapical at shoulder, abapical just above suture. Interspaces strongly concave bearing microsculpture of pustules arranged in rows. Last whorl 60% total height, broad concave subsutural ramp with axial riblets, concave below, strongly constricted ar base, one secondary cord delimiting subsutural ramp, four primaries mid-whorl, three over base, about ten weaker spirals over siphonal fasciole. Aperture ovate, 43% total height, outer lip simple; anal sinus asymmetrical with apex at suture, siphonal canal relatively long, open. Columella moderately excavated in upper third. Columellar callus not thickened, forming narrow rim.

Discussion – The European species of *Teretia* can be separated into two groups; those with a prominent carina on later adult whorls, such as *T. elegantissima* (Foresti, 1868), *T. monterosatoi* (Cipolla, 1914) and *T. turritelloides* (Bellardi, 1847) and those without a prominent carina, including *T. anceps* (Eichwald, 1830), *T. fusianceps* Nordsieck,

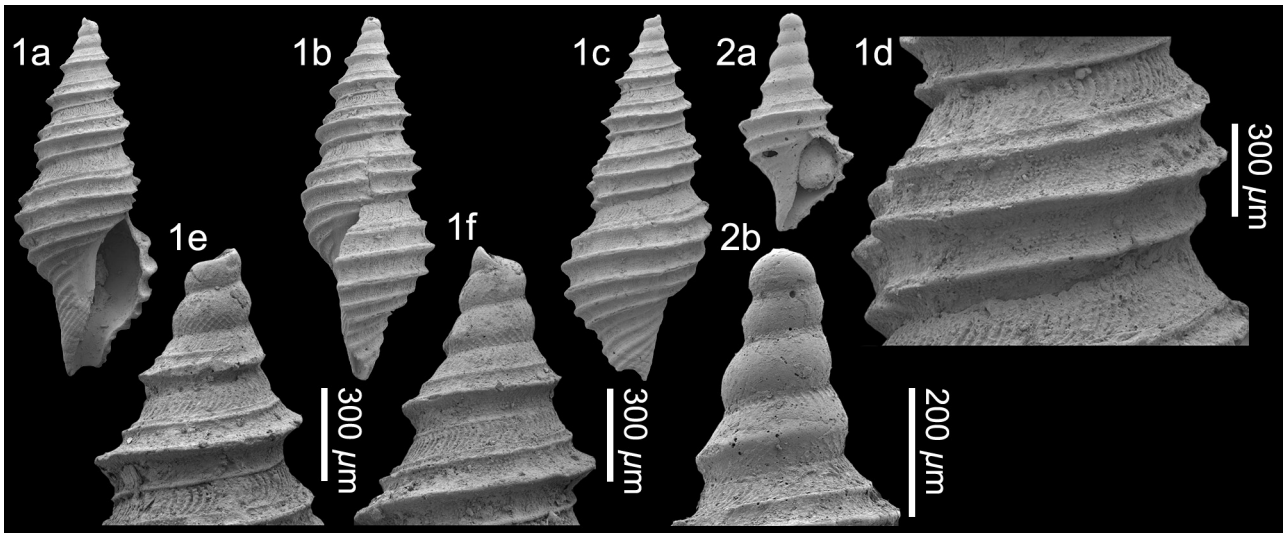

Plate 66. *Teretia horroi* nov. sp.; 1. **Holotype** NHMW 2016/0103/1730, height 4.4 mm, width 1.7 mm, 1d, detail of teleoconch microsculpture, 1 e, f, detail of protoconch. Renauleau. 2. **Paratype 1** NHMW 2016/0103/1389, height 1.4 mm, width 0.7 mm, 2b, detail of protoconch (all SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

1972 and *T. teres* (Reeve, 1844). The new species introduced by Vera-Peláez (2002, pl. 6, figs G-J, pl. 17, figs V-Y) from the early Pliocene of Estepona, southern Spain are difficult to evaluate due to the extremely poor figures, and are excluded from the discussion. The species from France has the first two whorls strongly carinate, but the last two regularly convex. The spiral sculpture consists of sharp elevated cords; two on the first two teleoconch whorls, the abapical carinate, three on the third whorl, the middle cord slightly stronger, four on the last whorl, with a single secondary cord above the adapical primary delimiting the subsutural ramp, three further primary cords over the base, and about ten over the siphonal fasciole. There is no further secondary spiral sculpture.

The fossil European Miocene-Pliocene species *T. anceps* differs in having more numerous spirals that are rounded. The present-day northeastern Atlantic and Mediterranean species *T. teres* also has 3-4 somewhat lamellar cords, not as sharp as in the French species, but also has 4-6 secondary cords per whorl (see Horro & Rolán, 2017, figs A-D). In *T. teres* three equal cords appear simultaneously at the protoconch-teleoconch boundary (Fretter & Graham, 1984, fig. 374; Brunetti & Vecchi, 2003, pl. 3, fig. 2), whereas in the French species only two, of which the abapical is far stronger (Pl. 66, fig. 1e). *Teretia fusianceps* from the Miocene North Sea Basin has a more slender turreted shell, with two equal primaries on spire whorls, a third primary develops only on the penultimate whorl appearing just above the suture.

Two species have recently been described from the coast of West Africa comparable in sculpture to the French species. *Teretia hoisaeteri* Horro & Rolán, 2017 is immediately separated by having carinate spire whorls and numerous fine spirals over the base and siphonal fasciole. *Teretia candelae* Horro & Rolán, 2017 is far more similar to the French species in having sharp cords, however, the shell reaches a greater maximum size (7.4 mm). It is possible that the holotype of the French species is not fully grown, but we have found no fragments suggesting a larger fully adult size. In *T. candelae* a few secondary cords are present in the interspaces in larger specimens. Nevertheless, if specimens of similar size are compared (Pl. 66 fig. 1, and Horro & Rolán, 2017, fig. 4C, D) they are closely similar. We do not, however, consider them conspecific, as the West African species has three cords at the teleoconch boundary, of which the mid-cord is strongest (Horro & Rolán, 2017, fig. 5), whereas the French species has only two.

The surface of all these species is covered with micropustules and not smooth as described by Brunetti & Vecchi (2003). This can be seen in their own figures (Brunetti & Vecchi, 2003, pl. 3, figs 1-2). The micropustules seem to be a generic character.

Brébion (1964, p. 616) recorded the genus *Teretia* only from the Assemblage III locality of Le Pigeon Blanc, a record that was not confirmed by Ceulemans *et al*. (2018). *Teretia horroi* nov. sp. is here recorded from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, although it is uncommon at all localities.

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

Family Drilliidae Olsson, 1964
Genus *Crassopleura* Monterosato, 1884

Type species – Pleurotoma maravignae Bivona, 1838, by monotypy, Pleistocene, Italy.

1884 *Crassopleura* Monterosato, p. 127.

***Crassopleura maravignae* (Bivona, 1838)**
Plate 67, figs 1-2

1836 *Pleurotoma elegans* Scacchi, p. 43, pl. 1, fig. 8 (*non* Defrance, 1826).
1837 *Pleurotoma incrassata* Dujardin, p. 292, pl. 20, fig. 28 (*non* G.B. Sowerby, I 1834).
*1838 *Pleurotoma Maravignae* Bivona, Ant. *in* Bivona And., p. 13, pl. 1, fig. 12.
1839 *Pleurotoma Maravignae* Biv. – Calcara, p. 8, pl. 1, fig. 3.
1841 *Pleurotoma elegans* Scacchi – Calcara, p. 54.
1844 *Pleurotoma elegans* Scacchi – Philippi, p. 168, pl. 26, fig. 5.
1847 *Raphitoma incrassata* Duj. – Bellardi, p. 108, pl. 4, fig. 27.
1852 *Pleurotoma subincrassata* d'Orbigny, p. 62 (*nom. nov. pro. P. incrassata* Dujardin, 1837, *non* G.B. Sowerby, I 1834).
1853 *Pleurotoma incrassata* Duj. – Hörnes, p. 383, pl. 40, fig. 14.
1854 *Pleurotoma Hybrida* Millet, p. 161 (*nomen nudum*).
1865 *Pleurotoma hybrida* Millet, p. 588, p. 161 (*non* Grateloup, 1845).
1877 *Drillia incrassata* (Duj.) – Bellardi, p. 140, pl. 5, fig. 1.
non 1878 *Pleurotoma incrassata* Duj. – Nyst, pl. 3, fig. 10 [= *Elaeocyma nysti* (Harmer, 1915)].
non 1882 *Pleurotoma incrassata* Duj. – Nyst, p. 45 [= *Elaeocyma nysti* (Harmer, 1915)].
1879 *Drillia incrassata* var. *rhodanica* Fontannes, p. 46, pl. 4, fig. 10.
1904 *Drillia* (*Cymatosyrinx*) *incrassata* var. *acutespirata* Sacco, p. 46.
1904 *Drillia* (*Cymatosyrinx*) *incrassata* var. *magnocostulata* Sacco, p. 47.
1904 *Drillia* (*Cymatosyrinx*) *incrassata* var. *miominor* Sacco, p. 47, pl. 12, figs 47, 48.
1904 *Drillia* (*Cymatosyrinx*) *incrassata* var. *dertomagna* Sacco, p. 47.
1914 *Drillia* (*Cymatosyrinx*) *incrassata* Dujardin – Cipolla, p. 122, pl. 12, fig. 10.
1914 *Drillia* (*Cymatosyrinx*) *incrassata* mut. *Maravignae* Biv. – Cipolla, p. 123, pl. 12, fig. 11.
1914 *Drillia* (*Cymatosyrinx*) *incrassata* var. *miominor* Sacco – Cipolla, p. 123, pl. 12, fig. 12.
1915 *Drillia incrassata* (Dujardin) – Harmer (*partim*), p. 222, pl. 27, fig. 28.
non 1915 *Drillia incrassata* var. *dertomagna* Sacco – Harmer, p. 223, pl. 27, fig. 29 [= *Elaeocyma nysti* (Harmer, 1915)].
non 1915 *Drillia incrassata* var. *miominor* Sacco – Harmer, p. 223, pl. 27, fig. 30 [= *Elaeocyma nysti* (Harmer, 1915)].
non 1915 *Drillia incrassata* var. *nysti* Harmer, p. 224, pl. 27, fig. 31 [= *Elaeocyma nysti* (Harmer, 1915)].
non 1915 *Drillia incrassata* var. *crassa* (A. Bell) – Harmer, p. 224, pl. 27, fig. 32 [= *Elaeocyma nysti* (Harmer, 1915)].
1937 *Drillia* (*Cymatosyrinx*) *incrassata* var. *minor* Montanaro, p. 159, pl. 7, figs 41-43.
1938 *Drillia* (*Cymatosyrinx*) *subincrassata* Peyrot, p. 275.
non 1953 *Drillia incrassata* Duj. – Csepreghy-Meznerics, p. 8, pl. 1, figs 5, 6 [= *'Crassopleura' sigmoidea* (Bronn, 1831)].
1954 *Clavus* (*Crassopleura*) *maravignae* Bivona, 1838 – Glibert, p. 33, pl. 1, fig. 12, pl. 5, fig. 4.
1964 *Clavus* (*Crassopleura*) *maravignae* Bivona, 1838 – Brébion, p. 553.
1966 *Crassopleura maravignae* (Bivona, 1838) – Powell, p. 93, pl. 14, fig. 12.
1977 *Crassopleura maravignae* (Bivona, 1938 [*sic*]) – Nordsieck, p. 11, pl. 1, fig. 3.
1984 *Crassopleura incrassata* (Dujardin, 1837) – Bernasconi & Robba, p. 270, pl. 2, fig. 1.
1984 *Crassopleura maravignae* (Bivona, 1838) – Van Aartsen *et al*., p. 43, fig. 207.
1997 *Crassopleura incrassata* (Dujardin, 1837) – Chirli, p. 43, pl. 12, figs 2-5.
2002 *Crassopleura incrassata* (Dujardin, 1837) – Vera-Pelàez, p. 197, pl. 3, figs D, E. F, pl. 11, figs I, J.
2003 *Crassopleura maravignae* (Bivona Ant. In Bivona And., 1838) – Scarponi & Della Bella, p. 21, figs 2, 3, 14.
2010 *Crassopleura maravignae* (Bivona Ant. In Bivona And., 1838) – Sosso & Dell'Angelo, p. 44, p. 60 unnumbered fig. bottom left.
2011 *Crassopleura maravignae* (Bivona Ant. In Bivona And., 1838) – Landau *et al*., p. 36, pl. 18, fig. 12.

Material and dimensions – Maximum height 10.6 mm, width 3.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0940-0941 (2), NHMW 2016/0103/0942 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0944 (50+), RGM.1349001 (50+), RGM.718140 (50+), RGM.1352294 (50+), RGM.1352331 (15), RGM.1352362 (20), RGM 1352546 (50+), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/0943 (50+), LC (50+), FVD (50+). **Beugnon**: RGM.1348486 (2), RGM.1349124 (7), RGM.1352346 (9), RGM.1352428 (13), RGM.1352441 (2).

Distribution – As discussed by Scarponi & Della Bella (2003, p. 22), the correct name for this species is *Crassopleura maravignae* (Bivona 1838), Dujardin's (1837) name *Pleurotoma incrassata* being a primary homonym of *P. incrassata* G. B. Sowerby I, 1834.
This species is characterised by its multispiral high dome-shaped protoconch composed of 2.5-3.25 whorls and strongly opisthocline axial ribs, sinuous over the subsutural ramp. The anal sinus is deep and forms a notch behind the parietal tubercle. Some specimens with fewer ribs resemble specimens of *'Crassopleura' sigmoidea* (Bronn, 1831), but can be differentiated in that the anal sinus is evenly U-shaped and does not produce a notch on the parietal wall. Scarponi & Della Bella (2003) considered this difference to be of generic significance and placed Bronn's species in the genus with exclamation marks.

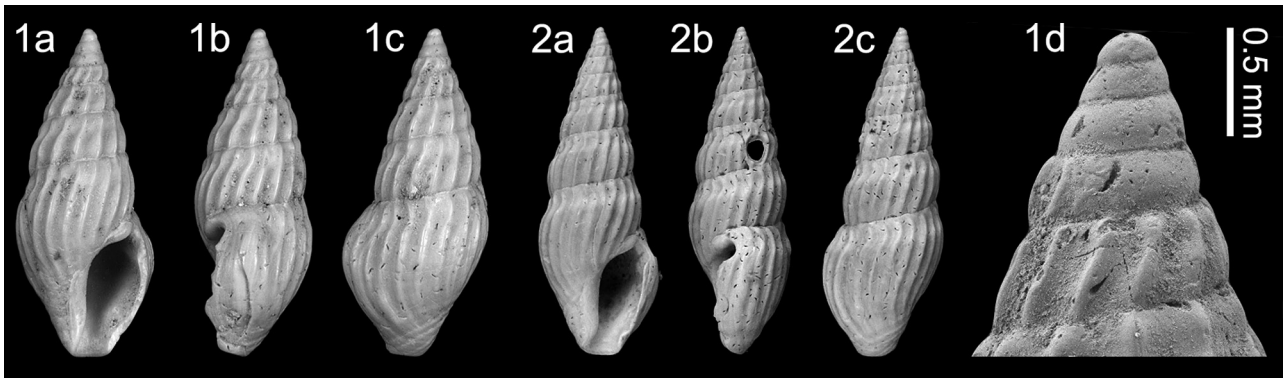

Plate 67. *Crassopleura maravignae* (Bivona 1838); 1. NHMW 2016/0103/0940, height 6.2 mm, width 2.6 mm, 1d, detail of protoconch (SEM image); 2. NHMW 2016/0103/0941, height 10.6 mm, width 3.6 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Crassopleura maravignae (Bivona 1838) is widespread from the middle Miocene to present-day European assemblages, although there are small differences between populations. Glibert (1954, p. 33) commented that the middle Miocene specimens from the Loire Basin were slightly more slender than those from the Holocene Mediterranean and that the ribs were less serrated and more oblique. These middle Miocene French specimens had anything between 15 and 30 axial ribs per whorl. Scarponi & Della Bella (2003, p. 23) noted that the most common Mediterranean Pliocene form had slightly fewer and less sinuous axial ribs (14-18 vs. 21-25) that present-day specimens. The Assemblage I specimens have most commonly between 15-20 axial ribs that are quite strongly sinuous and, as is usual for Assemblage I, most specimens are small compared to other populations. Some references to *Crassopleura maravignae* (as *Pleurotoma* or *Drillia incrassata*) (Nyst, 1878, 1882; Harmer, 1915) are not this species, but *Elaeocyma nysti* (Harmer, 1915) (Marquet, 1998a, b).
Brébion (1964, p. 563) recorded this species from numerous Assemblage I (Sceaux-d'Anjou, Renauleau, Thorigné, St-Clément-de-la-Place, St-Michel, Les Pierres Blanches) and Assemblage II (Apigné, le Temple du Cerisier, Carcé, Lillion) localities. He also recorded numerous specimens from the Assemblage III locality of Le Pigeon Blanc. This locality was thoroughly revised by our group (Ceulemans *et al*., 2018), but we did not find any specimen. It is therefore provisionally excluded from Assemblage III.

Distribution – Middle Miocene: Atlantic (Langhian), Loire Basin, France (Dujardin, 1837; Glibert, 1954); Paratethys, Austria (Hörnes, 1853); Proto-Mediterranean, Italy (Bellardi, 1877). Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Millet, 1854, 1865; Glibert, 1954; Brébion, 1964); Proto-Mediterranean, Italy (Bellardi, 1877; Montanaro, 1937). Lower Pliocene: ?NSB, Coralline Crag, England (Harmer, 1915); Atlantic, Guadalquivir Basin, Spain (Landau *et al*., 2011); western Mediterranean, S. France (Fontannes, 1879); central Mediterranean, Italy (Chirli, 1997; Scarponi & Della Bella, 2003; Sosso & Dell'Angelo, 2010). Upper Pliocene: western Mediterranean, Estepona Basin, S. Spain (Vera-Pelàez, 2002), central Mediterranean, Italy (Calcara, 1839, 1841; Bellardi, 1877; Cipolla, 1914; Bernasconi & Robba, 1984). Present-day: Eastern Atlantic frontage from Norway to the Azores and into the Mediterranean (Nordsieck, 1977).

Genus *Spendrillia* Hedley, 1922

Type species – Drllia woodsi Beddome, 1883, by original designation, present-day, Tasmania.

1922 *Spendrillia* Hedley, p. 250.

***Splendrillia clavulina clavulina* (Desmoulins, 1842)**
Plate 68, figs 1-4

1837 *Pleurotoma terebra* Dujardin, p. 292, pl. 20 fig. 30 (*non* de Basterot, 1825).
1842 *Pleurotoma clavulina* Desmoulins, p. 173.
1854 *Pleurotoma Larva* Millet (*partim*), p. 161 (*nomen nudum*).
1865 *Pleurotoma larva* Millet (*partim*), p. 588.
1931 *Drillia* (*Cymatosyrinx*) *clavulina* Desmoulins – Peyrot, p. 172, pl. 9, figs 14, 16.
1954 *Clavus* (*Cymatosyrinx*) *clavulina* Desmoulins forme *clavulina* ss. – Glibert, p. 42, pl. 5, fig. 3a.
1964 *Clavus* (*Cymatosyrinx*) *clavulina* Desmoulins, 1842 – Brébion (*partim*), p. 550.

Material and dimensions – Maximum height 10.7 mm, width 3.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0935-0938 (4), NHMW 2016/0103/0939 (50+), RGM.1352278 (50+), RGM.1352296 (50+), RGM.1352700 (17), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0946 (50+), NHMW 2016/0103/1933 (1), RGM.1348920 (50+), RGM.718139 (50+), RGM.739227 (50+), RGM.1352280 (50+), RGM.1352313 (10), RGM.1352361 (18), RGM.1352518 (31), LC (50+), FVD (50+).

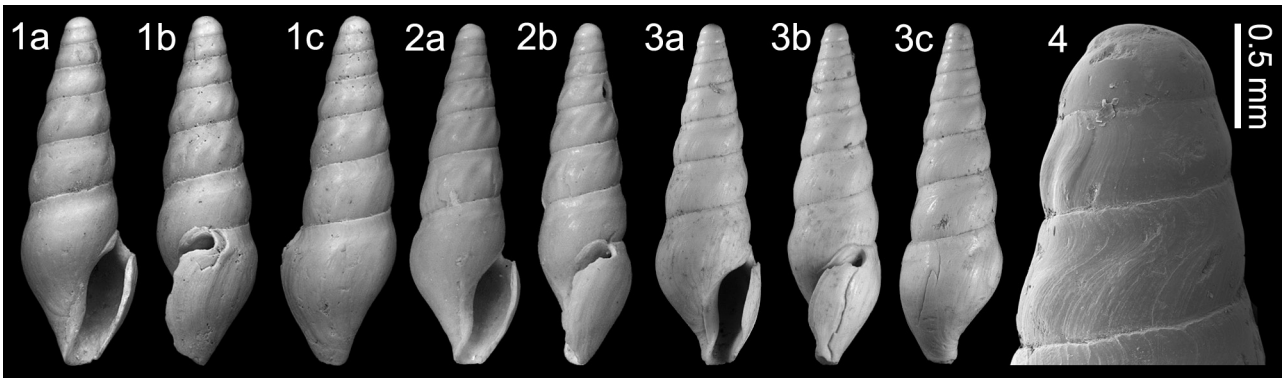

Plate 68. *Splendrillia clavulina clavulina* (Desmoulins, 1842); 1. NHMW 2016/0103/0935, height 7.8 mm, width 2.4 mm; 2. NHMW 2016/0103/0936, height 9.0 mm, width 2.6 mm; 3. NHMW 2016/0103/0937, height 8.6 mm, width 2.7 mm; 4. NHMW 2016/0103/0938, height 7.6 mm, width 2.5 mm, detail of protoconch (SEM image). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Renauleau: LC (1). **Beugnon**: RGM.1352398 (3), RGM. 1352429 (1).

Discussion – As pointed out by Glibert (1954, p. 33), the differences between the lower Miocene Tortonian Assemblage I specimens of *Splendrillia clavulina clavulina* (Desmoulins, 1842) and those from the lower Pliocene Zanclean Assemblage III locality of Le Pigeon Blanc are small but consistent. Both populations have a low dome-shaped paucispiral protoconch composed of about two smooth whorls (Pl. 68, fig. 4) and the teleoconch in both can have a more or less elevated spire and weaker or stronger sculpture. The number of ribs is also variable; some specimens have a greater number of ribs so that the shell superficially resembles *Crassopleura maravignae* (Bivona, 1838), but that species has a multispiral protoconch. However, the stratigraphically younger Le Pigeon Blanc specimens generally have a squatter shell, a more concave subsutural ramp, more convex whorls, the last whorl is comparatively larger and more inflated, the ribs are generally more strongly developed (although they are subobsolete in some specimens), and the narrow U-shaped anal sinus is even deeper and more constricted in the Assemblage III specimens. We accept that some specimens of *S. clavulina clavulina* from Assemblage I, especially some of the more strongly sculptured forms from Sceaux-d'Anjou, are very similar to the Assemblage III form, but they can usually be separated by being more slender and the last whorl less inflated. Dollfus (1907) erected the name *Pleurotoma* (*Drillia*) *incrassata* var. *brugnonei* for the specimens from Le Pigeon Blanc, which we provisionally consider to be a valid chronosubspecies of *S. clavulina*. A lectotype was assigned and figured by Glibert (1954, pl. 5, fig. 3b). However, this might be a case of genetic drift within a species, in which the more strongly sculptured forms survived into, and predominated in the lower Pliocene.

Distribution – Middle Miocene: Atlantic (Langhian and Serravallian), Aquitaine Basin (Peyrot, 1931), Loire Basin (Peyrot, 1938; Glibert, 1954). Upper Miocene (Tortonian): Atlantic, NW France (Millet, 1854, 1865; Brébion, 1964).

***Splendrillia larva* (Millet, 1865)**
Plate 69, figs 1-3

1854 *Pleurotoma Larva* Millet (*partim*), p. 161 (*nomen nudum*).
1865 *Pleurotoma larva* Millet (*partim*), p. 588.
1964 *Clavus* (*Cymatosyrinx*) *clavulina* Desmoulins, 1842 – Brébion (*partim*), p. 550.

Material and dimensions – Maximum height 14.0 mm, width 3.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1928-1931 (4), NHMW 2016/0103/1932 (10), RGM.1352341 (10), RGM.1352360 (7), RGM.1352527 (15), LC (6), FVD (3). **Renauleau**: LC (2).

Original description – 'Pleurotoma larva. *Millet. Coq. petite, allongée, très-mince, à peine canaliculée; composée de sept tours de spire, séparés entre eux par une légère dépression faisant cordon et joignant la suture; tous sont marqués de petites côtes obliques. Ouverture étroite, à peine canaliculée; bord droit recouvrant. Longueur: 10 millimètres; diamètre: 3 millimètres. Th., Sc., Ren., St-Mich*.' (Millet, 1865, p. 588).

Discussion – We cannot agree with Brébion (1964, p. 551) who considered *Splendrillia clavulina* (Desmoulins, 1842) a highly variable species and considered this form to fit within the species concept. As discussed above we consider the Assemblage III specimens a separate chronosubspecies, *Splendrillia clavulina brugnonei* (Dollfus, 1907). In the Assemblage I locality of Sceaux-d'Anjou a further form occurs that differs in being even more elongate than *S. clavulina* and the teleoconch whorls have a broad, almost vertical, concave, smooth subsutural ramp, below which develop short, strongly prosocline axial ribs. *Splendrillia clavulina* has weak prosocline ribs on early teleoconch whorls that weaken and disappear in most specimens by the penultimate whorl, whereas in

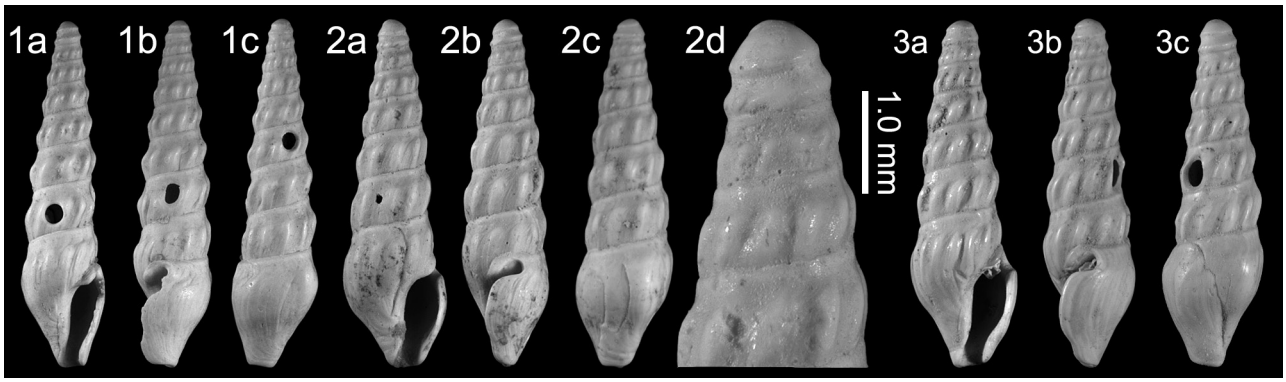

Plate 69. *Splendrillia larva* (Millet, 1865); 1. NHMW 2016/0103/1928, height 14.0 mm, width 3.2 mm; 2. NHMW 2016/0103/1929, height 10.4 mm, width 3.2 mm, 2d, detail of protoconch; 3. NHMW 2016/0103/1930, height 10.8 mm, width 3.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

S. larva (Millet, 1865) they continue strong throughout onto the last whorl. Moreover, they differ in their protoconch. Both *Splendrillia clavulina clavulina* (Pl. 68, fig. 4) and *S. clavulina brugnonei* (Ceulemans *et al*., 2018, pl. 2, fig. 4) have a regularly dome-shaped protoconch of just over two whorls, with just the suggestion of a carina mid-whorl on the last quarter whorl. In *S. larva* the protoconch is more depressed and the last protoconch whorl is strongly carinate (Pl. 69, fig. 2d). This difference is constant. We have only found this form at Sceaux-d'Anjou and Renauleau.

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

Family Pseudomelatomatidae Morrison, 1965
Genus *Crassispira* Swainson, 1840

Type species – Pleurotoma bottae (Valenciennes *in* Kiener, 1839), by subsequent designation (ICZN Opinion 754, 1965), present-day, tropical East Pacific.

1840 *Crassispira* Swainson, p. 153, 313.

***Crassispira chavani* Glibert, 1960**
Plate 70, figs 1-2

1854 *Pleurotoma Gradata* Defr. – Millet, p. 161 (*non* Defrance, 1826).
1954 *Crassispira powelli* Glibert (*partim*), p. 27 ('Redonian' specimens only) (*non* pl. 4, fig. 12 = *C. powelli* Glibert, 1954).
*1960 *Crassispira chavani* Glibert, p. 26, pl. 5, fig. 10.
?1964 *Crassispira dollfusi* Brébion, p, 561, pl. 13, fig. 34 (*nomen nudum*).
1964 *Crassispira chavani* Glibert, 1960 – Brébion, p. 562, pl. 13, figs 35, 36.

Material and dimensions – Maximum height 19.0 mm, width 6.2 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1019-1020 (2), NHMW 2016/0103/1021 (13), RGM. 1352685 (6 juveniles), LC (15), FVD (15). **Sceaux-d'Anjou**: NHMW 2016/0103/1022 (6), RGM.1352477 (8), LC (5), FVD (5). **Renauleau**: LC (20). **Beugnon**: RGM. 717788 (1).

Discussion – Crassispira chavani Glibert, 1960 is characterised by its bulbous paucispiral protoconch, strongly scalate spire, narrow subsutural collar and narrow concave subsutural ramp, axially dominant sculpture of about 12 straight, slightly opisthocline ribs overrun by narrow spiral cords, relatively short aperture, deep, narrow U-shaped anal sinus and short siphonal canal. It differs from *C. powelli* Glibert, 1954 from the middle Miocene Loire Basin of France in having a paucispiral protoconch; *C. powelli* has a multispiral protoconch, in having a higher scalate spire and not regularly biconic shell shape and by having a narrower subsutural collar. *Crassispira pseudobeliscus* (Fischer & Tournouër, 1873) from the middle Miocene Loire Basin and lower Pliocene Assemblage III deposits of NW France has a larger, more elongate shell, with a multispiral protoconch, a wider subsutural collar, wider concave subsutural ramp, and fewer axial ribs. Brébion (1964, p. 561) recorded *C. pseudobeliscus* from the Assemblage I locality of St-Michel, however, we cannot confirm this record based on the collections consulted. *Crassispira brocchii* (Bonelli, *in* Bellardi & Michelotti, 1840) from the Pliocene Portuguese Atlantic coast and Mediterranean also has a paucispiral protoconch, but differs in being larger, more slender with a comparatively taller last whorl and longer siphonal canal, the subsutural concavity is broader and the axial ribs are fewer and wider. *Crassispira geslini* (Desmoulins, 1842) from the middle Miocene to Pliocene of Italy also has a paucispiral protoconch and is closer in shape and sculpture to *C. chavani* in having a scalate spire and narrow ribs, but these are fewer than in *C. chavani*, the last whorl is taller with a slightly longer siphonal canal, the subsutural collar is more swollen and the concavity below broader. Brébion (1964, p. 561, pl. 13, fig. 34) described *Crassispira dollfusi* nov. sp. (*nomen nudum*) based on a single specimen from Beaulieu. It is very similar to

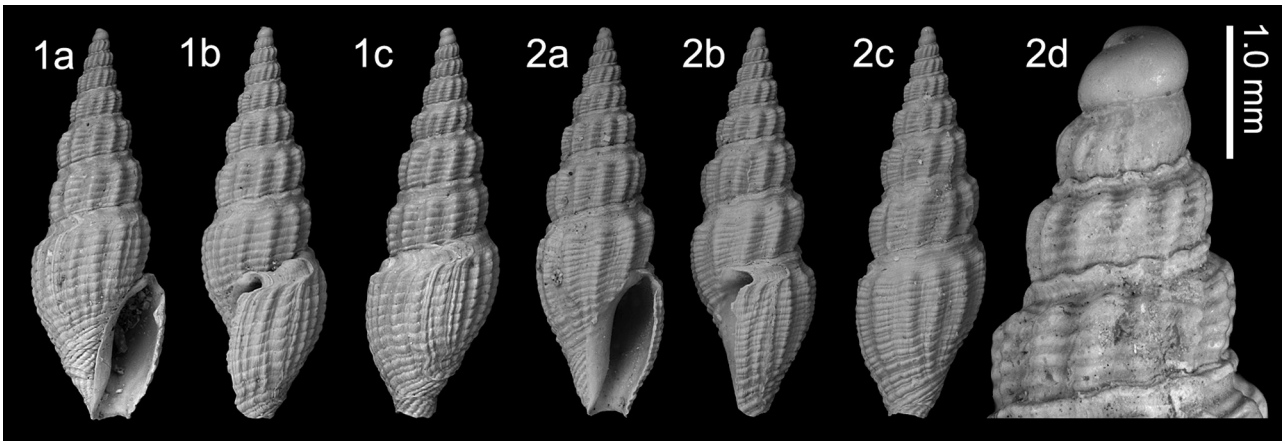

Plate 70. *Crassispira chavani* Glibert, 1960; 1. NHMW 2016/0103/1019, height 18.7 mm, width 6.0 mm; 2. NHMW 2016/0103/1020, height 19.0 mm, width 6.2 mm, 2d, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

C. chavani, but *C. chavani* was said to differ in being smaller (*C. dollfusi*: height 26 mm, width 9.0 mm), in having finer spiral sculpture and 'excavation des tours mieux marquées'. We have not found any specimens as large as *C. dollfusi*, but suspect it is probably a gerontic specimen of *C. chavani*.
Brébion (1964, p. 563) recorded this species from numerous Assemblage I (Sceaux-d'Anjou, Renauleau, Thorigné, Contigné, St-Michel, Beaulieu) and Assemblage II (Apigné, le Temple du Cerisier) localities.

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian), NW France (Millet, 1854, 1865; Glibert, 1960; Brébion, 1964).

***Crassispira detrita* (Peyrot, 1938)**
Plate 71, figs 1-4

*1938	*Drillia* (*Crassispira*) *detrita*	Peyrot, p. 273, pl. 4, fig. 64.
1954	*Clavus* (*Crassispira*) *detrita*	Peyrot, 1938 – Glibert, p. 28, pl. 4, fig. 13a, b.
1964	*Crassispira detrita*	Peyrot, 1938 – Brébion, p. 559.

Material and dimensions – Maximum height 17.6 mm, width 6.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1882-1883 (2), NHMW 2016/0103/1996-1997 (2), NHMW 2016/0103/1998 (4), RGM.718143 (8), RGM.718145 (50+), RGM.1352476 (7), LC (2), FVD (1).

Discussion – *Crassispira detrita* (Peyrot, 1938) is characterised by its small, slender shell, tall spire, broad concave subsutural ramp, below which ten broad opisthocline ribs, roughly equal in width to their interspaces, are developed from the shoulder to the abapical suture. The last whorl is comparatively short and only weakly constricted at the base, the aperture is small and the siphonal canal is short. We ascribe these specimens to *Crassispira detrita* (Peyrot, 1938) originally described from the middle Miocene Loire Basin of France. The Assemblage I specimens are smaller than those from the Loire Basin and the subsutural collar is not swollen, but otherwise they conform in shell shape and in the number of ribs. Peyrot's material did not have the protoconch preserved; we can add that it is paucispiral, composed of 1.5 smooth whorls with a large nucleus, typical for species reproducing by direct development. It differs from *C. obeliscus* (Desmoulins, 1842) from the lower Miocene Aquitaine Basin of France in

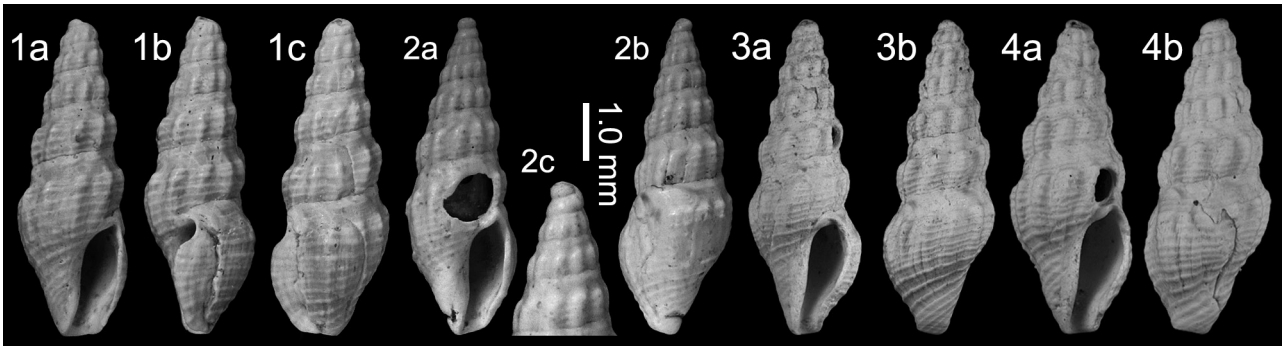

Plate 71. *Crassispira detrita* (Peyrot, 1938); NHMW 2016/0103/1996, height 10.8 mm, width 3.6 mm; 2. NHMW 2016/0103/1997, height 9.8 mm, width 3.3 mm; 3. NHMW 2016/0103/1882, height 9.3 mm, width 3.4 mm; 4. NHMW 2016/0103/1883, height 7.6 mm, width 3.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

being smaller and more slender, in having more flat-sided spire whorls with broader ribs, a less excavated base and a shorter siphonal canal. *Crassispira pseudobeliscus* (Fischer & Tournoüer, 1873) from the middle Miocene Aquitaine Basin is also closely similar, but has taller whorls with longer axial ribs, a taller last whorl and a larger aperture.
As in this work, Brébion (1964, p. 559) recorded this species only from the Assemblage I locality of Sceaux-d'Anjou.

Distribution – Middle Miocene, Atlantic (Langhian), Loire Basin, France (Peyrot, 1938; Glibert, 1954). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

Family Clavatulidae Gray, 1853
Genus *Clavatula* Lamarck, 1801

Type species – *Clavatula coronata* Lamarck, 1801, by monotypy, present-day, West Africa.

1801 *Clavatula* Lamarck, p. 84.

***Clavatula anaglypta* (Millet, 1865)**
Plate 72, figs 1-4

1854 *Pleurotoma Anaglypta* Millet, p. 161 (*nomen nudum*).
*1865 *Pleurotoma anaglypta* Millet, p. 587.
1964 *Clavatula anaglypta* Millet, 1854 [*sic*] – Brébion, p. 540, pl. 13, fig. 21.

Type material – Cotypes: Thorigné, Sceaux-d'Anjou, Renauleau, St-Michel; Musée d'Angers (*fide* Brébion, 1964, p. 541).

Material and dimensions – Maximum height 24.1 mm, width 8.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1278-1280 (3), NHMW 2016/0103/1281 (12), NHMW 2016/0103/1878 (1), RGM.1352344 (23 juveniles + fragments), RGM.1352444 (1 adult, 1 subadult and 7 juveniles), LC (20), FVD (12). **Sceaux-d'Anjou**: NHMW 2016/0103/1282 (14), RGM.718136 (50+), RGM.1352380 (7 + 26 juveniles and fragments), RGM.13522625 (25 all showing signs of predation), LC (10), FVD (9). **Renauleau**: NHMW 2016/0103/1494 (14 incomplete adults and juveniles), LC (20 incomplete adults), FVD (10 incomplete adults).

Original description – 'Pleurotoma anaglypta. *Millet. Coq. fusiforme, à canal court, composée de dix tours de spire légèrement creusés vers le centre. Ces tours, en outre, sont bordés par des espèces de crénelures que sépare la suture qui les touche. Echancrure peu profonde, laisant tomber sur le bord droit quelques petites côtes effilées, arquées et coupées par des stries transversales. Longueur: 25-26 millimètres; diamètre: 9-10 millimètres. Th., Se, Ren., Saint-Michel*' (Millet, 1865, p. 587).

Discussion – *Clavatula anaglypta* (Millet, 1865) is the most abundant *Clavatula* species in the Assemblage I deposits. Following the paucispiral protoconch of just under two whorls with a few riblets on the last quarter whorl, the neanic teleoconch whorls are strongly sculptured by close set axial ribs, strongly flexuous at the position of the anal sinus and irregular spirals. Abapically, a narrow, slightly swollen subsutural band develops and a broader, more swollen suprasutural band, separated by a narrow, slightly depressed or concave section placed at about two-thirds whorl height. On the last 2-3 whorls the axial sculpture weakens and is only strongly developed over the suprasutural band. On the last whorl they developed only mid-whorl into axially elongated tubercles, or are altogether absent. As with all the *Clavatula* species encountered in these deposits the adult sculpture is variable and the species are best identified based on the neanic whorls. *Clavatula neogradata* Glibert, 1954, with which it co-occurs in Assemblage I, differs in having less strongly sculptured neanic whorls, with ribs that are not flexuous, and on adult whorls the concave section between the sub- and suprasutural bands is

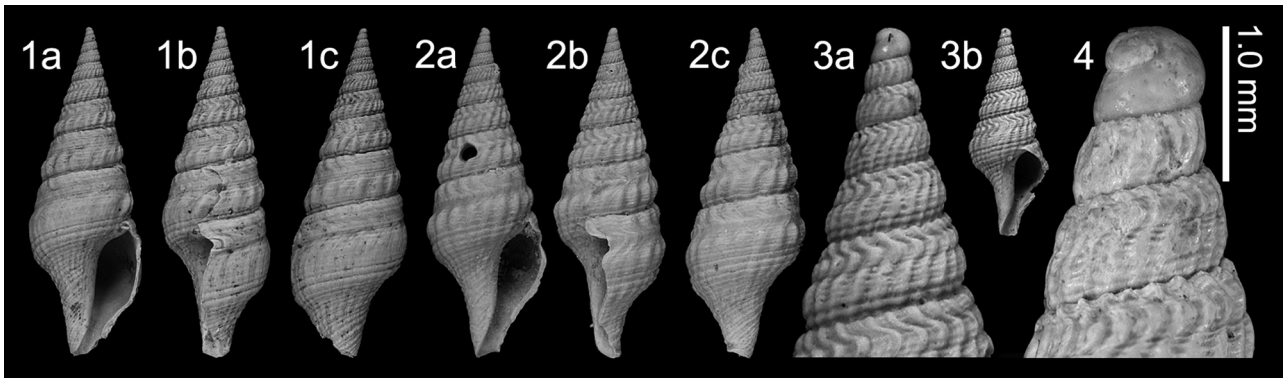

Plate 72. *Clavatula anaglypta* (Millet, 1865); 1. NHMW 2016/0103/1278, height 24.1 mm, width 8.1 mm; 2. NHMW 2016/0103/1279, height 23.0 mm, width 7.5 mm; 3. NHMW 2016/0103/1878, height 11.6 mm (juvenile), 3a, detail of early teleoconch sculpture; 4. NHMW 2016/0103/1280, height 13.6 mm, width 4.9 mm (juvenile), detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

much broader.
Brébion (1964, p. 542) recorded this species from almost all Assemblage I localities (St-Michel, Sceaux-d'Anjou, Thorigné, Renauleau, Beaulieu).

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

***Clavatula dujardini* Peyrot, 1938**
Plate 73, figs 1-5

*1938	*Clavatula Dujardini* Peyrot, p. 264, pl. 5, figs 42, 48.
1954	*Clavatula dujardini* Peyrot, 1938 – Glibert, p. 16, pl. 3, fig. 5.
1964	*Clavatula dujardini* Peyrot, 1938 – Brébion, p. 541, pl. 13, fig. 22.
1964	*Clavatula baccifera* Bellardi, 1877 – Brébion, p. 542 (*non* Bellardi, 1877).

Material and dimensions – Maximum height 20.6 mm, width 7.7 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1863 (1), NHMW 2016/0103/1875 (1), RGM.1352301-303 (3), RGM.1352619 (2), RGM.719029 (5), LC (?1).

Discussion – *Clavatula dujardini* Peyrot, 1938 is characterised by its rather squat, broad shape and coarse sculpture. The protoconch is paucispiral, consisting of just under 2 smooth whorls, with a large nucleus. This sculpture changes with ontogeny. Early teleoconch whorls bear sinuous axial riblets that are swollen towards the adapical suture. On the 3rd or 4th teleoconch whorl the axial sculpture fades and two swollen band develop adjacent to the suture, bearing large tubercles, separated by a relatively broad concave mid-whorl section. The entire surface is covered in fine spiral cords of irregular strength. The last whorl is roundly angled at the shoulder and base, which coincided with the two rows of tubercles, and the base is constricted and concave. Axial ribs reappear between the tubercles mid-whorl, and continue weakening onto the base. The siphonal canal is medium to short in length, the last portion slightly bent and notched at the tip. The anal sinus is deeply U-shaped and occupies the entire concave portion of the subsutural ramp. There is some intraspecific variability especially concerning the apical angle, so that some specimens are squatter than others, and the size of the tubercles. We have compared the Assemblage I material with middle Miocene specimens at hand from the Loire Basin (Ferrière-Larçon; NHMW coll.) and note that the tubercles in the Assemblage I shells tend to be larger and less numerous.
Clavatula dujardini is easily separated from its Assemblage I congeners by its coarse nodular sculpture. Several similar species occur in the upper Miocene of Italy illustrated by Ferrero Mortara *et al*. (1981, pl. 14). Of these the most similar is *C. baccifera* Bellardi, 1877. We have not seen this species, but it seems to differ in having a shorter, more scalate spire and the subsutural ramp is less concave. It also has a shallower anal sinus (see Ferrero Mortara *et al*., 1981, pl. 14, fig. 1b). We do not know the intraspecific variability of the Italian species, and it is possible they are conspecific, but we provisionally prefer to consider them distinct.
Indeed, Brébion (1964, p. 542) argued that Glibert's (1954) *C. dujardini* was not that species, but *C. baccifera*, and recorded both species as occurring in Assemblage I and also noted some variability in the sculpture. In our opinion, and after comparison with specimens from the type locality of Ferrière-Larçon, we consider all these French middle and upper Miocene shells to represent *C. dujardini*. *Clavatula reginae* (Hoernes & Auinger, 1891) from the middle Miocene Paratethys is also similar in shape and in having ill-defined rugose tubercles mid-whorl, but that species is coronate with spinous tubercles developed on the subsutural band.
Brébion (1964, p. 542) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou, St-Michel).

Distribution – Middle Miocene (Langhian), Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1954). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964).

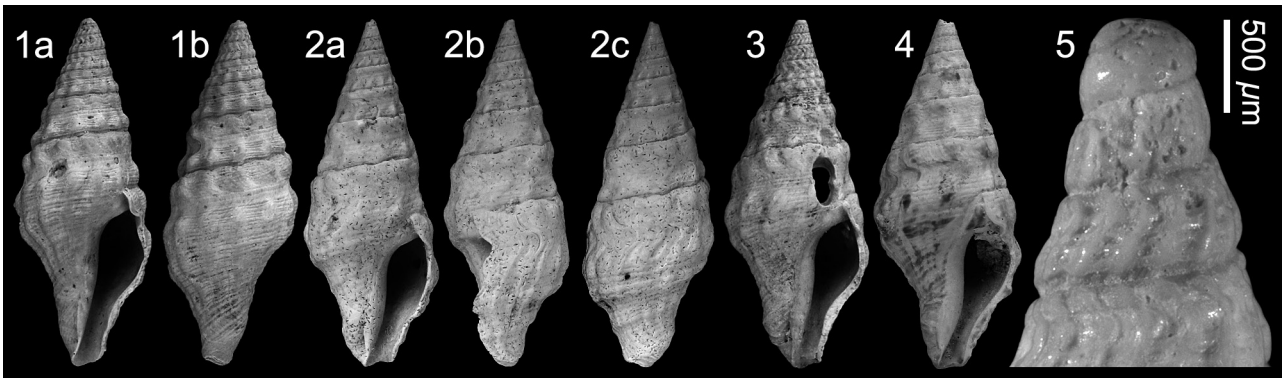

Plate 73. *Clavatula dujardini* Peyrot, 1938; 1. NHMW 2016/0103/1875, height 18.9 mm, width 7.2 mm; 2. NHMW 2016/0103/1863, height 20.6 mm, width 7.7 mm; 3. RGM.1352301, height 17.9 mm, width 7.1 mm; 4. RGM.1352302, height 19.8 mm, width 8.0 mm; 5. RGM.1352303, (juvenile), detail of protoconch. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

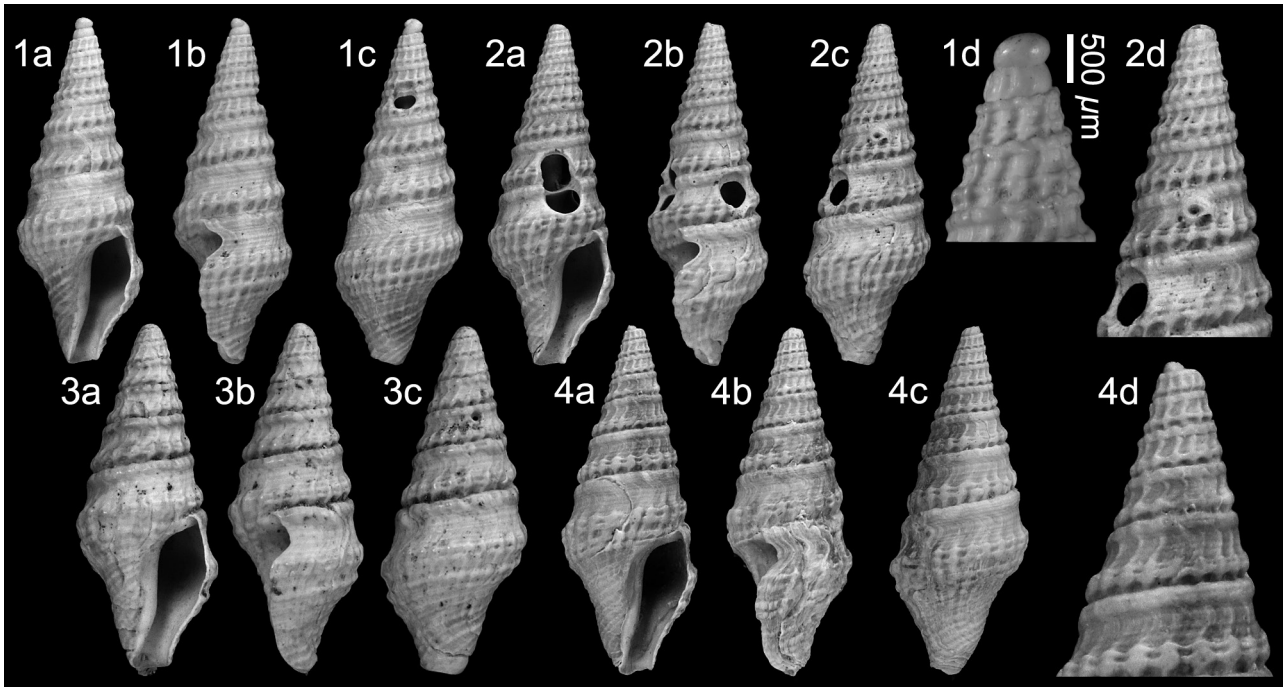

Plate 74. *Clavatula neogradata* Glibert, 1954; 1. NHMW 2016/0103/1876, height 10.0 mm, width 3.7 mm, 1d, detail of protoconch; 2. RGM.1352304, height 10.8 mm, width 3.5 mm, 2d, detail of early teleoconch sculpture; 3. NHMW 2016/0103/1877, height 11.2 mm, width 4.7 mm; 4. RGM.1352305, height 12.8 mm, width 4.8 mm, 4d, detail of early teleoconch sculpture. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Clavatula neogradata* Glibert, 1954**
Plate 74, figs 1-4

1886	*Clavatula gradata* Defr. – Dollfus & Dautzenberg, p. 9 (*non* Defrance, 1826).
1938	*Clavatula gradata* Defrance – Peyrot, p. 266, pl. 4, fig. 17.
*1954	*Clavatula neogradata* Glibert, p. 18, pl. 3, fig. 10.
1964	*Clavatula neogradata* Glibert, 1954 – Brébion, p. 538.
1964	*Clavatula gradata* Defrance, 1826 – Brébion, p. 539, pl. 13, fig. 20 (*non* Defrance, 1826).

Material and dimensions – Height 12.8 mm, width 4.8 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1286 (1), NHMW 2016/0103/1876-1877 (7), RGM.1352304-305 (2), RGM.718135 (32), RGM.1352622 (9), LC (8), FVD (3). **Beugnon**: RGM.1352445 (1).

Discussion – As discussed by Glibert (1954, p. 19), Defrance (1926) included various species under his name *Pleurotoma gradata*, and as Siena (Italy) was the first locality cited, Glibert considered the shell illustrated by Bellardi (1877, pl. 5, fig. 39) to represent true *C. gradata*. He erected the name *C. neogradata* for the French middle Miocene specimens from the Loire Basin. Glibert considered the French specimens to differ from *C. gradata* in having a narrower spire and more numerous, but weaker tubercles above the suture. As seen in the series illustrated some specimens have the slender shell typical of *C. neogradata* (Pl. 74, figs 1, 2), whereas others have a slightly wider apical angle (Pl. 74, figs 3, 4). This probably led Brébion (1964) to record both species from Assemblage I. However, if the neanic teleoconch whorls are compared, the sculpture is the same in both forms (Pl. 74, figs 2d, 4d). The number of tubercles above the suture, 18-20, is similar to that recorded by Glibert for the Loire Basin population. In comparing *C. neogradata* to *C. ligeriana* Peyrot, 1938, also from the Loire Basin, Glibert described the protoconch of *C. neogradata* as '*à costules axiales coudées, très rapprochées, …*' (1954, p. 19). However, the protoconch is paucispiral and consists of under two smooth whorls with a few axial ribs just before the teleoconch junction. It is possible he was referring to the earliest teleoconch whorls. We have not seen specimens of *C. gradata* from the upper Miocene if Italy, but provisionally consider them distinct based on the finer sculpture and more numerous tubercles. It is possible that with more comparative material the two fall within the range of a single species, in which case Defrance's name has priority. However, *Clavatula* species are all direct developers and hence tend to be geographically restricted.
Brébion (1964, p. 539, 540) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou, St-Michel) and Assemblage II (Apigné, Carcé, Le Temple du Cerisier).

Distribution – Middle Miocene (Langhian), Atlantic, Loire Basin, France (Peyrot, 1938; Glibert, 1954). Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964).

***Clavatula obtruta* (Millet, 1865)**
Plate 75, figs 1-7

1854 *Pleurotoma Obtruta* Millet, p. 161 (*nomen nudum*).
*1865 *Pleurotoma obtruta* Millet, p. 587.
?1954 *Clavatula ligeriana* Peyrot, 1938 – Glibert, p. 17, pl. 3, fig. 8c only (*non* Peyrot, 1938).
1964 *Clavatula obtruta* Millet, 1854 [*sic*] – Brébion, p. 544, pl. 13, fig. 24.

Type material – Syntypes: Sceaux-d'Anjou, Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 545).

Material and dimensions – Maximum height 13.2 mm, height 5.0 mm. **St-Clément-de-la-Place**: LC (1). **Sceaux-d'Anjou**: NHMW 2016/0103/1283-1285 (3), NHMW 2016/0103/1879-1880 (2), 2016/0103/1881 (3), RGM.1352306-307 (2), RGM.718134 (44), RGM.1352623 (14), LC (12), FVD (2). **Renauleau**: LC (?15).

Original description – 'Pleurotoma obruta, *Millet. Coq. de moyenne taille, comme fusiforme, à canal court, composée de huit à dix tours de spire, tous couverts de ciselures obliques, perlées ou non perlées, et dont l'obliquité se contrarie d'un tour à l'autre. Le dernier tour porte un large sillon légèrement creusé en gouttière et dont l'intérieur est garni, dans sa longueur, de fines stries qui se touchent. Ce sillon repose sur un rang de perles situées sur un petit canal transversal plus ou moins bien marqué; le reste de la coq. montre des stries transverales. Longueur: 16-18 millimètres; diamètre: 7 millimètres. Th., Sc.*' (Millet, 1865, p. 587).

Discussion – *Clavatula obtruta* (Millet, 1865) has a paucispiral protoconch of just under two smooth whorls. Early teleoconch whorls are strongly beaded, with two rows of beads on the subsutural band and one row of stronger beads on the suprasutural band. The sub- and suprasutural bands are separated by a narrow groove. Abapically comma-shaped axial ribs develop, roughly equal in width to their interspaces. The entire surface is covered in weak, narrow spiral cords. On the last whorl the subsutural ramp is strongly concave and the whorl swollen at the shoulder. This is particularly evident in juvenile specimens (Pl. 75, figs 1, 2) in which the base is strongly constricted and the siphonal canal relatively short and narrow. With ontogeny the peripheral swelling on the last whorl becomes less prominent and the base less excavated (Pl. 75, figs 4-7). Intermediate subadult forms exist (Pl. 75, fig. 3). Brébion (1964) recorded a similar species from Assemblage I under the name *Clavatula raphana* Millet, 1854 (*nomen nudum*; validated by Millet, 1865, p. 587). That species differs in having a wider apical angle, the subsutural band seems to be predominant, whereas in *C. obtruta* the beads on the suprasutural band are stronger, and the canal, if complete, in very short. We have not identified this species in the Assemblage I material examined.

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

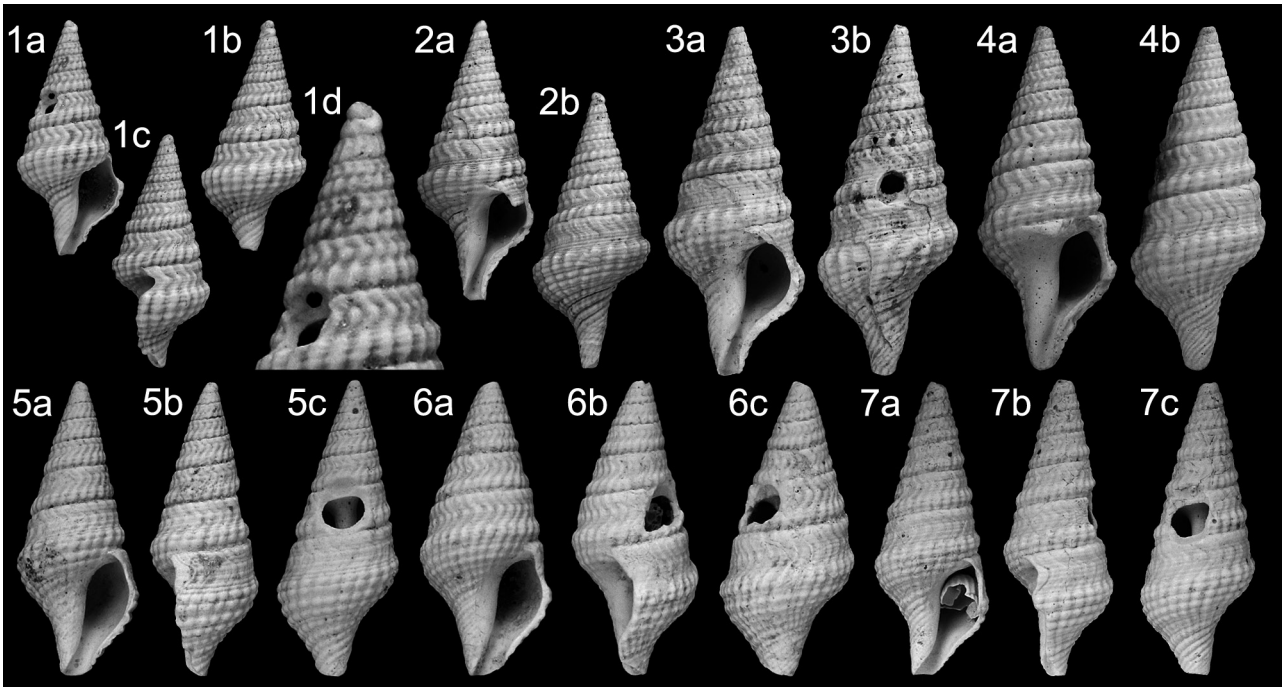

Plate 75. *Clavatula obtruta* (Millet, 1865); 1. NHMW 2016/0103/1879, height 9.4 mm, width 4.0 mm (juvenile), 1d, detail of protoconch; 2. RGM.1352306, height 9.1 mm, width 3.7 mm (juvenile); 3. NHMW 2016/0103/1880, height 12.8 mm, width 4.8 mm; 4. RGM.1352307, height 13.4 mm, width 5.0 mm; 5. NHMW 2016/0103/1283, height 12.5 mm, width 4.9 mm; 6. NHMW 2016/0103/1284, height 12.1 mm, width 5.1 mm; 7. NHMW 2016/0103/1285, height 13.2 mm, height 5.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Clavatula raphana* (Millet, 1865)**
Plate 76, fig. 1

1854 *Pleurotoma Raphana* Millet, p. 160 (*nomen nudum*).
*1865 *Pleurotoma raphana* Millet, p. 587.
1964 *Clavatula raphana* Millet, 1854 [*sic*] – Brébion, p. 543, pl. 13, fig. 23.

Type material – Syntypes: Sceaux-d'Anjou or Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 544).

Material and dimensions – Height 18.9 mm, width 9.0 mm (incomplete). **Sceaux-d'Anjou**: RGM.1352624 (1). **Reanauleau**: NHMW 2016/0103/2195 (1).

Original description – 'Pleurotoma raphana. *Millet. Coq. en ovale renflée dans sa partie moyenne, aiguë au sommet et a canal court; composée de 9-10 tours de spire, couverts de rangs de perles mal définies et alternant de grosseur sur les derniers tours. Les derniers tours en outre, présentent un canal ouvert, qui n'est que la continuation de l'échancrure du bord droit. Le bord gauche montre un grand nombre de stries bien prononcées. Longueur: 15-16 millimètres; diamètre: vers la partie renflée, 10-12 millimètres. Assez rare. Sc., Ren*.' (Millet, 1865, p. 587).

Discussion – Two specimens are herein tentatively ascribed *Clavatula raphana* (Millet, 1865). The shell from Renauleau (Pl. 76, fig. 1) has a well-preserved teleoconch, but the protoconch is missing. The second is an incomplete specimen from Sceaux-d'Anjou (Pl. 76, fig. 2). The early whorls sculpture is similar in the two specimens, but there are some small sculptural differences on the last whorl, where the Sceaux-d'Anjou specimen has a more prominent subsutural band and the axial ribs are slightly stronger at the periphery.
The original description states that the tubercles are poorly defined and alternate in strength on later teleoconch whorls, which is not the case in the specimen at hand. The description given by Brébion '*Forme élargie. Tours creusés en gorge à la partie médiane, ornés de cordons spiraux trés atténués dans la zone excavée et de côtes arquées dans les premiers tours, progressivement réduites à des rangées de nodules crénelés par les cordons, au nombre de 25, à la partie antérieure et postérieure des tours, moins nets dans cette dernière. Base couverte de cordons irréguliers faiblement noduleux; canal court*.' (1964, p. 543) is much closer to the specimens illustrated here. Brébion considered one of the specimens from the middle Miocene Loire Basin of France illustrated by Glibert (1954, pl. 3, fig. 8f only) as *Clavatula ligeriana* (Peyrot, 1938) to belong to *C. raphana*. However, Glibert's specimen does not have a well-developed subsutural band, as seen in *C. raphana*, whereas another of his figures for *C. ligeriana* does (1954, pl. 3, fig. 8c). We cannot make any definitive conclusion about the relationship between these species with the scant material at hand, however, if they were synonyms, Millet's name would have priority. As interpreted here, *C. raphana* is the broadest of the Assemblage I *Clavatula* species. The peripheral tubercles are larger that they are in *C. anaglypta* (Millet, 1865), *C. neogradata* Glibert, 1954 and *C. obtruta* (Millet, 1865), but not as large as in *Clavatula sceauxensis* nov. sp. In *C. dujardini* Peyrot, 1938 the peripheral tubercles are also broader, but poorly delimited.
Brébion (1964, p. 544) recorded this species from the Assemblage I localities of Sceaux-d'Anjou, Renauleau, St-Clément-de-la-Place and Beaulieu, but we have only been able to ascibe a single specimen from Sceaux-d'Anjou to this species.

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

***Clavatula sceauxensis* nov. sp.**
Plate 77, figs 1-2

Type material – Holotype RGM.739224, height 9.0 mm, width 4.7 mm; paratype 1 RGM.739226, height 9.4 mm, width 4.3 mm.

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

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

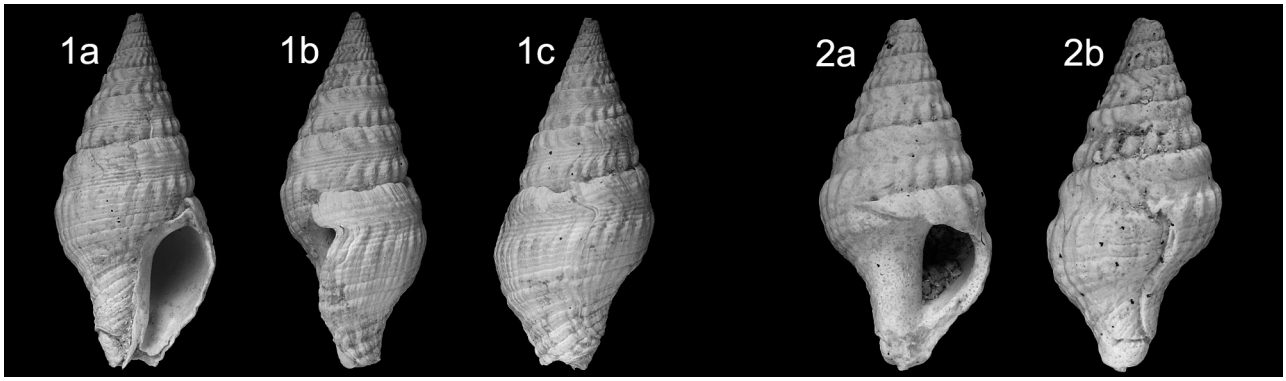

Plate 76. *Clavatula raphana* (Millet, 1865); 1. NHMW 2016/0103/2195, height 28.5 mm, width 12.2 mm. Renauleau. 2. RGM.1352624, height 18.9 mm, width 9.0 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Clavatula* species of small size, biconic, coeloconoid spire, teleoconch whorls with two coarsely nodular bands abutting suture, band above suture bearing larger tubercles, separated by concave mid-section, weak spiral cords cover entire surface, base strongly concave, siphonal canal relatively short.

Description – Shell small, biconic, coeloconoid spire. Protoconch not preserved. Teleoconch of 5-6 whorls. Spire whorls with broad subsutural band, even broaded suprasutural band abutting suture, both bearing coarse tubercles, larger on lower band; interspace between cords concave. Weak flattened spiral cords cover entire surface. Last whorl 60% total height, weakly tubercular subsutural cord, concave below to peripheral cord, peripheral cord bearing 9-14 large rounded axially-elongated tubercles, cords strengthen over base and siphonal fasciole. In some specimens single cord placed just below periphery bisecs peripheral tubercles unequally into larger adapical portion at periphery and smaller abapical portion delimiting base. Base strongly constricted, concave. Aperture 43% total height, outer lip thin, smooth within, anal sinus moderately wide and deep, with apex placed on concave portion of subsutural ramp; siphonal canal relatively short, open. Columella moderately excavated in upper third, Columellar callus slightly thickened forming narrow callus rim, parietal callus not developed, but small parietal pad present adapically immediately adjacent to insertion outer lip. Siphonal fasciole not sharply delimited, bearing stronger spiral cords.

Discussion – Unfortunately only two specimens are available to us, of which neither has the protoconch preserved and both have been drilled by predators. However *Clavatula sceauxensis* nov. sp. differs from all its Assemblage I congeners in having large rounded axially-elongated tubercles developed at the periphery. The two specimens show little variation, except that in paratype 1 (Pl. 77, fig. 2) the peripheral tubercles are bisected unequally by a spiral cord. This type of sculpture composed of a broad, nodular infra- and suprasutural band separated by broad concave interspace is shared by numerous species from the upper Miocene Tortonian of Italy, such as *Clavatula coppii* Bellardi, 1877, *C. agassizi* Bellardi, 1877, *C. stazzanensis* Bellardi, 1877 and *C. aradasi* Bellardi, 1877, but they are all larger and differ is shell shape. *Clavatula doderleini* (Hörnes, 1854) from the middle Miocene Paratethys also has tubercular bands bordering the suture, but again differs in shell shape.

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

Genus *Perrona* Schumacher, 1817

Type species – *Perrona tritonum* Schumacher, 1817, by monotypy, present-day, West Africa.

1817 *Perrona* Schumacher, p. 66, 218.

***Perrona obeliscoides* (Millet, 1854)**
Plate 78, figs 1-2

*1854 *Pleurotoma Obeliscoides* Millet, p. 161.
1865 *Pleurotoma obeliscoides* Millet, p. 587.
1954 *Clavatula* (*Perrona*) *semimarginata* Lamarck, 1822 – Glibert, p. 20, pl. 4, fig. 1 [*non Perrona semimarginata* (Lamarck, 1822)].
1964 *Clavatula obeliscoides* Millet, 1854 – Brébion, p. 546, pl. 13, fig. 25.
1964 *Clavatula* (*Perrona*) *semimarginata* var. *servata* Sacco, 1890 – Brébion, p. 549, pl. 13, fig. 27 [*non Perrona servata* (Sacco, 1890)].

Type material – Syntypes: Thorigné, Sceaux-d'Anjou, Genneteil or Renauleau; musée d'Angers (*fide* Brébion, 1964, p. 546).

Material and dimensions – Maximum height 35.5 mm, width 11.4 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1884 (2), RGM.718137 (19), RGM.1352443 (5 large adult speci-

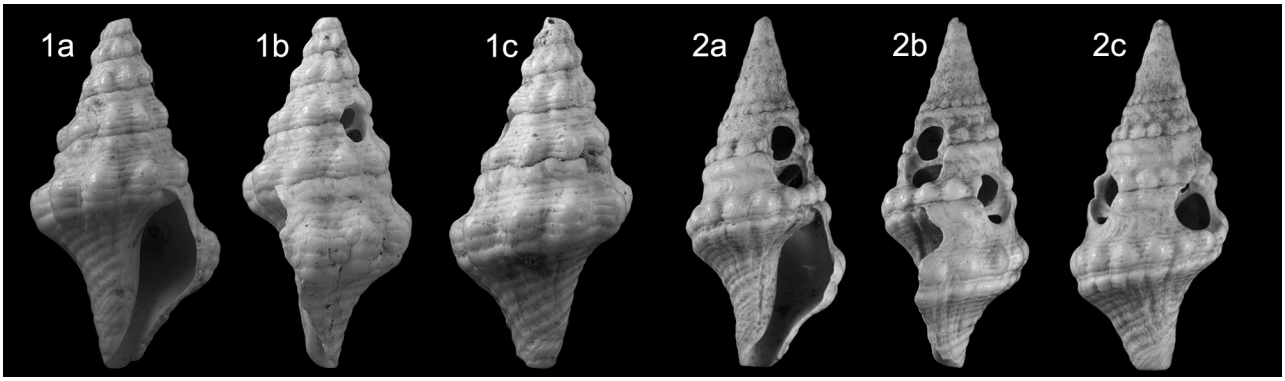

Plate 77. *Clavatula sceauxensis* nov. sp.; 1. **Holotype** RGM.739224, height 9.0 mm, width 4.7 mm; 2. **Paratype 1** RGM.739226, height 9.4 mm, width 4.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

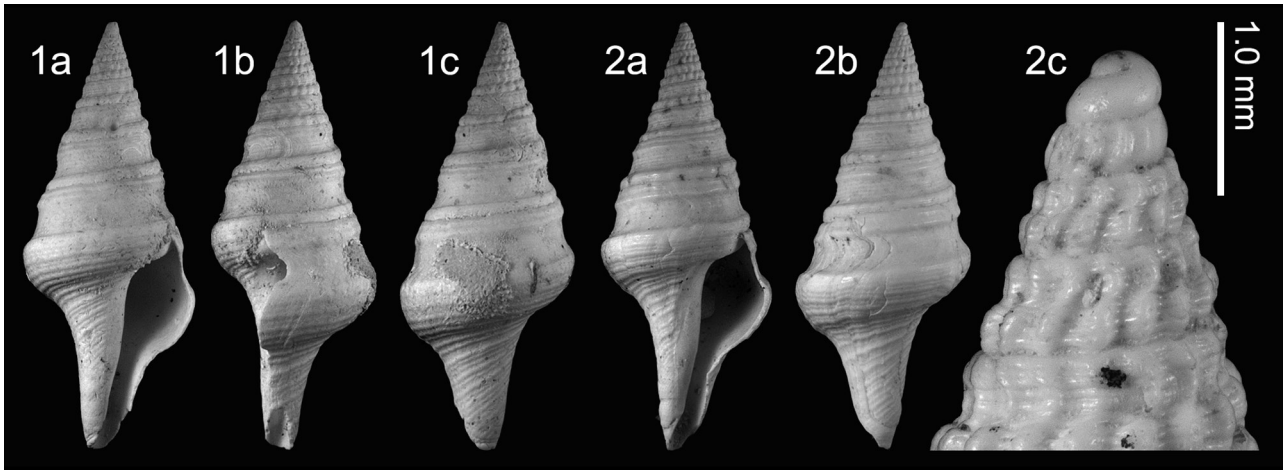

Plate 78. *Perrona obeliscoides* (Millet, 1854); 1. NHMW 2016/0103/1491, height 20.1 mm, width 7.8 mm; 2. NHMW 2016/0103/1492, height 21.5 mm, width 8.5 mm, 2c, detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

mens showing signs of predation), RGM 1352549 (1 + 2 juveniles), LC (10), FVD (1). **Renauleau**: NHMW 2016/0103/1491-1492 (2), NHMW 2016/0103/1493 (21), LC (50+), FVD (25). **Beugnon**: RGM.1352442 (1).

Original description – 'Obeliscoides*, Millet. —Thorigné. Sceaux. — Cette espèce a des rapports de forme et de grosseur avec le P. transversaria, Lamk.; mais les dessins dont la coquille est ornée l'en distinguent facilement*' (Millet, 1854, p. 160).
'Pleurotoma obeliscoides, *Millet. Coq. fusiforme composée de 10-11 tours de spire: les derniers, portant une large et profonde gouttière, bordée de chaque côté par une espèce de carène plus ou moins prononcée et que délimite chaque suture. Ces tours sont ou lisses ou légèrement striés transversalement; mais les stries de la base du dernier tour sont toujours apparentes. Sur d'autres points, des stries verticales, irrégulières et peu marquées, prennent par l'accroissement de la coquille, la forme que lui donne le bord droit; enfin les premiers tours de spire présentent de petits cordons perlés. Longueur: 45-48 millimètres; diamètre: 15-16 millimètres. Th., Sc., Genn., Ren.*' (Millet, 1865, p. 587).

Discussion – Perrona obeliscoides (Millet, 1854) is characterised by its paucispiral protoconch of two smooth whorls. Earliest teleoconch whorls are strongly sculptured by a narrow infrasutural band and a wider suprasutural band separated by a concave portion roughly equal in width to the subsutural band. This is overlain by strong sinuous axial ribs and numerous weaker, close-set spiral cords. Abapically, the interspace between the sub- and suprasutural bands widens, leaving a broad, concave mid-whorl area. The sculpture weakens, axials disappear on the 4-5 teleoconch whorl, leaving a smooth subsutural band bearing two spiral cords and a beaded suprasutural band. The last whorl bears a subsutural band with two cords, a broad concave smooth area below, is strongly, but narrowly swollen at the periphery and convex below, rapidly constricted at the base. The siphonal canal is long and straight. Spiral sculpture reappears over the base and siphonal canal.
The most similar species is *Perrona inedita* (Bellardi, 1877) from the lower Miocene of Italy and the middle Miocene of Turkey (Landau *et al*., 2013), but that species is much larger, the axial ribs on the earliest teleoconch whorls disappear weaken earlier and have disappeared by the third whorl and the base is subangular. Brébion (1964) identified this species (in part) as *Perrona semimarginata* var. *servata* (Sacco, 1890), from the Italian upper Miocene, but *P. semimarginata* (Lamark, 1822) from the lower Miocene Aquitaine Basin and *P. servata* are both quite different; larger, without a clearly delimited suprasutural band, they are less inflated mid-whorl on the last whorl and they lack spiral cords on the base. Specimens at hand of *P. semimarginata* also have very weak spiral sculpture on the first two teleoconch whorls. We note that *Pleurotoma obeliscoides* Schauroth, 1865 is a junior homonym.
Millet (1854, 1865) recorded this species from Assemblage I (Thorigné, Sceaux-d'Anjou, Genneteil, Renauleau), to which Brébion (1964, p. 618) added St-Clément-de-la-Place. He also recorded it from the middle Miocene locality of La Beurelière.

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

Genus *Fusiturris* Thiele, 1929

Type species – *Pleurotoma undatiruga* Bivona Ant. in Bivona And., 1838, by monotypy, Pleistocene, Italy.

1929 *Fusiturris* Thiele, p. 361.
1929 *Tyrrhenoturris* Coen, p. 297. Type species (by subsequent designation Powell, 1942): *Pleurotoma undatiruga* Bivona Ant. in Bivona And., Pleistocene, Italy.

***Fusiturris strigosa* (Millet, 1865)**
Plate 79, figs 1-5

1854 *Pleurotoma Strigosa* Millet, p. 161 (*nomen nudum*).
*1865 *Pleurotoma strigosa* Millet, p. 588 (*pars*).
1964 *Turris* (*Fusiturris*) *aquensis* Grateloup, 1832 – Brébion, p. 554, pl. 13, figs 28, 29 [*non Fusiturris aquensis* (Grateloup, 1832)].
1964 *Turris* (*Fusiturris*) *inermis* Partsch, 1842 [*sic*] – Brébion, p. 556, pl. 13, figs 30, 31 (= *Pleurotoma inermis* Hörnes, 1854].
2018 *Fusiturris strigosa* (Millet, 1865) – Ceulemans *et al*., p. 96, pl. 1, figs 13-15.

Type material – Plesiotype: Thorigné; musée d'Angers (*fide* Brébion, 1964, p. 557).

Material and dimensions – Maximum height 35.1 mm, width 7.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1033-1035 (3), NHMW 2016/0103/1036 (15), RGM.1352284 (1 fragment), RGM.1352285 (26), RGM. 1352297 (27), RGM.1352699 (4 juveniles), LC (40), FVD (19). **Sceaux-d'Anjou**: NHMW 2016/0103/1037-1038 (2), NHMW 2016/0103/1039 (7), RGM.718141 (50+), RGM.718142 (8 juveniles), RGM.1352281 (15), RGM. 1352287 (5), RGM.1352288 (35), RGM.1352289 (5), RGM.1352550 (50+), LC (10), FVD (13).

Discussion – This species was fully discussed by Ceulemans *et al*. (2018, p. 96). Brébion (1964, p. 554) considered this species a synonym of *F. aquensis* (Grateloup, 1832) from the lower Miocene of the Aquitaine Basin, also recorded from the lower-middle Miocene of the North Sea Basin (A.W. Janssen, 1984). However, despite the teleoconch of the two being similar, *F. aquensis* has a multispiral protoconch composed of four whorls (Glibert, 1954, p. 11; A.W. Janssen, 1984, pl. 10, fig. 13), suggestive of planktotrophic development. Although the teleoconch sculpture is somewhat variable in *F. aquensis* and similar to that of *F. strigosa* (Millet, 1865), the siphonal canal is shorter in *F. aquensis*. This teleoconch variability is even more marked in the Assemblage I specimens than those from Assemblage III. Specimens from Sceaux-d'Anjou tend to have axials persisting onto the last whorl (Pl. 79, figs 4, 5), whereas in gerontic specimens from St-Clément-de-la-Place the axials often weaken and disappear on the last whorl (Pl. 79, figs 1,2), however numerous intermediate forms exist at both localities.
Millet (1854, p. 161; 1865, p. 588) described this species from Assemblage I localities if Thorigné, Sceaux-d'Anjou, Renauleau, and Saint-Michel. Brébion (1964, p. 555) added St-Clément-de-la-Place and Beaulieu, Assemblage II (Apigné, Le Temple du Cerisier) and Assemblage III (Palluau, Le Pigeon Blanc).

Distribution – Upper Miocene: Atlantic (Tortonian and Messinian): NW France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al*., 2018).

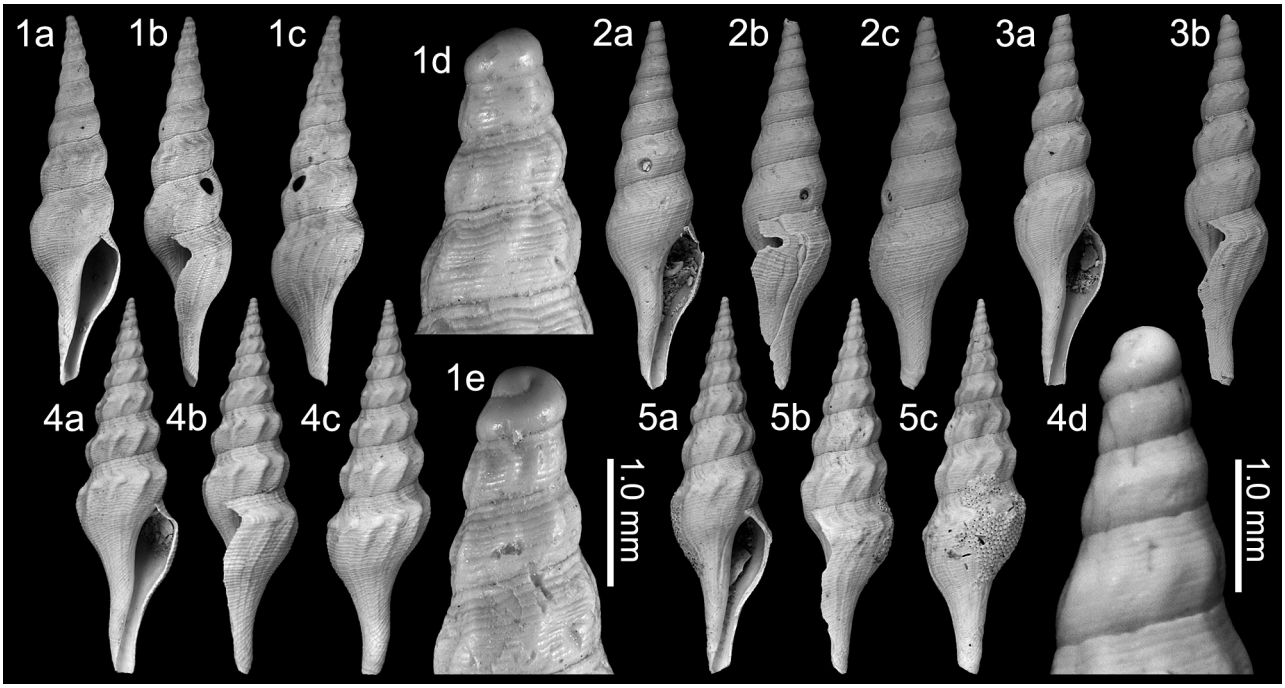

Plate 79. *Fusiturris strigosa* (Millet, 1865); 1. NHMW 2016/0103/1033, height 21.5 mm, width 5.2 mm, 1d, e, detail of protoconch; 2. NHMW 2016/0103/1034, height 29.0 mm, width 7.2 mm; 3. NHMW 2016/0103/1035, height 27.6 mm, width 5.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place. 4. NHMW 2016/0103/1037, height 27.9 mm, width 7.7 mm, 1d, detail of protoconch; 5. NHMW 2016/0103/1038, height 28.5 mm, width 7.5 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene. Maine-et-Loire, NW France, Tortonian, upper Miocene.

Family Horiaclavidae Bouchet, Kantor, Sysoev & Puillandre, 2011
Genus *Haedropleura* Bucquoy, Dautzenberg & Dollfus, 1883

Type species – Pleurotoma septangularis Montagu, 1803, by original designation, present-day, Mediterranean.

1883 *Haedropleura* Bucquoy, Dautzenberg & Dollfus, p. 85, 110.

***Haedropleura brebioni* nov. sp.**
Plate 80, figs 1-2

1964 *Bellaspira* (*Haedropleura*) *couffoni* Brébion, p. 567, pl. 13, fig. 39.

Type material – Holotype MNHN.F.A57932, height 6.1 mm, width 2.6 mm; paratype 1 MNHN.F.A57933, height 6.7 mm, 3.2 mm; paratype 2 NHMW 2016/0103/1040, height 7.8 mm, width 3.1 mm; paratype 3 NHMW 2016/0103/1041, height 7.5 mm, width 2.8 mm; paratype 4 NHMW 2016/0103/1042, height 6.4 mm, width 2.7 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1352478, height 8.1 mm, width 3.1 mm; paratype 6 RGM.1352479, height 7.6 mm, width 3.0 mm; paratype 7 RGM.1352561, height 7.7 mm, width 3.2 mm; paratype 8 RGM.1352562, height 7.5 mm, width 3.2 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 12.4 mm, width 5.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1043 (30), LC (40), FVD (45). **Sceaux-d'Anjou**: NHMW 2016/0103/1045 (50+), RGM.718146 (50+), RGM.718147 (43), RGM.1352363 (2), RGM.1352480 (20), RGM.1352557 (8), RGM.1352563 (22), RGM.1352670 (1), LC (30), FVD (50+). **Renauleau**: NHMW 2016/0103/1044 (32), LC (45), FVD (38). **Beugnon**: RGM.1352350 (1), RGM.1352430 (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – Haedropleura species of small size, squat-fusiform shape, with smooth paucispiral protoconch of 1.75 whorls, convex teleoconch whorls with 10-12 rounded sinuous ribs, fine crowded spiral sculpture, short siphonal canal, without parietal pad or tooth.

Description – Shell small, of moderate thickness, squat-fusiform. Protoconch paucispiral, composed of 1.75 smooth, strongly convex whorls with large nucleus. Junction with teleoconch marked by beginning of axial sculpture. Teleoconch of 4.5 convex whorls, somewhat swollen in abapical half, with periphery placed between mid-whorl and suture; subsutural ramp and shoulder poorly delimited. Suture impressed, undulating. Axial sculpture of sinuous, rounded ribs, half width of their interspaces, extending between sutures, weakening slightly over subsutural ramp, 10-12 on last whorl, in some specimens aligned axially, in other not. Spiral sculpture of very fine, crowded, equal spiral cords covering entire surface. Last whorl 62-64% total height, convex, subsutural ramp narrow, hardly delimited, moderately constricted at base; base not sharply delimited. Aperture 39-42% total height, ovate, relatively wide, outer lip convex, weakly thickened by narrow labial varix; anal sinus shallow U-shape with apex at shoulder; siphonal canal short, open, wide. Columella moderately excavated in upper half. Columellar and parietal callus not thickened, forming narrow indented callus rim, slightly everted over siphonal fasciole. Siphonal fasciole not delimited.

Discussion – The genus *Haedropleura* can have a multispiral or paucispiral protoconch. *Haedropleura brebioni* nov. sp. is a paucispiral species, with a protoconch suggesting direct development. Others with a paucispiral protoconch are *H. secalina* (Philippi, 1844), which was relatively widespread in the European late Miocene and Pliocene and today is found in the western and central Mediterranean, *H. flexicostata* Monterosato, 1884, en-

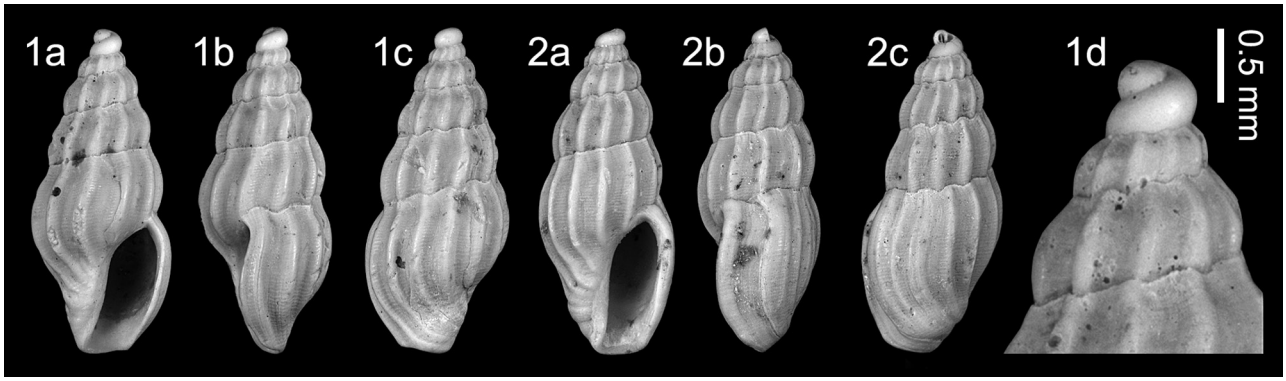

Plate 80. *Haedropleura brebioni* nov. sp.; 1. **Holotype** MNHN.F.A57932, height 6.1 mm, width 2.6 mm, 1d, detail of protoconch; 2. **Paratype 1** MNHN.F.A57933, height 6.7 mm, width 3.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

demic to the present-day coast of Tunisia, that is similar in having sinuous axial ribs, but differs in having a more pointed spire, the spire whorls are more swollen in the abapical half, and the siphonal canal is wider, and *H. fratemcontii* Ceulemans, Van Dingenen & Landau, 2018 from the lower Pliocene Assemblage III of NW France. *Haedropleura secalina* differs in having a more elongated shell, the ribs are less sinuous and tend to fade on the last half whorl, whereas in *H. brebioni* they continue strongly over the outer lip. *Haedropleura fratemcontii* has far more convex whorls, a more inflated last whorl, slightly more numerous axials that weaken over the base of the last whorl, and stronger spiral sculpture.
Brébion (1964, p. 568) recorded this species from the Assemblage I locality of St-Michel, to which we add St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, and he recorded it from the Assemblage II locality of Apigné.

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

***Haedropleura gallica* nov. sp.**
Plate 81, figs 1-7

1964 *Bellaspira* (*Haedropleura*) *secalina* Philippi, 1844 – Brébion (*partim*), p. 565, pl. 13, fig. 38 [*non Haedropleura secalina* (Philippi, 1844)].
2018 *Haedropleura secalina* (Philippi, 1844) – Ceulemans *et al*., p. 98, pl. 2, fig. 7.

Type material – Holotype MNHN.F.A70530, height 7.8 mm, width 2.8 mm; paratype 1 MNHN.F.A70531, height 6.7 mm, width 2.6 mm; paratype 2 NHMW 2016/0103/1948, height 6.8 mm, width 2.7 mm; paratype 3 NHMW 2016/0103/1949, height 6.8 mm, width 2.6 mm; paratype 4 NHMW 2016/0103/1950, height 7.0 mm, width 2.7 mm; paratype 5 NHMW 2016/0103/1951, height 7.8 mm, width 2.8 mm; paratype 6 NHMW 2016/0103/1952, height 5.5 mm (juvenile), **St-Clément-de-la-Place**. Paratype 7 RGM.1352453, height 7.6 mm, width 3.1 mm; paratype 8 RGM.1352466, height 7.9 mm, 3.0 mm; paratype

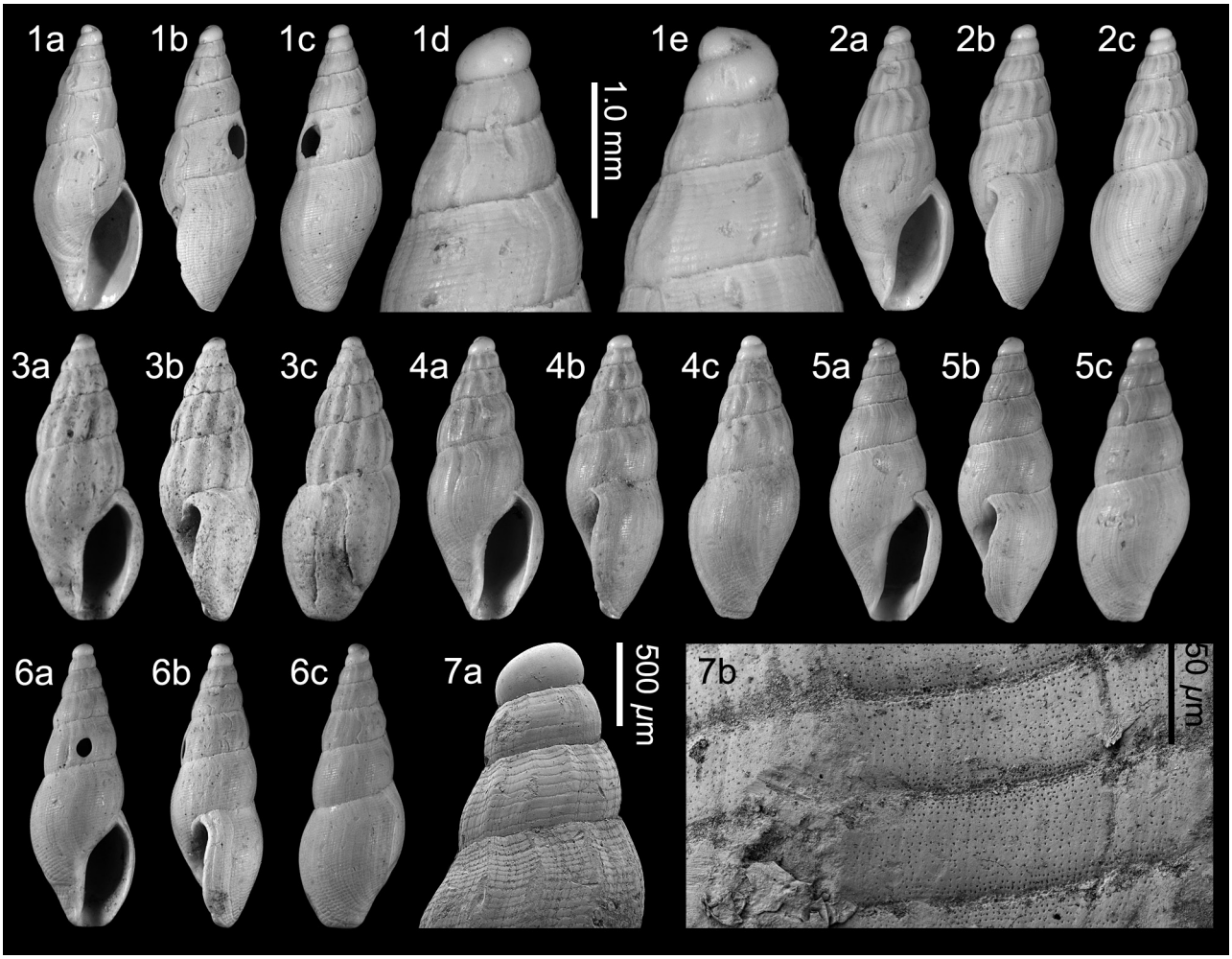

Plate 81. *Haedropleura gallica* nov. sp.; 1. **Holotype** MNHN.F.A70530, height 7.8 mm, width 2.8 mm, 1d, e, detail of protoconch; 2. **Paratype 1** MNHN.F.A70531, height 6.7 mm, width 2.6 mm; 3. **Paratype 2** NHMW 2016/0103/1948, height 6.8 mm, width 2.7 mm; 4. **Paratype 3** NHMW 2016/0103/1949, height 6.8 mm, width 2.6 mm; 5. **Paratype 4** NHMW 2016/0103/1950, height 7.0 mm, width 2.7 mm; 6. **Paratype 5** NHMW 2016/0103/1951, height 7.8 mm, width 2.8 mm; 7. **Paratype 6** NHMW 2016/0103/1952, height 5.5 mm (juvenile), 7a, detail of protoconch, 7b, detail of teleoconch microsculpture (SEM images). Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

9 RGM.1352467, height 7.5 mm, width 2.9 mm, paratype 10 RGM.1352556, height 8.1 mm, width 3.1 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 13.9 mm, width 4.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1048 (50+), RGM.1352660 (50+), RGM.1352696 (12), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1053 (39), RGM.718148 (32), RGM.734987 (50+), RGM.1352454 (2), RGM.1352468 (5), RGM.1352481 (3), RGM.1352557 (7), LC (20), FVD (23).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Haedropleura* species of small size, fusiform shape, with smooth paucispiral protoconch of 1.75 whorls, weakly convex teleoconch whorls with 10-11 ribs on second teleoconch whorl, last two whorls smooth or almost so in most specimens, fine flattened spiral sculpture, short siphonal canal, without parietal pad or tooth, siphonal canal short.

Description – Shell small, of moderate thickness, fusiform. Protoconch paucispiral, composed of 1.75 smooth, strongly convex whorls with medium-sized nucleus. Junction with teleoconch marked by beginning of axial sculpture. Teleoconch of four weakly convex whorls, somewhat swollen in abapical half, with periphery placed between mid-whorl and suture; subsutural ramp and shoulder hardly developed. Suture impressed, linear. Weak axial sculpture of prosocline ribs, weakening further abapically, obsolete or almost so on last two whorls in most specimens, 10-11 on second teleoconch. Weak spiral sculpture of fine flattened cords separated by narrow grooves covering entire surface. Last whorl 61% total height, subsutural ramp slightly concave, poorly delimited, whorl profile convex below, hardly constricted at base; base not delimited. Aperture 41% total height, ovate, relatively wide, outer lip convex, weakly thickened by labial varix; anal sinus shallow U-shape with apex at shoulder; siphonal canal short, open, wide. Columella moderately excavated in upper half. Columellar and parietal callus not thickened, forming narrow callus rim, slightly everted over siphonal fasciole. Siphonal fasciole not delimited.

Discussion – Scarponi & Della Bella (2003, p. 55) and Micali (2010, p. 4) discussed the confusion surrounding *Haedropleura septangularis* (Montagu, 1803) and *Haedropleura secalina* (Philippi, 1844), which has often been considered a subspecies of *H. septangularis*.
Haedropleura secalina (Philippi, 1844) and *H. septangularis* form a species pair; *H. septangularis* has a multispiral protoconch of about 2.5-3 whorls with sigmoid axial riblets on the last half whorl, whereas *H. secalina* has a paucispiral protoconch of 1.5-2.0 whorls covered with micropustular sculpture to a variable degree. Their teleoconch shells are difficult to separate consistently and rather variable.
Ceulemans *et al*. (2018, p. 98) regarded the material from the lower Pliocene Assemblage III of NW France conspecific with *H. secalina*, but drew attention to the difference in sculpture between the Assemblage III specimens and *H. secalina* described by Scarponi & Della Bella (2003) from the Pliocene of Italy and present-day Mediterranean.
With the plentiful and better-preserved material at hand from Assemblage I we consider this position to be incorrect. The fossil specimens from France differ from *H. secalina* in having far weaker spiral sculpture that weakens even further abapically, and disappears on the last two whorls in most specimens, whereas in *H. secalina* the ribs remain strong throughout. About one-third of the French specimens do have subobsolete axial sculpture persisting onto the last whorl (Pl. 81, fig. 2), but it is never as strong as in *H. secalina*.
We therefore consider both the Assemblage I and III specimens a separate species, *H. gallica* nov. sp., that was probably endemic to the late Miocene and Pliocene of the Ligerian Gulf.
Interestingly, the specimen illustrated by Glibert (1954, pl. 6, fig. 12a) from the middle Miocene of the Loire Basin has strong ribs developed on the last whorl and is more similar to *H. secalina*, but this record needs to be verified with more material.

Distribution – Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Ceulemans *et al*., 2018).

***Haedropleura ligeriana* nov. sp.**
Plate 82, figs 1-5

1964 *Bellaspira* (*Haedropleura*) *secalina* Philippi, 1844 – Brébion (*partim*), p. 565, pl. 13, fig. 38 [*non Haedropleura secalina* (Philippi, 1844)].

Type material – Holotype MNHN.F.A70532, height 7.6 mm, width 2.7 mm; paratype 1 MNHN.F.A70533, height 8.4 mm, width 2.9 mm; paratype 2 NHMW 2016/0103/1046, height 7.5 mm, width 2.8 mm; paratype 3 NHMW 2016/0103/1047, height 8.2 mm, width 3.2 mm; paratype 4 NHMW 2016/0103/1049, height 8.2 mm, width 3.2 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1352558, height 7.0 mm, width 2.8 mm; paratype 6 RGM.1352559, height 7.3 mm, width 2.7 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 13.9 mm, width 4.9 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/1051 (50+), RGM.1352661 (30), RGM.1352697 (8), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1052

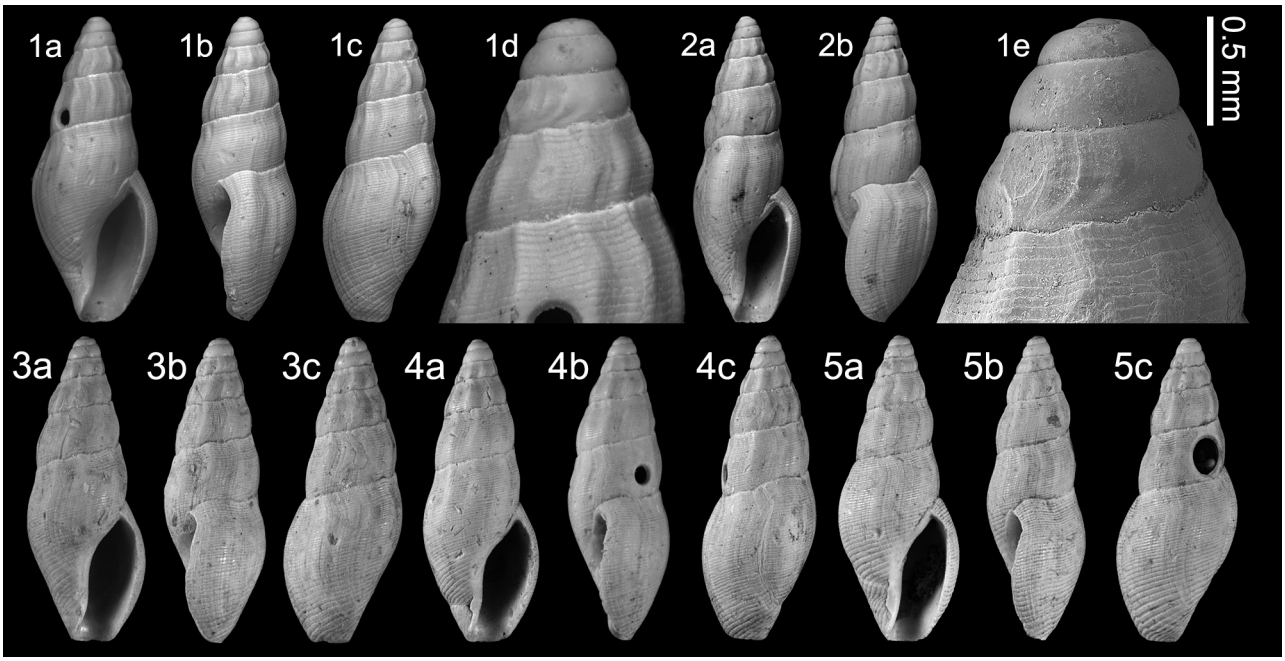

Plate 82. *Haedropleura ligeriana* nov. sp.; 1. **Holotype** MNHN.F.A70532, height 7.6 mm, width 2.7 mm, 1d, e, detail of protoconch (1e, SEM image); 2. **Paratype 1** MNHN.F.A70533, height 8.4 mm, width 2.9 mm; 3. **Paratype 2** NHMW 2016/0103/1046, height 7.5 mm, width 2.8 mm; 4. **Paratype 3** NHMW 2016/0103/1047, height 8.2 mm, width 3.2 mm; 5. **Paratype 4** NHMW 2016/0103/1049, height 8.2 mm, width 3.2 mm. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

(5), RGM.718149 (36), RGM.1352469 (5), RGM.1352482 (2), RGM.1352560 (9), RGM.1352618 (1 large adult, height 13.9 mm, width 4.9 mm, much larger than average), FVD (2). **Beugnon**: RGM.1352352 (1).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Haedropleura* species of small size, fusiform shape, with dome-shaped multispiral protoconch of 3.25-3.5 whorls, weakly convex teleoconch whorls with 9-10 ribs on second teleoconch whorl, last two whorls smooth or almost so in most specimens, fine flattened spiral sculpture, strong varix on last whorl in most specimens, short siphonal canal, without parietal pad or tooth, siphonal canal short.

Description – Shell small, of moderate thickness, fusiform. Protoconch multispiral, dome-shaped, composed of 3.25-3.5 smooth, convex whorls with small nucleus. Junction with teleoconch marked by beginning of axial sculpture. Teleoconch of four weakly convex whorls, slightly swollen in abapical half, with periphery placed just above suture; subsutural ramp and shoulder hardly developed. Suture impressed, linear. Weak axial sculpture of prosocline ribs, weakening further abapically, obsolete or almost so on last two whorls in most specimens, 9-10 on second teleoconch. Weak spiral sculpture of fine flattened cords separated by narrow grooves covering entire surface. Last whorl 61-65% total height, subsutural ramp slightly concave, poorly delimited, whorl profile convex below, hardly constricted at base; base not delimited. Strong varix on last whorl developed in most specimens, Aperture 38-43% total height, ovate, moderately wide, outer lip convex, weakly thickened by labial varix; anal sinus shallow U-shape with apex at shoulder; siphonal canal short, open, wide. Columella moderately excavated in upper half. Columellar and parietal callus not thickened, forming narrow callus rim, slightly everted over siphonal fasciole. Siphonal fasciole not delimited.

Discussion – If *Haedropleura secalina* (Philippi, 1844) and *H. septangularis* (Montagu, 1803) can be considered to form a species pair, one with a paucispiral, the other with a multispiral protoconch, in the upper Miocene of Assemblage I *H. gallica* nov. sp. and *H. ligeriana* nov. sp. can be considered to form another species pair. Their shells cannot be separated with confidence without their protoconchs. In *H. ligeriana* the spiral sculpture tends to be even weaker than in *H. gallica*, and in most specimens a strong, randomly placed varix forms on the last whorl, but there is so much intraspecific variability that neither of these characters can be used to reliably separate them. The protoconch on the other hand is quite different; of a typically direct developing type in *H. gallica* and typically planktotrophic in *H. ligeriana*. The protoconch of

H. ligeriana is similar to that of *H. septangularis*, but the teleoconch differs in having far weaker axial sculpture. Axials are present on the last whorl of all specimens of H. *septangularis* seen, both fossil and present-day. The specimens reported by Ceulemans *et al*. (2018) from the lower Pliocene Assemblage III of NW France do have relatively strong axials on the last whorl and we continue to consider them closer to *H. septangularis*. In the middle Miocene of the Paratethys and eastern Mediterranean H. *avenacea* Boettger, 1906 is similar to *H. ligeriana*, with a dome-shaped multispiral protoconch, but in that species the axial sculpture is stronger and persists or only becomes subobsolete on the second half of the last whorl (see Bałuk, 2003, pl. 14, figs 4-6; Landau *et al*., 2013, pl. 51, figs 1, 2).
We record *H. ligeriana* from the Assemblage I localities of St-Clément-de-la-Place, Sceaux-d'Anjou and Beugnon.

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

Family Terebridae Mörch, 1852
Genus *Strioterebrum* Sacco, 1891

Type species – Terebra basterotii Nyst, 1845, by original designation, Miocene, Belgium.

1891 *Strioterebrum* Sacco, 1891.

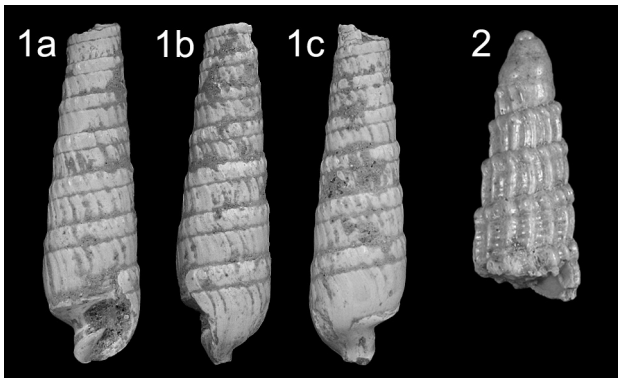

Plate 83. 1. *Strioterebrum acuminatum* (Borson, 1820), RGM.1349099, height 25.3 mm, width 8.5 mm. La Presselière, Sceaux-d'Anjou. 2. *Strioterebrum* cf. *basterotii* (Nyst, 1845), NHMW 2016/0103/1050, height 2.6 mm, width 1.0 mm, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Strioterebrum acuminatum* (Borson, 1820)**
Plate 83, fig. 1

*1820 *Terebra acuminata*, Borson, p. 224, pl. 1, fig. 17.
1854 *Terebra Rugulosa* Millet, p. 165 (*nomen nudum*).
1854 *Terebra rugulosa* Millet, p. 597.
1964 *Terebra acuminata* Borson, 1820 – Brébion, p. 634, pl. 15, fig. 17.
2013 *Terebra acuminata* Borson, 1820 – Landau *et al*., p. 297, pl. 51, figs 10-13 (*cum syn*.).

Material and dimensions – Maximum height 25.3 mm, width 8.5 mm (incomplete). **Sceaux-d'Anjou**: RGM.1349099 (1 fragment). **Beugnon**: RGM.1352397 (1 fragment).

Discussion – Landau *et al*. (2013, p. 297) followed Bałuk (1997), in considering *Terebra acuminata* Borson, 1820 and *Terebra neglecta* Michelotti, 1847 synonyms. This species is extremely uncommon in the Assemblage I deposits. Only a few fragments are available to us that show well developed axial sculpture.
Brébion (1964, p. 636) recorded this species from the Assemblage I localities of Renauleau, Sceaux-d'Anjou, St-Clément-de-la-Place and Beaulieu.

Distribution – Lower Miocene: Atlantic (Aquitanian and Burdigalian): Aquitaine Basin, France (Peyrot, 1931; Lozouet *et al*., 2001); Proto-Mediterranean Sea (Burdigalian): Colli Torinesi, Italy (Sacco, 1891). Lower-middle Miocene: North Sea Basin (upper Burdigalian-Langhian): Belgium (Glibert, 1952b), Germany (Beyrich, 1854; Kautsky, 1925; Anderson, 1964; Wienrich, 2007; Moths *et al*., 2010), The Netherlands (Nordsieck, 1972; A.W. Janssen, 1984). Middle Miocene: Atlantic (Langhian and Serravallian): Aquitaine Basin, France (Peyrot, 1931), (Langhian): Loire Basin (France (Glibert, 1952a); Paratethys (Langhian and Serravallian): Austria (Hörnes, 1852), Bulgaria (Kojumdgieva & Strachimirov, 1960), Romania (Hoernes & Auinger, 1880; Stancu & Andreescu, 1968), Hungary (Strausz, 1954, 1966; Csepreghy-Meznerics, 1954, 1956, 1972; Bohn-Havas, 1973), Poland (Friedberg, 1928; Bałuk, 1997), eastern Paratethys (Iljina, 1993); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958; Landau *et al*., 2013). Upper Miocene: Atlantic (Tortonian): NW France (Brébion, 1964), Cacela Basin, Portugal (Pereira da Costa, 1866); Proto-Mediterranean Sea (Tortonian): Po Basin, Italy (Sacco, 1891; Davoli, 1977), Tunisia (Stchepinsky, 1938). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (González Delgado, 1992; Landau *et al*., 2011); western Mediterranean, Estepona Basin (NHMW collection), northeastern Spain (Martinell, 1982b); central Mediterranean, Italy (Sacco, 1891), Tunisia (Fekih, 1975). Upper Pliocene: central Mediterranean, Italy (Sacco, 1891; Malatesta, 1974; Caprotti & Vescovi, 1973; Chirli, 1988; Cavallo & Repetto, 1992), Crete (Symeonidis, 1966). Pleistocene: central Mediterranean, Italy (Malatesta, 1960).

***Strioterebrum* cf. *basterotii* (Nyst, 1845)**
Plate 83, fig. 2

cf.*1845 *Terebra Basterotii* Nyst, p. 582.
cf. 1952b *erebra* (*Myurella*) *basteroti* (Nyst, 1843 [*sic*]) – Glibert, p. 138, pl. 10, fig. 8.

cf. 1984 *Strioterebrum* (*Strioterebrum*) *basteroti* (Nyst, 1845) – A.W. Janssen, p. 336, pl. 13, fig. 8, pl. 77, figs 1, 2.

cf. 2007 *Strioterebrum basteroti* (Nyst, 1845) – Wienrich, p. 722, pl. 116, fig. 6, pl. 156, figs 1-3.

Material and dimensions – height 2.6 mm, width 1.0 mm (incomplete). **St-Clément-de-la-Place**: NHMW 2016/0103/1050 (1 fragment).

Discussion – A small apical fragment from St-Clément-de-la-Place might represent *Strioterebrum basterotii* (Nyst, 1845), which is widespread in the Miocene of the NE Atlantic, Mediterranean and North Sea Basin (Davoli, 1977). However, with such scant material at hand we cannot be sure and provisionally ascribe itto this species.

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

Discussion

In this paper we record 84 conoidean species (of which four are left in open nomenclature), representing 40 genera. Fourty-two species are described as new: *Eoconus cambieni* nov. sp., *Eoconus vanhoutenae* nov. sp., *Aphanitoma roesti* nov. sp., *Pleurotomoides barnardi* nov. sp., *Pleurotomoides vanderdoncki* nov. sp., *Mitromorpha* (*s.s.*) *mulderi* nov. sp., *Bactrocythara pascaleae* nov. sp., *Bela henkmulderi* nov. sp., *Bela keukelaari* nov. sp., *Bela pseudomegastoma* nov. sp., *Bela pseudovulpecula* nov. sp., *Bela redoniana* nov. sp., *Bela scarponii* nov. sp., *Bela sceauxensis* nov. sp., *Mangelia burgersae* nov. sp., *Andonia delgadoi* nov. sp., *Buccinaria minuscula* nov. sp., *Clathromangelia daisyae* nov. sp., *Clathromangelia densecostata* nov. sp., *Clathromangelia hakkennesi* nov. sp., *Clathromangelia helwerdae* nov. sp., *Clathromangelia karinneae* nov. sp., *Clathromangelia pereirae* nov. sp., *Clathromangelia vannieulandei* nov. sp., *Clathromangelia wopkeae* nov. sp., *Cyrillia michalidesi* nov. sp., *Daphnella* (*Paradaphne*) *groeneveldi* nov. sp., *Leufroyia annegienae* nov. sp., *Leufroyia hesseli* nov. sp., *Leufroyia ligeriana* nov sp., *Leufroyia renauleauensis* nov. sp., *Leufroyia riccardoi* nov. sp., *Leufroyia seani* nov sp., *Raphitoma breitenbergeri* nov. sp., *Raphitoma dellabellaorum* nov. sp.*Raphitoma soniusae* nov. sp., *Raphitoma vogeli* nov. sp., *Teretia horroi* nov. sp., *Clavatula sceauxensis* nov. sp., *Haedropleura brebioni* nov. sp., *Haedropleura gallica* nov. sp., and *Haedropleura ligeriana* nov. sp. Of the 84 conoidean species recorded here, 64 (76%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. If we include the middle Miocene, 76 (90%) are restricted to northwestern France. Stratigraphically (see Fig. 1), 17 (20%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1952a). 10 (11%) 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. Only 6 (7%) are relatively cosmopolitan in the Pliocene, found in the Atlantic and Mediterranean and even fewer, 2 (2%) are still living in European Atlantic and/or Mediterranean waters.

In this part of the series we have recognised almost all the taxa discussed by Brébion, with the exception of *Clavatula raphana* (Millet, 1865) (Brébion, 1964, p. 543, pl. 13, fig. 23) and *Crassispira pseudobeliscus* (Fischer & Tournouer, 1873) (Brébion, 1964, p. 560, pl. 13, fig. 34) within the turrids, and the terebrid *Hastula striata* var. *subcinerea* (d'Orbigny, 1852) (Brébion, 1964, p. 634). Brébion discussed, but did not figure this species, and counted on seven specimens from Renauleau. Despite extensive collecting from this locality we have not encountered a single fragment of *Hastula*, therefore, this record requires confirmation.

The assemblage is highly endemic with 76 (90%) species occurring exclusively in the middle Miocene and Assemblage I-III of northwestern French. This concurs with the observation that there is a strong predisposition for non-planktotrophic-type protoconchs, especially amongst the endemic species, but is even more strongly amongst the Conoidea. The rate of endemism is far greater than that found in other parts of this series. Part 1 (Patellogastropoda and Vetigastropoda) and Part 2 (Caenogastropoda) found 63% (Landau *et al*., 2017, 2018) and Part 4 Neogastropoda 66%. Endemism amongst the muricids (Part 3) was lower at 33% (Landau *et al*., 2019a). We hope to discuss the implications of this preferred non-planktotrophic mode of development seen in Assemblage I in a separate paper.

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

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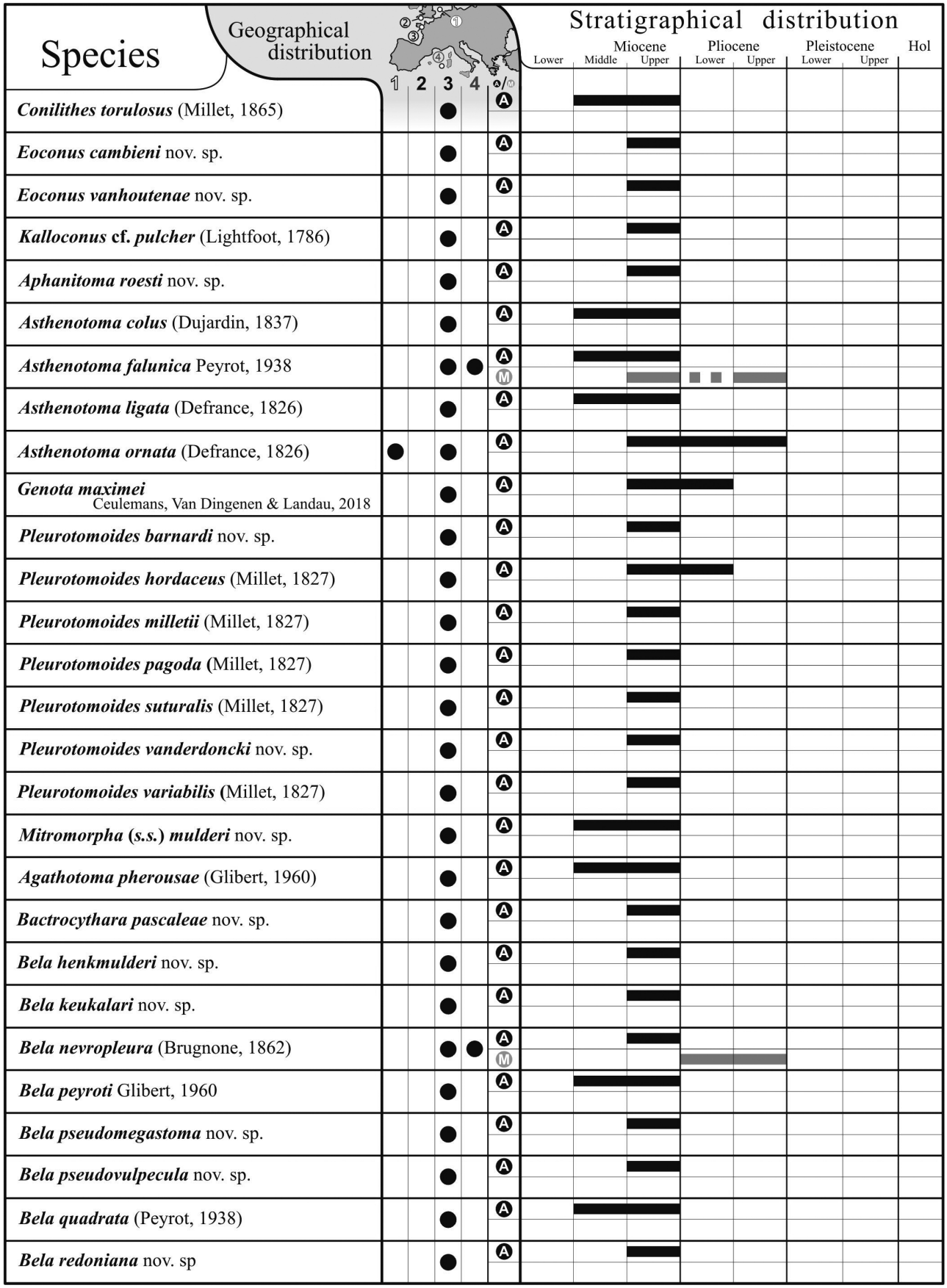
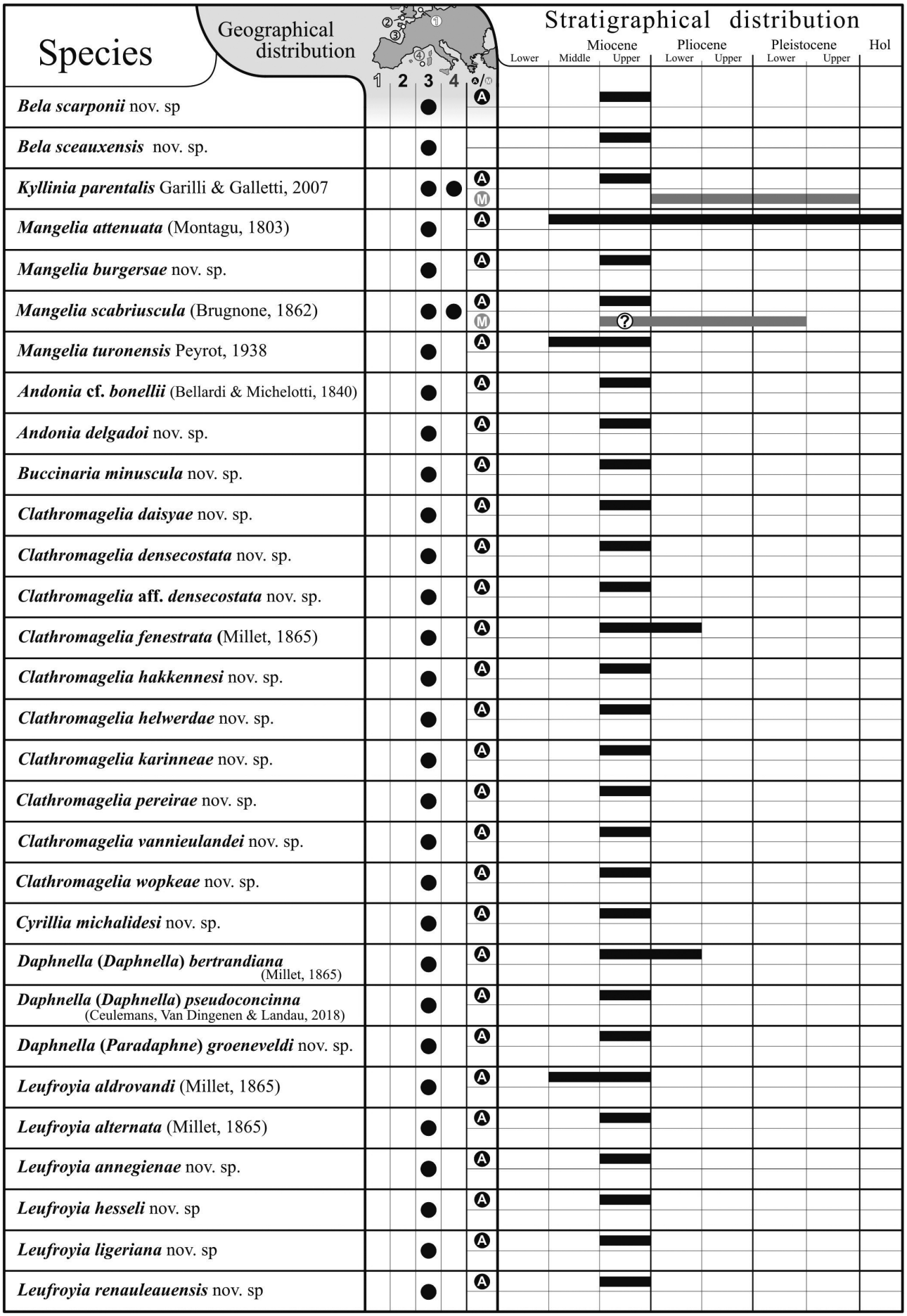
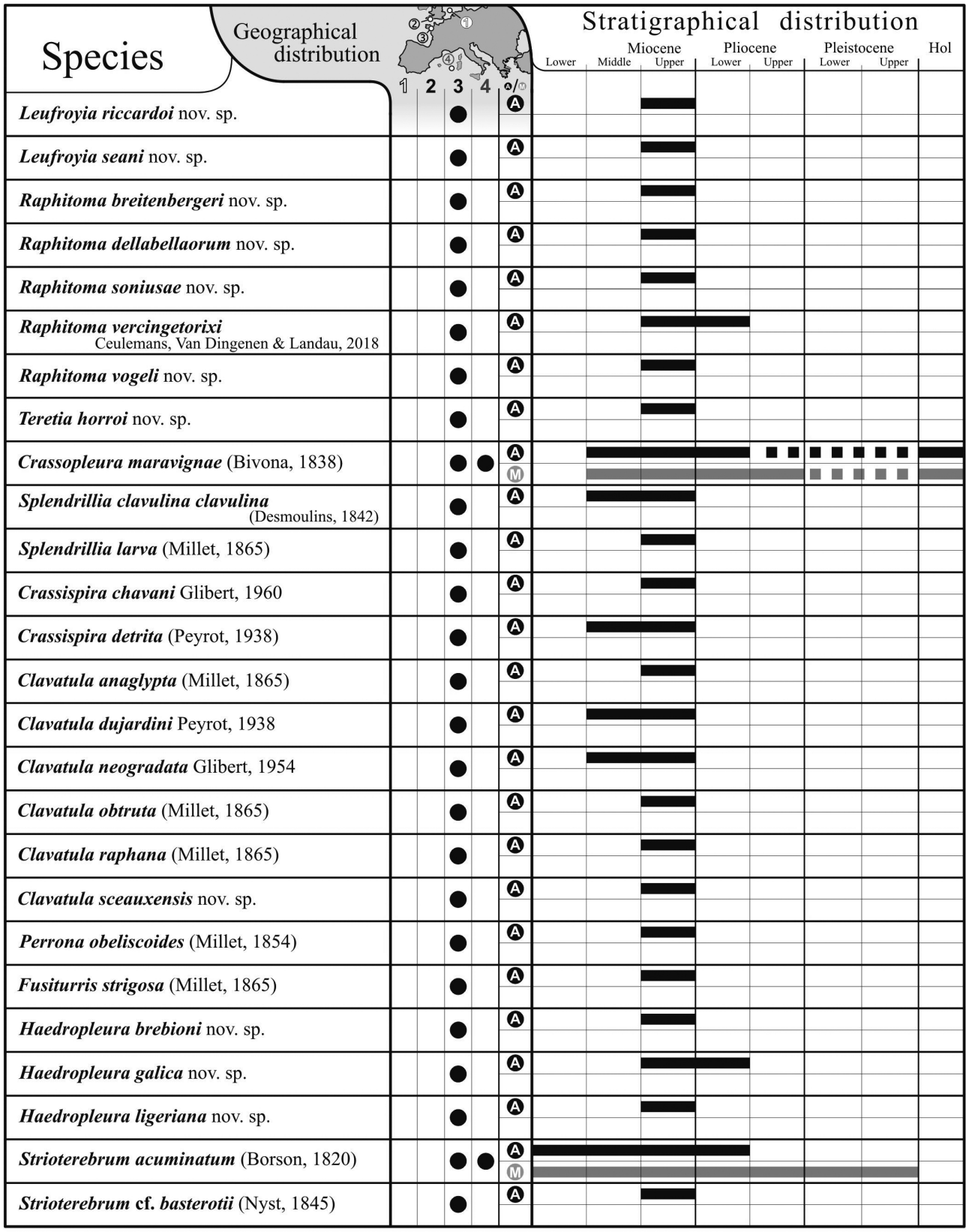


Figure 1. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black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


Species
Geographical distribution
1 2 3 4 A/M
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower Middle Upper Lower Upper Lower Upper
Bela scarponii nov. sp
Bela sceauxensis nov. sp.
Kyllinia parentalis Garilli & Galletti, 2007
Mangelia attenuata (Montagu, 1803)
Mangelia burgersae nov. sp.
Mangelia scabriuscula (Brugnone, 1862)
Mangelia turonensis Peyrot, 1938
Andonia cf. bonellii (Bellardi & Michelotti, 1840)
Andonia delgadoi nov. sp.
Buccinaria minuscula nov. sp.
Clathromagelia daisyae nov. sp.
Clathromagelia densecostata nov. sp.
Clathromagelia aff. densecostata nov. sp.
Clathromagelia fenestrata (Millet, 1865)
Clathromagelia hakkennesi nov. sp.
Clathromagelia helwerdae nov. sp.
Clathromagelia karinneae nov. sp.
Clathromagelia pereirae nov. sp.
Clathromagelia vannieulandei nov. sp.
Clathromagelia wopkeae nov. sp.
Cyrillia michalidesi nov. sp.
Daphnella (Daphnella) bertrandiana (Millet, 1865)
Daphnella (Daphnella) pseudoconcinna (Ceulemans, Van Dingenen & Landau, 2018)
Daphnella (Paradaphne) groeneveldi nov. sp.
Leufroyia aldrovandi (Millet, 1865)
Leufroyia alternata (Millet, 1865)
Leufroyia annegienae nov. sp.
Leufroyia hesseli nov. sp
Leufroyia ligeriana nov. sp
Leufroyia renauleauensis nov. sp


Species
Geographical distribution
1 2 3 4
A/D
Stratigraphical distribution
Miocene
Pliocene
Pleistocene
Hol
Lower
Middle
Upper
Lower
Upper
Lower
Upper
Leufroyia riccardoi nov. sp.
Leufroyia seani nov. sp.
Raphitoma breitenbergeri nov. sp.
Raphitoma dellabellaorum nov. sp.
Raphitoma soniusae nov. sp.
Raphitoma vercingetorixi Ceulemans, Van Dingenen & Landau, 2018
Raphitoma vogeli nov. sp.
Teretia horroi nov. sp.
Crassopleura maravignae (Bivona, 1838)
Splendrillia clavulina clavulina (Desmoulins, 1842)
Splendrillia larva (Millet, 1865)
Crassispira chavani Glibert, 1960
Crassispira detrita (Peyrot, 1938)
Clavatula anaglypta (Millet, 1865)
Clavatula dujardini Peyrot, 1938
Clavatula neogradata Glibert, 1954
Clavatula obtruta (Millet, 1865)
Clavatula raphana (Millet, 1865)
Clavatula sceauxensis nov. sp.
Perrona obeliscoides (Millet, 1854)
Fusiturris strigosa (Millet, 1865)
Haedropleura brebioni nov. sp.
Haedropleura galica nov. sp.
Haedropleura ligeriana nov. sp.
Strioterebrum acuminatum (Borson, 1820)
Strioterebrum cf. basterotii (Nyst, 1845)

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