

The upper Miocene gastropods of northwestern France, 3. Muricidae

Bernard M. Landau^{1,5}, Didier Merle², Luc Ceulemans³ & Frank Van Dingenen⁴

¹ Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; Instituto Dom Luiz da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal; and International Health Centres, Av. Infante de Henrique 7, Areias São João, P-8200 Albufeira, Portugal; email: bernardmlandau@gmail.com

² Sorbonne Université (CR2P, MNHN, CNRS, UPMC), Muséum national d'Histoire naturelle, 8 rue Buffon, F75005 Paris CP 43, France; e-mail: didier.merle@mnhn.com

³ Avenue Général Naessens de Loncin 1, B-1330 Rixensart, Belgium; email: luc.ceulem@skynet.be

⁴ Cambeenboslaan A 11, B-2960 Brecht, Belgium; email: fvd@telenet.be

⁵ Corresponding author

Received: 21 January 2019, revised version accepted 26 April 2019

In this paper we review the Muricidae of the Tortonian (Assemblage I of Van Dingenen *et al.*, 2015) of northwestern France. Thirty species are recorded of which five are new: *Paziella (Flexopteron) gallica* nov. sp., *Paziella (Flexopteron) gracilentia* nov. sp., *Attiliosa gallica* nov. sp., *Attiliosa poweri* nov. sp. and *Ocinebrina houarti* nov. sp. The muricid generic composition is moderately strongly thermophilic, with a considerable number of genera present that do not extend northwards to the latitude of NW France today, and more strongly thermophilic than the muricid fauna of the lower Pliocene Assemblage III of the same geographical area, suggesting some lowering of Sea Surface Temperatures (SSTs) between the late Miocene and early Pliocene.

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

Introduction

In this paper we continue our studies on the Neogene gastropod fossil assemblages of northwestern France (see Ceulemans *et al.*, 2014, 2016; Van Dingenen *et al.*, 2014, 2015). Here the Muricidae are revised, and the study is restricted to the locality of Le Pigeon Blanc, which we consider to be the 'type' locality for Assemblage III gastropods (of Van Dingenen *et al.*, 2015).

In his unpublished thesis, Brébion (1964) recorded 22 muricid species from Assemblage I localities, one was described as new and one new name was proposed. However, as the thesis was never published, the names do not comply with article 13 of the ICZN code (1999) and must be considered *nomina nuda*.

Geological setting and material and methods

Landau *et al.* (2017, p. 78) gave a list of the private collections consulted during this work that had been donated to the Naturalis Biodiversity Center in Leiden (The Netherlands). Since the publication of Part 2 of this series, a large collection of material from Sceaux-d'Anjou has been donated to Naturalis and been made available to the authors. This collection is an amalgamation from two collectors,

B.G. Roest and A.M. Mulder. We thank them and Naturalis for making this vast amount of material available.

For the rest of this section see Landau *et al.* (2017, pp. 76-78).

Abbreviations:

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

Systematic palaeontology

Systematics has been updated following Bouchet *et al.* (2017). The muricids are a group of marine predatory gastropods. The classification adopted here is mainly according to Houart (2018). According to Oliverio & Mari-

ottini (2001) and Barco *et al.* (2010), the Coralliophilinae are also arranged within the Muricidae.

The descriptions adopt the terminology suggested by Merle (1999, 2001, 2005), see below:

P	primary cord
s	secondary cord
t	tertiary cord
Ad	adapical (or abapertural)
Ab	abapical (or adapertural)
SP	subsutural cord
IP	infrasutural primary cord (primary cord on shoulder)
adis	adapical infrasutural secondary cord (shoulder)
abis	abapical infrasutural secondary cord (shoulder)
P1	shoulder cord
P2-P6	primary cords of the convex part of the teleoconch whorl
s1-s6	secondary cords of the convex part of the teleoconch whorl example: s1 = secondary cord between P1 and P2; s2 = secondary cord between P2 and P3, etc.
ADP	adapertural primary cord on the siphonal canal
MP	median primary cord on the siphonal canal
ABP	abapertural primary cord on the siphonal canal
ads	adapertural secondary cord on the siphonal canal
ms	median secondary cord on the siphonal canal
abs	abapertural secondary cord on the siphonal canal

Aperture:

ID	infrasutural denticle
D1-D6	abapical denticles

Corrections to Assemblage III Part 3 Ceulemans *et al.* (2016)

p. 46: Plate 3, figures 8 and 9 have been reversed. Figure 8 is *Hirtomurex* aff. *squamosus* (Bivona Ant. in Bivona And., 1838), figure 9 is *Coralliophila* cf. *burdigalensis* (Tournouër, 1874).

Corrections to Assemblage I Part 2 Landau *et al.* (2018)

p. 298: *Leachia* Risso, 1826 is a junior homonym of *Leachia* Lesueur, 1821. The originally included species *Leachia viridescens* Risso, 1826 is not *Hydrobia acuta* (Draparnaud 1805) and is best regarded as a *nomen dubium* or *species inquirenda*. *Bythinella* Moquin-Tandon 1856 is a replacement name for *Leachia* Risso. Its type species was fixed by the ICZN (2006, Opinion 2161) as *Bulimus viridis* Poiret, 1801. As both original and replacement name have to have the same type species, the type species of *Leachia* Risso, 1826 is *Bulimus viridis* Poiret, 1801.

p. 298: *Litorinella* Braun, 1843. The type species is *Cyclostoma acutum* Draparnaud, 1805 by monotypy. All other species-group names attributed by Braun (1843) to

Litorinella are *nomina nuda*.

p. 298: *Hydrobia tournoueri* Sandberger, '1875'. The correct date of publication is 1872, when plate 26 with the species-group name in the legend was published.

p. 301: Potamiopsidae and Potamiopsinae should spell Pomatiopsidae and Pomatiopsinae Stimpson, 1865.

My thanks to Dietrich Kadolsky for pointing out these errors.

Superfamily Muricoidea Rafinesque, 1815

Family Muricidae Rafinesque, 1815

Subfamily Muricinae Rafinesque, 1815

Genus *Bolinus* Pusch, 1837

Type species (by original designation) – *Murex brandaris* Linnaeus, 1758, present-day, Atlantic and Mediterranean Sea.

1837 *Bolinus* Putsch, p. 134.

1853 *Rhinocantha* H. & A. Adams, p. 72. Type species (by subsequent designation, Vokes, 1964): *Murex brandaris* Linnaeus, 1758, present-day, Atlantic and Mediterranean Sea. Junior objective synonym of *Bolinus* Pusch, 1837.

1917 *Brandaria* Monterosato, p. 20. Type species (by original designation): *Murex brandaris* Linnaeus, 1758, present-day, Atlantic and Mediterranean Sea. Junior objective synonym of *Bolinus* Pusch, 1837.

Bolinus brandaris torularius (Lamarck, 1822)

Plate 1, figs 1-3

*1822 *Murex torularius* Lamarck, p. 576.

1958 *Murex* (*Murex*) *torularius* Lamarck – Erünal-Er-entöz, p. 53, pl. 8, figs 1, 2.

1964 *Murex torularius* Lamarck, 1822 – Brébion, p. 370, pl. 9, figs 1, 2.

2007 *Bolinus brandaris torularius* (Lamarck, 1822) – Landau *et al.*, p. 5, pl. 1, figs 3-6 (*cum syn.*).

2011 *Bolinus brandaris torularius* (Lamarck, 1822) – Landau *et al.*, p. 22, pl. 10, figs 2-4 (*cum syn.*).

2011 *Bolinus brandaris torularius* (Lamarck, 1822) – Merle *et al.*, p. 302, pl. 29, figs 5-8.

2013 *Bolinus brandaris torularius* (Lamarck, 1822) – Landau *et al.*, p. 144, pl. 21, fig. 4 (*cum syn.*).

2013 *Bolinus brandaris torularius* (Lamarck, 1822) – Goret *et al.*, p. 5, text-fig. 7, pl. 1, fig. 2.

2013 *Bolinus brandaris torularius* (Lamarck, 1822) – Goret & Pons, p. 55, pl. 1, fig. 2.

Material and dimensions – Maximum height 46.5 mm, width 39.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0759 (1 juvenile), NHMW 2016/0103/0760 (5

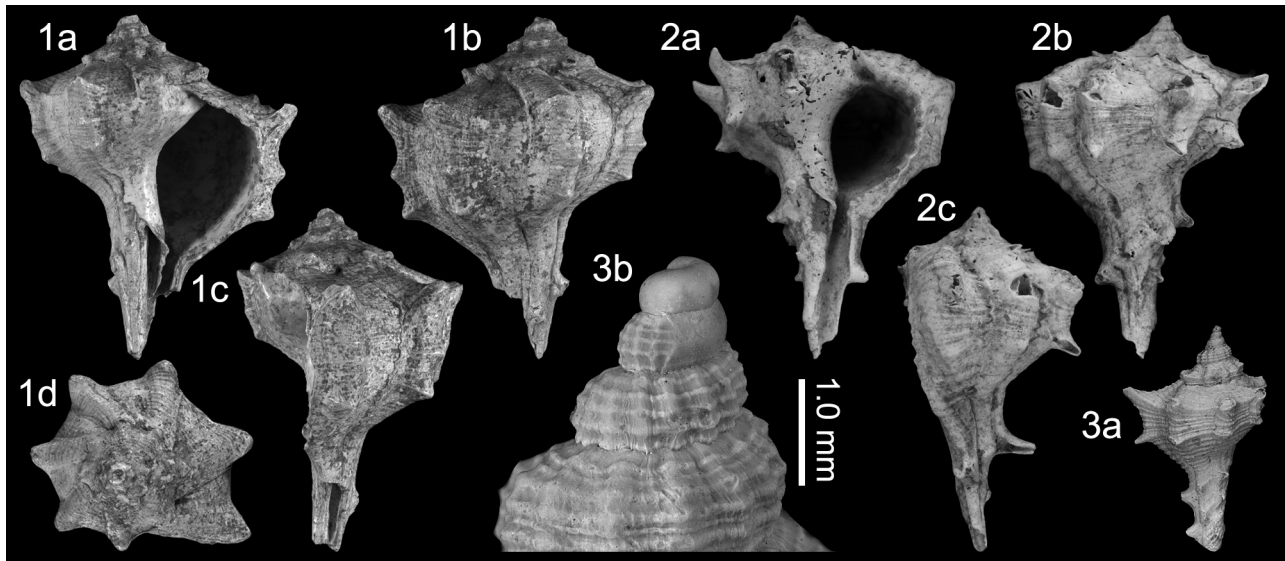


Plate 1. *Bolinus brandaris torularius* (Lamarck, 1822); 1. MNHN.F.A71204, height 35.0 mm, width 27.0 mm; 2. NHMW 2016/0103/1682, height 38.3 mm, width 29.3 mm. La Presselière, Sceaux-d'Anjou; 3. NHMW 2016/0103/0758 (juvenile); 3b. detail of protoconch. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

juveniles), RGM.1349158 (6 juveniles), RGM.1349215 (7 juveniles), RGM.1349219 (2 juveniles), LC (4 + 20 juveniles), FVD (2). **Sceaux-d'Anjou:** MNHN.F.A71204 (1), NHMW 2016/0103/0757 (1 juveniles), NHMW 2016/0103/1682 (1), NHMW 2016/0103/0758 (5 juveniles), RGM.1348088 (5 fragments + 4 juveniles), RGM.1348090 (2 subadult), RGM.1348103 (6 juveniles), RGM.1348114 (6 juveniles), RGM.1348117 (16 fragments and juveniles), RGM.1348119 (1 adult), RGM.1348123 (2 fragments), RGM.1348129 (1 juvenile), RGM.1348130 (1 juvenile), RGM.1348135 (1 juvenile), RGM.1348171 (3 incomplete adults), RGM.1348174 (2 incomplete), RGM.1348198 (2 juveniles), RGM.1348769 (1 large adult, height 36.6 mm), RGM.1348771 (15 fragments), RGM.718075 (1 adult + 50+ juveniles), RGM.734964 (13 juveniles), LC (3 juveniles), FVD (1 + 4 juveniles). **Renauleau:** NHMW 2016/0103/1486 (1 adult + 5 fragments and juveniles), LC (9 + 2 fragments), FVD (3 + 1 juvenile).

Discussion – Caretto (1967) showed that fossil shells differed from the Recent *Bolinus brandaris brandaris* (Linnaeus, 1758) in having a lower spire, a deeper suture, an aperture extending further adaperturnally and two rows of spines on the siphonal fasciole as opposed to only one in *B. brandaris brandaris*. This is clearly illustrated in the juvenile specimen from St-Clément-de-la-Place illustrated (Pl. 1, fig. 3a). The fossil shells also tend to be more robust, with stronger, larger spines than in the modern specimens. These characters are not as evident in the French Assemblage I material, where the specimens are all small compared to those from other assemblages. We consider all the Miocene and Pliocene specimens to belong to a single chronosubspecies, *Bolinus brandaris torularius* (Lamarck, 1822), which was replaced in the Pleistocene by the living taxon *B. b. brandaris*. The transition from one subspecies to another may not have been abrupt, as

B. b. brandaris occurs in the Assemblage IV (upper Pliocene-Pleistocene) of France (DM personal observation 2006). This species has not been found in the Paratethys, where it is replaced by *Bolinus subtorularius* (Hoernes & Aunger, 1885), which differs in having a stockier shell, with a higher spire, a less pronounced sutural canal and stronger ribs bearing less developed spines. For further discussion see Landau *et al.* (2007, p. 6).

Brébion (1964, p. 372) recorded this species widespread in the Assemblage I localities (Sceaux-d'Anjou, Thorigné, St-Michel, St-Clément-de-la-Place, Renauleau, Beaulieu) and also recorded it for Assemblage II (Le temple du Cerisier).

Distribution – Middle Miocene: Atlantic (Serravallian): Aquitaine Basin, France (Cossmann & Peyrot, 1924); Proto-Mediterranean (Langhian): Kasaba Basin, Turkey (İslamoğlu, 2004), (Serravallian): Karaman Basin, Turkey (Erünal-Erentöz, 1958). Upper Miocene: Atlantic (Tortonian and Messinian): northwestern France (Millet, 1854, 1865; Brébion, 1964), Cacela, Portugal (Pereira da Costa, 1867); Proto-Mediterranean (Tortonian): Po Basin, Italy (Montanaro, 1935). Miocene (indeterminate): western Proto-Mediterranean, France (Goret & Pons, 2013). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (González-Delgado, 1989; Landau *et al.*, 2011); western Mediterranean, northeastern Spain (Almera & Bofill, 1893; Martinell, 1979), Roussillon Basin, France (Fontannes, 1879; Cataliotti-Valdina, 1975; Chirli & Richard, 2008; Goret *et al.*, 2013); central Mediterranean, Italy (Chirli, 2000), Tunisia (Stchepinsky, 1938; Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001; Landau *et al.*, 2007); western Mediterranean, Estepona, Spain (Landau *et al.*, 2007); central Mediterranean (Sacco, 1904; Ruggieri *et al.*, 1959; Palla, 1967; Caretto, 1963, 1967; Annoscia, 1970; Malatesta,

1974; Caprotti, 1976; Cavallo & Repetto, 1992; Andreoli & Marsigli, 1992; Damarco, 1993; Merle *et al.*, 2011); eastern Mediterranean, Turkey (Karakus & Taner, 1994). Lower Pleistocene: central Mediterranean, Italy (Cerulli-Irelli, 1911; Malatesta, 1960).

Genus *Chicoreus* de Montfort, 1810

Type species – *Murex ramosus*, Linnaeus, 1758, by original designation (ICZN Opinion 911, 1970), present-day, Indo-Pacific.

- 1810 *Chicoreus* de Montfort, p. 610.
- 1834 *Cichoreum* Voigt, p. 359. Error pro *Chicoreus* de Montfort, 1810.
- 1834 *Cichoracea* Griffith & Pidgeon, p. 79. Error pro *Chicoreus* de Montfort, 1810.
- 1838 *Frondosaria* Schlüter, p. 20. Type species (by subsequent designation, Vokes, 1964): *Murex inflatus* Lamarck, 1822 [= *Murex ramosus*, Linnaeus, 1758], present-day, Indo-Pacific.
- 1846 *Cichoreus* Agassiz, p. 80. Unnecessary emmedation.
- 1847 *Cichoraceus* Hermannsen, p. 234. Unnecessary emmedation.
- 1880 *Euphyllon* Jousseume, p. 335. Type species (by original designation): *Murex monodon* G.B. Sowerby I, 1825 [= *Purpura cornucervi* Röding, 1798], present-day, Indo-Pacific.

Subgenus *Triplex* Perry, 1810

Type species – *Murex foliatus* Perry, 1811 (rejected ICZN = *T. rosaria* Perry, 1810; see Petit, 2003, p. 47), by monotypy, present-day, Indo-Pacific.

- 1810 *Triplex* Perry, p. M7, pl. 23.
- 1885 *Pirtus* de Gregorio, p. 257. Type species (by monotypy): *Murex fiatus* de Gregorio, 1885, Mioocene, France.

- 1936 *Torvamurex* Iredale, p. 323. Not available (no description).
- 1941 *Foveomurex* Wenz, p. 1091. Error pro *Torvamurex* Iredale, 1936.
- 1962 *Torvamurex* Macpherson & Gabriel, p. 167. Type species (by original designation): *Triplex denudatus* Perry, 1811, present-day, Australia.

Chicoreus (Triplex) foliosus (Bellardi, 1873)

Plate 2, figs 1-3

- *1873 *Murex foliosus* Bellardi, p. 80, pl. 6, fig. 5.
- 1875 *Murex dujardini* Tournouër, p. 151, pl. 5, fig. 4.
- 1964 *Chicoreus dujardini* Tournouër, 1875 – Brébion, p. 366.
- 2007 *Chicoreus (Triplex) foliosus* (Bellardi, 1873, Bonelli ms.) – Landau *et al.*, p. 15, pl. 3, fig. 7 (*cum syn.*).
- 2011 *Chicoreus (Triplex) foliosus* (Bellardi, 1872 [*sic*]) – Merle *et al.*, p. 105, pl. 52, figs 4-7 (*cum syn.*).
- 2013 *Chicoreus (Triplex) foliosus* (Bonelli *in* Bellardi, 1873) – Goret *et al.*, p. 8, pl. 2, figs 3, 4.

Material and dimensions – Maximum height 48.6 mm, width 28.5 mm (incomplete). **St-Clément-de-la-Place:** RGM.1348168 (1 juvenile), LC (2). **Sceaux-d’Anjou:** RGM.1348102 (1 incomplete), RGM.1348106 (1 juvenile), RGM.1348112 (1), RGM.1348143 (4 incomplete), RGM.1348147 (3 fragments), RGM.719016 (3 subadult + 10 juveniles), RGM.718080 (4 juveniles). **Renauleau:** NHMW 2016/0103/1657-1659 (3), NHMW 2016/0103/1660 (14 juveniles and fragments), LC (10 + 5 fragments), FVD (7 + 5 juveniles).

Discussion – This species was fully discussed by Landau *et al.* (2007, p. 15). In the Assemblage I deposits only juvenile specimens are well preserved. Larger specimens reaching at least 75 mm in height occur in the Renauleau deposits, but they are always represented by fragments or strongly worn specimens, suggesting transport. The protoconch is multispiral (Pl. 2, fig. 3), as reported by Lozouet *et*

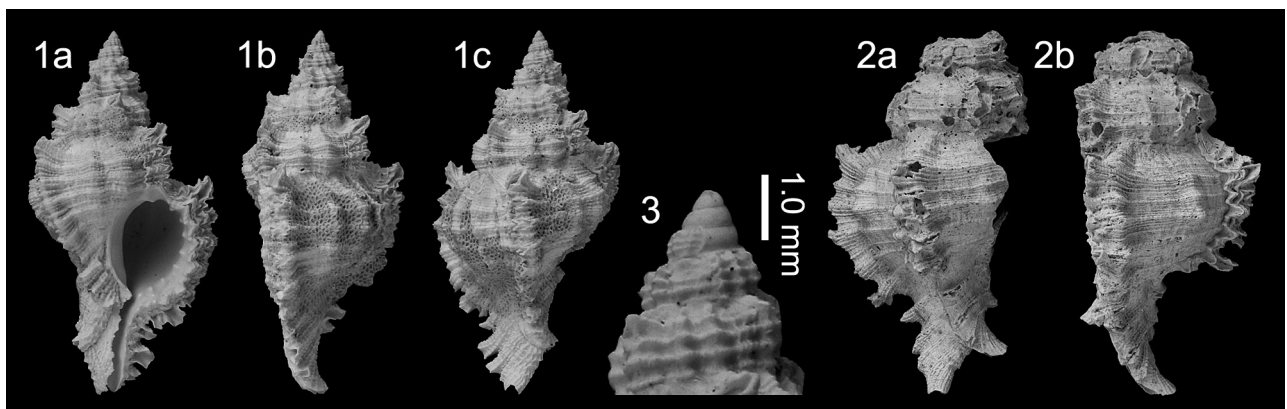


Plate 2. *Chicoreus (Triplex) foliosus* (Bellardi, 1873); 1. NHMW 2016/0103/1657, height 29.2 mm, width 14.4 mm; 2. NHMW 2016/0103/1658, height 48.6 mm, width 28.5 mm; 3. NHMW 2016/0103/1659 (juvenile), detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

al. (2001, p. 54), suggesting planktotrophic development. Brébion (1964, p. 367) recorded this species from the Assemblage I locality of Sceaux-d'Anjou, to which we add St-Clément-de-la-Place and Renauleau.

Distribution – Lower Miocene: Atlantic, Aquitaine Basin, France (Cossmann & Peyrot, 1924, Lozouet *et al.*, 2001; Merle *et al.*, 2011). Middle Miocene: Atlantic, Loire Basin, France (Tournouër, 1875; Glibert, 1952; Merle *et al.*, 2011). Upper Miocene: Atlantic (Tortonian): north-western France (Brébion, 1964). Lower Pliocene: western Mediterranean, Roussillon Basin, France (Goret *et al.*, 2013). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2007); central Mediterranean, Tunisia (Fekih, 1975); central Mediterranean, Italy (Bellardi, 1873; Cavallo & Repetto, 1992; Merle *et al.*, 2011).

Genus *Hexaplex* Perry, 1811

Type species (by subsequent designation, Iredale, 1915) – *Hexaplex foliacea* Perry, 1811 [junior synonym of *Hexaplex cichoreum* (Gmelin, 1791)], present-day, Philippines.

1811 *Hexaplex* Perry, sgn. M7.

Subgenus *Trunculariopsis* Cossmann, 1921

Type species (by typification of replaced name) – *Murex trunculus* Linnaeus, 1758, present-day, Mediterranean. *Nom. nov. pro Truncularia* Monterosato, 1917, *non* Wiegmann & Rütke, 1832.

1921 *Trunculariopsis* Cossmann, p. 79.

For generic synonymy see Ceulemans *et al.* (2016, p. 36).

Note – Species within the subgenus *Hexaplex* (*Trunculariopsis*) Cossmann, 1921 are solid, large shelled muricids. Their identification in Assemblage I is hindered by their scarcity and the lack of well-preserved adult speci-

mens. We recognise three groups within Assemblage I; the *arietinus/conglobatus* group, for which large shelled specimens are preserved, albeit usually incomplete or abraded, the cf. *bourgeoisituronensis* group represented only by juveniles with a multispiral protoconch, and the *ledoni/ cf. ledoni* group, also only represented by juveniles, with paucispiral or lecithotrophic-type protoconchs. Identifications made herein based on juvenile material are all provisional.

Hexaplex (*Trunculariopsis*) *arietinus* (Millet, 1865)

Plate 3, figs 1-2

1854 *Murex Arietinus* Millet, p. 163 (*nomen nudum*).

*1865 *Murex arietinus* Millet, p. 593.

2011 *Hexaplex* (*Trunculariopsis*) *arietinus* (Millet, 1866 [*sic*]) – Merle *et al.*, p. 88, 322, pl. 39, fig. 4.

Material and dimensions – Maximum height 54.5 mm, width 46.1 mm (incomplete). **Sceaux-d'Anjou**: RGM.1348172 (5 incomplete adults), RGM.1348364 (1 fragment), RGM.1348770 (1 fragment), FVD (1 adult). **Renauleau**: NHMW 2016/0103/1485 (3), LC (?1), FVD (4).

Type material – Syntypes: Thorigné, Sceaux-d'Anjou, not located (*vide* Merle *et al.*, 2011, p. 322).

Original description – ‘*Murex arietinus*, Millet. *Coq. de moyenne taille comme fusiforme, composée de 8 tours de spires: tous couverts par de grosses côtes verticales, arrondies et croisées par un grand nombre de stries d'inégale grosseur et tellement rapprochées, qu'elles semblent se toucher. Les derniers tours en outre présentent des côtes plus ou moins épineuses et dont la plus rapprochée de l'ouverture se termine en une corne arquée. L'ouverture qui est ovale, marquée d'un léger sinus au sommet et d'un certain nombre de stries sur la partie interne du bord droit, se termine par un canal ouvert, droit et arqué en dessus. Une fente ombilicale se montre dans la direction que suit le canal. Longueur: 34-36 millimètres; diamètre: 20-22 millimètres. Sc., Th. (Millet, 1865, p. 593)*

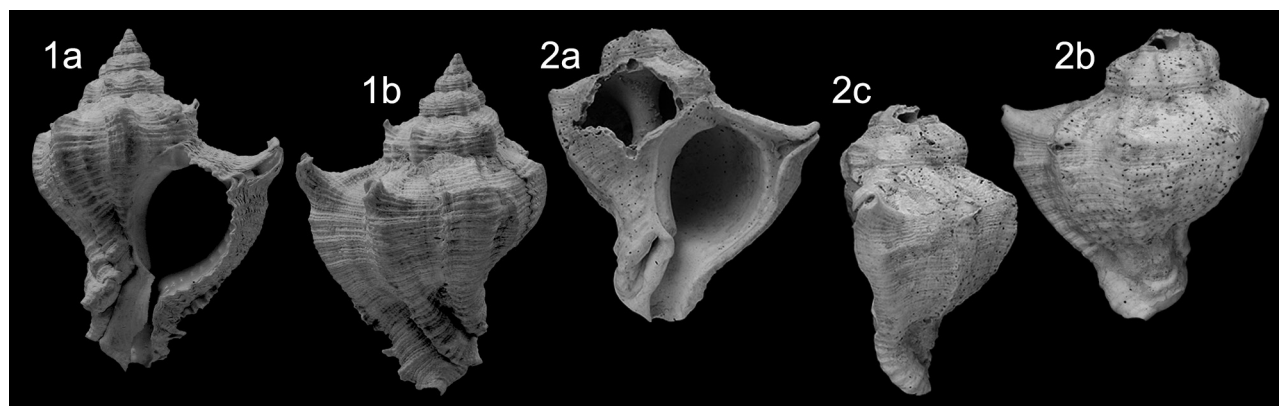


Plate 3. *Hexaplex* (*Trunculariopsis*) *arietinus* (Millet, 1865); 1. MNHN.F.J09268 (Bardin coll.), height 34.5 mm (photo C. Lemzaouda); 2. LC coll., height 54.5 mm, width 46.1 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – Millet first introduced *Murex arietinus* (*nomen nudum*) with the comment ‘*Cette espèce n’est peut-être qu’une variété de la suivante* (1854, p. 163)’ referring to *Murex subconglobatus* (*nomen nudum*). The name was later validated with the following description: ‘*Murex subconglobatus*, Millet. *Coq. grande, trapue, épaisse; composée de 9 à 10 tours de spire marqués de grosses côtes verruqueuses, terminées chacune par une corne légèrement arquée, dont l’épaisseur et la longueur augmentent avec l’âge. Le dernier tour, en outre, porte un grand nombre de stries transversales de diverses grosseurs, où elles forment comme de petits sillons peu profonds. Vers leur base l’on remarque que les côtes ont dévié de la verticale, qu’elles sont aplaties, terminées en pointe, légèrement relevées en arc et réunies ensemble pour former ce large et épais empâtement qui a précédé ce vaste et profond ombilic dont il porte les traces (1). L’ouverture qui est comme orbiculaire, présente sur le bord droit: 1° un sinus au sommet de celui-ci; 2° un sinus à l’entrée du canal de la dernière corne; 3° enfin, sur la partie interne de ce même bord, un grand nombre de stries élevées. Cette ouverture est terminée par un canal court, arqué et remonant. Cette grande coquille parvient à plus de 8 centimètres de longueur et 6 centimètres de diamètre. Sc., Th., Genneteil* (Millet, 1865, p. 593)’.

Brébion (1964, p. 364), like Millet, recognised the presence of two similar species in the Assemblage I deposits; *H. (T.) arietinus* and *H. (T.) trunculus conglobatus* (Michelotti, 1841), although he also commented that one may be a form of the other. In his discussion *H. (T.) arietinus* differed in having only five axial ribs, whereas *H. (T.) trunculus conglobatus* in the French upper Miocene had seven. Brébion noted that the ‘Redonian’ specimens of *H. (T.) trunculus conglobatus* had fewer ribs than seen in the Italian Pliocene populations which have 8-10 ribs and attributed this reduced rib count to the smaller shell size of the ‘Redonian’ specimens. However, even in the Pliocene the number of ribs varies slightly, Landau *et al.* (2007, p. 14) described 7-8 ribs for the lower Piacenzian Upper Pliocene specimens from the Estepona Basin, southern Spain. Merle *et al.* (2011, p. 88) in his list of European fossil *Hexaplex (Trunculariopsis)* species suggested that *M. subconglobatus* might be a synonym of *M. arietinus*, without further comment.

It is difficult to form any firm conclusions, as the number of complete specimens available from the Assemblage I deposits is small and most are juvenile or subadult worn or incomplete specimens. In our opinion, *H. (T.) trunculus conglobatus* occurs in the Assemblage I fauna (see below; Pl. 4, fig. 1) characterised by its very solid squat shell, strong rounded ribs forming spines at the periphery and broad umbilicus formed by the flaired abapical end of the axial ribs. The Assemblage I specimens have 6-7 axial ribs, fewer than the number seen in other populations, as mentioned by previous authors. A second form may be distinguished (Pl. 3, figs 1-2) which has 5-6 axial ribs in which only the last two ribs are raised and form significant spines at the shoulder and the umbilicus is much narrower than in *H. (T.) trunculus conglobatus*. It is

difficult to evaluate if these differences are due to ontogeny, but the larger specimen illustrated here (Pl. 3, fig. 2) is roughly equal in size to the adult specimens of *H. (T.) trunculus conglobatus* illustrated by Brébion (1964, pl. 8, figs 26, 27). As we have seen repeatedly when dealing with the Assemblage I fauna, the specimens present tend to be small, and it is possible also that *H. (T.) arietinus* is a nanitic form of *H. (T.) trunculus conglobatus*. However, as we recognise both forms in Assemblage I, we provisionally consider this second form distinct and to represent *H. (T.) arietinus*.

Millet (1854, p. 163; 1865, p. 594) described this species from the Assemblage I localities of Thorigné and Sceaux-d’Anjou. Brébion (1964, p. 366) added St-Clément-de-la-Place and we add Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian): northwestern France (Millet, 1854, 1865; Merle *et al.*, 2011).

Hexaplex (Trunculariopsis) trunculus conglobatus (Michelotti, 1841)

Plate 4, fig. 1

- *1841 *Murex conglobatus* Michelotti, p. 16, pl. 4, fig. 7.
- 1854 *Murex Subconglobatus* Millet, p. 163 (*nomen nudum*).
- 1865 *Murex subconglobatus* Millet – Millet, p. 592.
- 1964 *Hexaplex (Muricanthus) conglobatus* Michelotti, 1841 – Brébion, p. 364, pl. 8, figs 26, 27.
- 2007 *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841) – Landau *et al.*, p. 13, pl. 3, figs 1, 2 (*cum syn.*).
- 2011 *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841) – Landau *et al.*, p. 22, pl. 10, fig. 6 (*cum syn.*).
- 2011 *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841) – Merle *et al.*, p. 88, pl. 40, figs 2-4 (*cum syn.*).
- 2013 *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841) – Goret *et al.*, p. 7, pl. 1, figs 4, 5, pl. 2, fig. 1.

Material and dimensions – Height 75.6 mm, width 51.7 mm (incomplete). **Sceaux-d’Anjou**: RGM.1348173 (1 large incomplete adult), FVD (1 fragment). **Renauleau**: NHMW 2016/0103/1656 (1), FVD (1 incomplete), LC (1 fragment).

Discussion – The relationship between the extant *Hexaplex (Trunculariopsis) trunculus trunculus* (Linnaeus, 1758) and the Miocene-Pliocene *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841) was fully discussed by Landau *et al.* (2007, p. 14). The fossil subspecies tends to be more solid, flatter spired, more globose, with longer spines developed at the shoulder. Like most of the larger shelled species from the Assemblage I deposits specimens are either incomplete or strongly abraded, suggesting transport. Large fragments from Re-

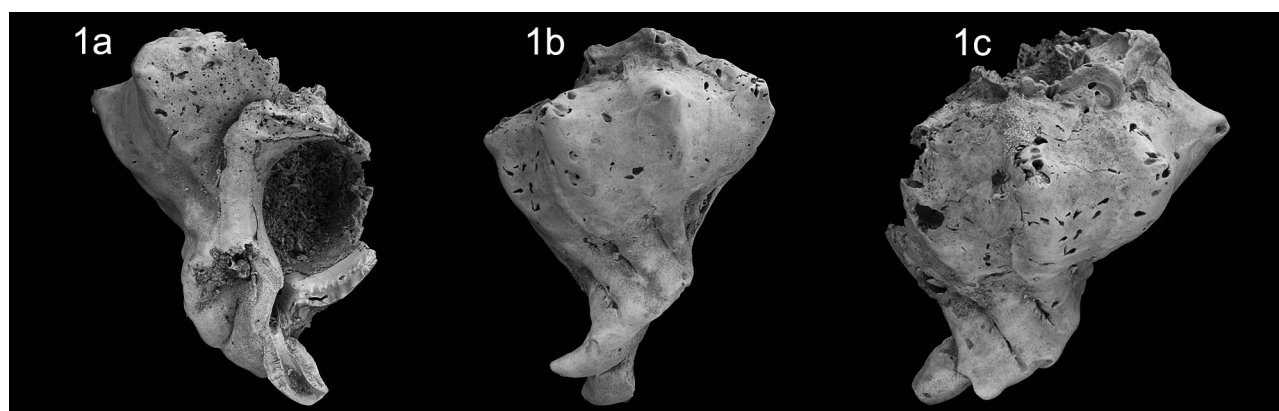


Plate 4. *Hexaplex (Trunculariopsis) trunculus conglobatus* (Michelotti, 1841); 1. RGM.1348173, height 75.6 mm, width 51.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

nauleau suggest a large adult size and solid shell, similar to specimens found in other European Neogene localities. For further discussion see above under *H. (T.) arietinus* (Millet, 1865).

Millet (1854, p. 163, 1865, p. 592) recorded this species in Assemblage I localities (Sceaux-d'Anjou, Thorigné), to which Brébion (1964, p. 365) added Contigné, and we add Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian): northwestern France (Millet, 1854, 1865; Brébion, 1964), Cacela, Portugal (Pereira da Costa, 1867); central Mediterranean, Po Basin, Italy (Montanaro, 1935). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (González-Delgado, 1989; Landau *et al.*, 2011); western Mediterranean, Roussillon, France (Fontannes, 1879; Merle *et al.*, 2011; Goret *et al.*, 2013); central Mediterranean, Italy (Chirli, 1988, 2000; Merle *et al.*, 2011), Tunisia (Stchepinsky, 1938; Fekih, 1975; Merle *et al.*, 2011). Upper Pliocene: western Mediterranean, Estepona Basin, Spain (Muñiz-Solís & Guerra-Merchán, 1994; Landau *et al.*, 2007), central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al.*, 1959; Caretto, 1963; Palla, 1967; Annoscia, 1970; Malatesta, 1974; Caprotti, 1976; Cavallo & Repet-

to, 1992; Andreoli & Marsigli, 1992; Damarco, 1993).

Hexaplex (Trunculariopsis) cf. bourgeoisi (Tournouër, 1875)

Plate 5, fig. 1

- 1854 *Murex Asper* Millet, p. 163 (*nomen nudum*).
- 1865 *Murex asper* Millet, p. 593 (*non* Linnaeus, 1758).
- cf. *1875 *Murex (Chicoreus) bourgeoisi* Tournouër, p. 156, pl. 5, fig. 5.
- cf. 1938 *Murex (Favartia) bourgeoisi* Tournouër [sic] – Peyrot, p. 180.
- cf. 1952 *Murex (Hexaplex) bourgeoisi* Tournouër, 1875 – Glibert, p. 289, pl. 5, fig. 5.
- 1964 *Hexaplex bourgeoisi* Tournouër, 1875 – Brébion (*partim*), p. 362 (part of Assemblage I specimens only).
- cf. 2011 *Hexaplex (?Trunculariopsis) bourgeoisi* (Tournouër, 1875) – Merle *et al.*, p. 88, pl. 40, figs 5-6.

Material and dimensions – Maximum height 13.0 mm, width 7.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0752 (1), LC (1). **Sceaux-d'Anjou:** RGM.1348136 (1).

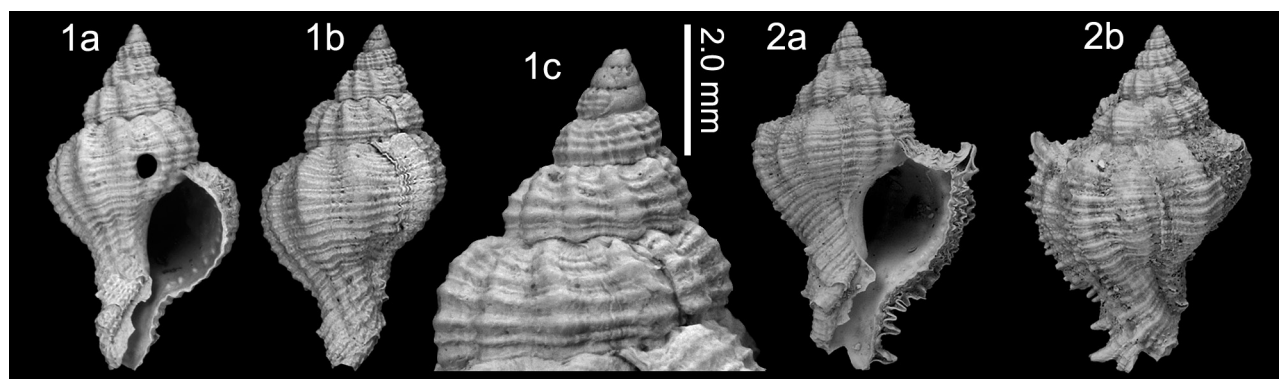


Plate 5. 1. *Hexaplex (Trunculariopsis) cf. bourgeoisi* (Tournouër, 1875), NHMW 2016/0103/0752, height 13.0 mm, width 7.0 mm; 1c, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene. 2. *Hexaplex (Trunculariopsis) turonensis* (Dujardin, 1837), NHMW 2016/0103/1675, height 19.8 mm, width 12.2 mm, Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

RGM.1348160 (3 juveniles), RGM.1348175 (3 subadults), RGM.1348188 (2 juveniles), RGM.718077 (6 juveniles), LC (?), FVD (1). **Renauleau**: LC (7), FVD (2).

Discussion – This identification is based on the protoconch type; typically planktotrophic: tall dome-shaped, multispiral, with a small nucleus characteristic of *Hexaplex (Trunculariopsis) bourgeoisi* (Tournouër, 1875) (see Ceulemans *et al.*, 2016, pl. 1, fig. 4). However, the aperture is less rounded than usual for that species. The teleoconch characters cannot reliably separate this species from *Hexaplex (Trunculariopsis) ledoni* Ceulemans, Van Dingenen, Merle & Landau, 2016, with which it co-occurs in the Assemblage I fauna (see below).

Brébion (1964, p. 362) recorded *Hexaplex bourgeoisi* from Assemblage I and III localities. However, each of these records will have to be reassessed individually and protoconch type assessed. We confirm the presence of a species close to, if not conspecific with *Hexaplex (T.) bourgeoisi* in the Assemblage I deposits of Sceaux-d'Anjou and St-Clément-de-la-Place, and await adult material to confirm the identification. The lower Pliocene Assemblage III record does not represent this species, but *H. (T.) ledoni*.

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

Hexaplex (Trunculariopsis) turonensis (Dujardin, 1837)
Plate 5, fig. 2

- *1837 *Murex turonensis* Dujardin, p. 295, pl. 19, fig. 27.
- 1875 *Murex (Chicoreus? Phyllonotus?) turonensis* var. *pontileviensis* Tournouër, p. 159, pl. 5, fig. 6.
- 1924 *Murex (Muricantha) turonensis* Dujardin – Cossmann & Peyrot, p. 116, pl. 13, figs 42, 43, pl. 18, fig. 11.
- 1938 *Murex (Favartia) turonensis* var. *pontileviensis* Tournouër [sic] – Peyrot, p. 182, pl. 3, fig. 20.
- 1952 *Murex (Muricantha) turonensis* Dujardin, 1837 – Glibert, p. 283, pl. 5, fig. 1.
- 1952 *Murex (Muricantha) turonensis pontileviensis* Tournouër, 1875 – Glibert, p. 285, pl. 4, fig. 8.
- 2011 *Hexaplex (Trunculariopsis) turonensis* (Dujardin, 1837) – Merle *et al.*, p. 88, pl. 37, figs 8-12.

Material and dimensions – Maximum height 19.8 mm, width 12.2 mm. **Renauleau**: NHMW 2016/0103/1675 (1), NHMW 2016/0103/1662 (7 juveniles), RGM.1348188 (1 juvenile), FVD (2).

Discussion – *Hexaplex (Trunculariopsis) turonensis* (Dujardin, 1837) has a typical planktotrophic-type multispiral protoconch (Merle *et al.* 2011, fig. 35D). In their adult forms that species and *H. (T.) bourgeoisi* (Tournouër, 1875) are easily separated (see Merle *et al.*, 2011, pls 37, 40). The material at hand from Assemblage I is all juvenile, but the specimen here illustrated, a subadult specimen (Pl. 5, fig. 2), differs from that here ascribed to *H. (T.)*

cf. *bourgeoisi* (Pl. 5, fig. 1) in not having clearly distinguishable primary and secondary spiral cords, in lacking developed primary spines (P1 to P6), and the aperture is not rounded as it is in *H. (T.) bourgeoisi*. Again, we await adult material to confirm this determination.

Distribution – Middle Miocene: Atlantic (Langhian and Serravallian), Aquitaine Basin (Cossmann & Peyrot, 1924; Merle *et al.*, 2011), Loire Basin, France (Dujardin, 1837; Tournouër, 1875; Peyrot, 1938; Glibert, 1952; Merle *et al.*, 2011). Upper Miocene: Atlantic (Tortonian): northwestern France (this paper).

Hexaplex (Trunculariopsis) ledoni Ceulemans, Van Dingenen, Merle & Landau, 2016
Plate 6, figs 1-3

- 1964 *Hexaplex bourgeoisi* Tournouër, 1875 – Brébion (*partim*), p. 362 (Assemblage III specimens only) (*non* Tournouër, 1875).
- *2016 *Hexaplex (Trunculariopsis) ledoni* Ceulemans, Van Dingenen, Merle & Landau, p. 36, text-fig. 1, pl. 1, figs 1-3.

Material and dimensions – Maximum height 46.1 mm, width 30.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0754 (1), NHMW 2016/0103/0755 (4), RGM.1348167 (1 juvenile), RGM.1348855 (1 juvenile), LC (3 + 10 juveniles), FVD (5). **Sceaux-d'Anjou**: NHMW 2016/0103/0756 (9), NHMW 2016/0103/1692 (1), RGM.1348107 (3 juveniles), RGM.1348133 (1 juvenile), RGM.1348154 (3), RGM.1348187 (4 juveniles), RGM.1348365 (2), RGM.1348768 (6), RGM.1348912 (2 juveniles), RGM.1349032 (8 juveniles), LC (1), FVD (2). **Renauleau**: NHMW 2016/0103/1676 (1), LC (1), FVD (2).

Discussion – *Hexaplex (Trunculariopsis) ledoni* Ceulemans, Van Dingenen, Merle & Landau, 2016 is characterised by its medium-size for the genus, its paucispiral protoconch consisting of two smooth whorls, its moderately elevated spire, its teleoconch whorls with four varices per whorl with one intervarical node, and the sculpture on the last whorl; P1-P6 subequal, forming a short spine on the apertural varix, secondary and tertiary spiral sculpture present, aperture with six pairs of denticles within, siphonal canal relatively long: ADP, MP, ABP well-developed, forming small spines where they cross the varices.

At first glance these shells resemble small specimens of *Hexaplex (Trunculariopsis) cf. bourgeoisi* (Tournouër, 1875) with which it co-occurs. However, *H. (T.) cf. bourgeoisi* has a tall dome-shaped multispiral protoconch, with a small nucleus (Pl. 5, fig. 1c), whereas *H. (T.) ledoni* has a paucispiral protoconch, with a large, bulbous nucleus. The teleoconch is similar to that of smaller specimens of *H. (T.) bourgeoisi* such as that illustrated by Merle *et al.* (2011, pl. 40, fig. 6). Only one well preserved adult specimen of *H. (T.) ledoni* from Assemblage I is available to us (Pl. 6, fig.1). In this specimen the primary cords

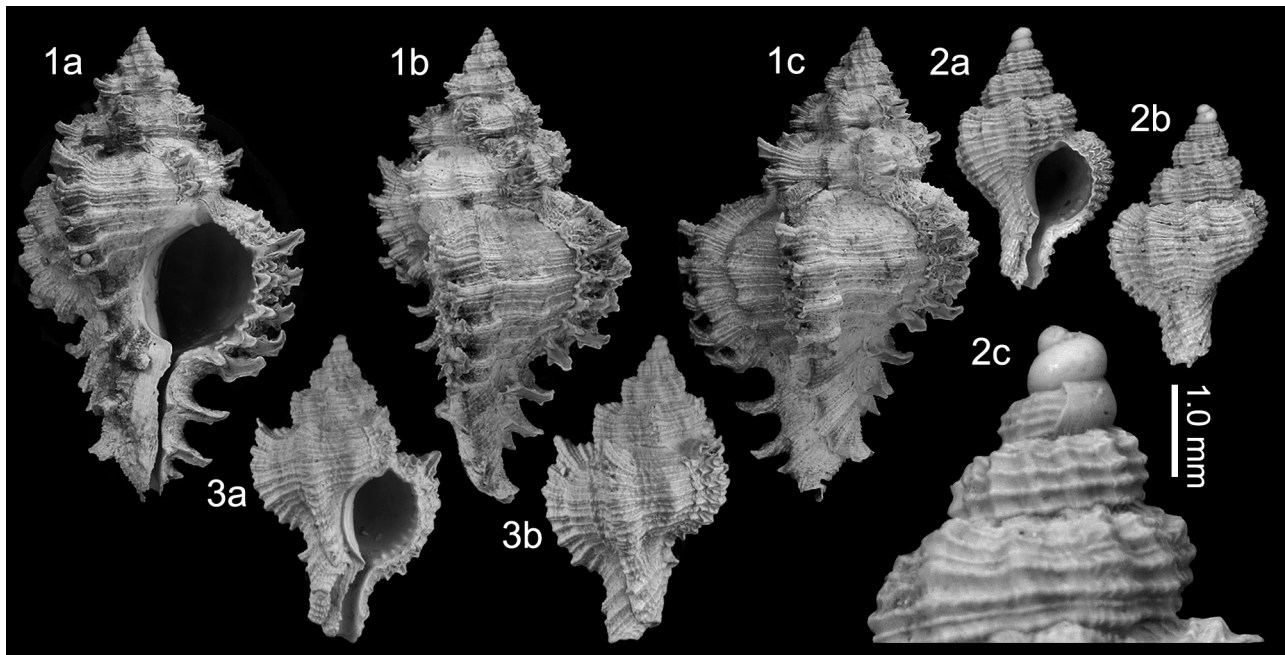


Plate 6. *Hexaplex (Trunculariopsis) ledoni* Ceulemans, Van Dingenen, Merle & Landau, 2016. 1. LC coll., 46.1 mm, width 30.1 mm; Renauleau. 2. NHMW 2016/0103/0754, height 10.4 mm, width 6.1 mm, 2c, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place. 3. NHMW 2016/0103/1692, height 16.1 mm, width 10.1 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

are strongly foliose at the aperture, forming adapically recurved open spines. The rest of the teleoconch features: height of spire, sculpture, aperture, do not distinguish it from *H. (T.) bourgeoisi*. Fortunately, the protoconch is preserved in this specimen showing it to be *H. (T.) ledoni*. Millet (1854, p. 163) erected the name *Murex asper* (*nomen nudum*), later made available by a description in Millet (1865, p. 593). This referred to the *Hexaplex*-like muricid from the 'Redonian'. Unfortunately this name is invalid as it is a junior primary homonym of *M. asper* Linnaeus, 1758. Millet's taxon was based on material from Assemblage I localities of Sceaux d'Anjou, Thorigné and Renauleau. This description could have applied to either *H. (T.) bourgeoisi* or *H. (T.) ledoni*.

Brébion (1964, p. 362) recorded *Hexaplex bourgeoisi* from Assemblage I and III localities. However, each of these records will have to be reassessed individually and protoconch type assessed. We confirm the presence of *H. (T.) ledoni* in the Assemblage I deposits of St-Clément-de-la-Place, Sceaux-d'Anjou and Renauleau, and the lower Pliocene Assemblage III deposit of Le Pigeon Blanc.

Distribution – Upper Miocene: Atlantic (Tortonian): northwestern France (Millet, 1854, 1865; Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016).

Hexaplex (Trunculariopsis) cf. ledoni Ceulemans, Van Dingenen, Merle & Landau, 2016
Plate 7, fig. 1

Material and dimensions – Height 7.3 mm, width 3.9 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0756 (1), LC (1 + 4 juveniles). **Sceaux-d'Anjou:** RGM.1349033 (10 juveniles).

Discussion – A form with the same type of teleoconch as *Hexaplex (Trunculariopsis) bourgeoisi* (Tournouër, 1875) and *H. (T.) ledoni* Ceulemans, Van Dingenen, Merle & Landau, 2016 occurs in the Assemblage I fauna that differs in having a multispiral protoconch with rounded whorls suggestive of lecithotrophic development rather than planktotrophic, as in *H. (T.) bourgeoisi*. It is possible that some specimens of *H. (T.) ledoni* were direct

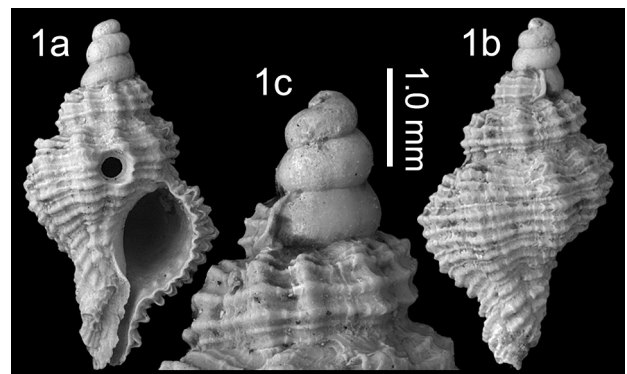


Plate 7. *Hexaplex (Trunculariopsis) cf. ledoni* Ceulemans, Van Dingenen, Merle & Landau, 2016; 1. NHMW 2016/0103/0756, height 7.3 mm, width 3.9 mm, 1c, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

developers (those with paucispiral protoconch of under two whorls), whereas others had a short planktrophic stage, resulting in a protoconch with more whorls. This is supported by the presence in Assemblage I of specimens with a number of protoconch whorls intermediate between the less than two whorls, typical for *H. (T.) ledoni* and that seen in the specimen illustrated here (Pl. 7, fig. 1c). It is also possible that we are dealing with a juvenile of yet another *Hexaplex (Trunculariopsis)* species. Recent work on larger Mediterranean cerithiids that can hardly be separated based on teleoconch characters showed that they could be separated by their paucispiral or multispiral planktrophic or lecithotrophic protoconchs (Garilli *et al.*, 2017)

We (BL) prefer to consider this a variant of *H. (T.) ledoni* and refrain from formally describing this species based on such immature material.

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

Hexaplex (Trunculariopsis) tapparonii (Bellardi, 1873)
Plate 8, figs 1-3

- *1873 *Murex Tapparonii* Bellardi, p. 93, pl. 7, fig. 3.
- 1893 *Murex Aquitanicus* Grateloup – Almera & Bofill, p. 170, pl. 5, figs 22-23 [*non Chicoreus (Triplex) aquitanicus* (Grateloup, 1833)].
- 1974 *Trunculariopsis tapparonii* (Bellardi, 1873) – Malatesta, p. 283, pl. 23, fig. 2.
- 1981 *Murex tapparonii* Bellardi, 1872 [*sic*] – Ferrero Mortara *et al.*, p. 36, pl. 2, fig. 8.
- 1985 *Trunculariopsis tapparonii* (Bellardi, 1872 [*sic*]) – Inzani & Bertarelli, p. 27, pl. 2, fig. 9.
- 1992 *Hexaplex tapparonii* (Bellardi, 1872 [*sic*]) – Cavallo & Repetto, p. 88, fig. 189.
- 2000 *Hexaplex tapparonii* (Bellardi, 1872 [*sic*]) – Chirli, p. 14, pl. 7, figs 1-4.

2011 *Hexaplex (Trunculariopsis) tapparonii* (Bellardi, 1872 [*sic*]) – Merle *et al.*, p. 88, pl. 39, fig. 3.

2013 *Hexaplex (Trunculariopsis) tapparonii* (Bellardi, 1873) – Goret *et al.*, p. 6, pl. 1, fig. 3.

Material and dimensions – Maximum height 52.8 mm, width 39.2 mm. **Sceaux-d'Anjou**: NHMW 2016/0103/1733 (2 juveniles). **Renauleau**: NHMW 2016/0103/1488-89 (1 incomplete adult + 1 subadult), LC (1 + 1 fragment).

Discussion – *Hexaplex (Trunculariopsis) tapparonii* (Bellardi, 1873) is easily separated from its congeners, characterised by its solid, squat, biconic shell shape, its small aperture and secondary spiral sculpture that is almost equal in strength to the primary cords. The six or seven axial ribs are low and broad, almost equal in width to their interspaces and produce short upturned spines at the sharp shoulder that delimits the concave subsutural ramp. The siphonal fasciole is broad, with the ribs strengthened and extending to the umbilical chink.

In the Assemblage I deposits we record this species from Sceaux-d'Anjou and Renauleau. This is the first published record for the species in the Miocene, although we (DM) have also found it in the upper Miocene Tortonian of Crete.

Distribution – Upper Miocene: Atlantic (Tortonian): northwestern France (this paper); proto-Mediterranean, Crete (DM personal data). Lower Pliocene: western Mediterranean, northeastern Spain (Almera & Bofill, 1893), Roussillon, France (Goret *et al.*, 2013); central Mediterranean, Italy (Chirli, 2000). Upper Pliocene: central Mediterranean, Italy (Bellardi, 1873; Malatesta, 1974; Ferrero Mortara *et al.*, 1981; Inzani & Bertarelli, 1985; Cavallo & Repetto, 1992; Merle *et al.*, 2011).

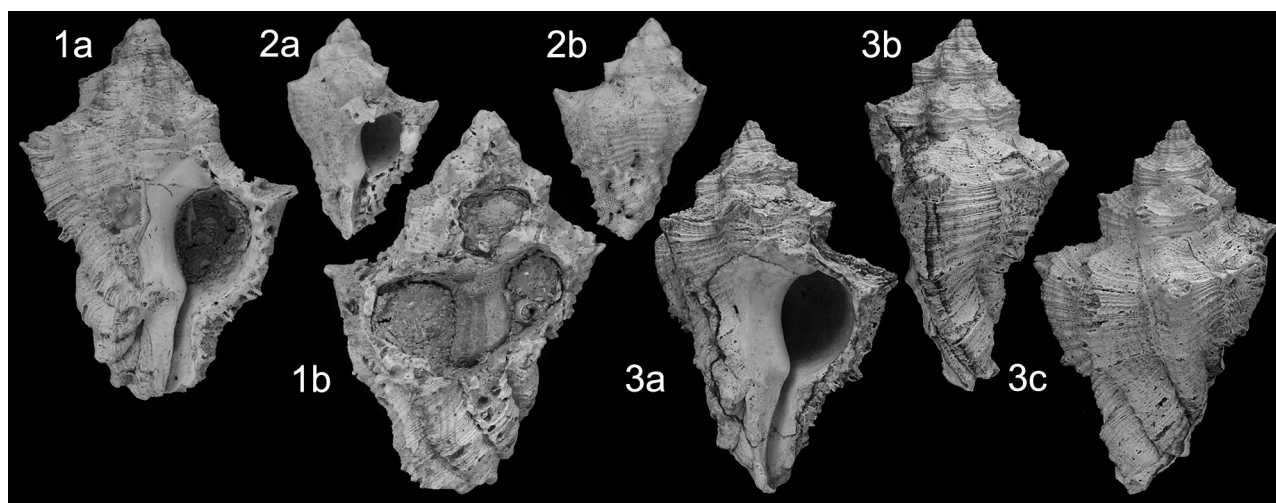


Plate 8. *Hexaplex (Trunculariopsis) tapparonii* (Bellardi, 1873); 1. NHMW 2016/0103/1488, height 52.8 mm, width 39.2 mm. 2. NHMW 2016/0103/1489, height 29.8 mm, width 19.3 mm. 3. LC coll., height 49.1 mm, width 32.1 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Incertae sedis in the subfamily Muricinae

Genus *Purpurellus* Jousseaume, 1880

Type species (by original designation) – *Murex gambien-sis* Reeve, 1845, present-day, West Africa.

1880 *Purpurellus* Jousseaume, p. 335.

Note – *Purpurellus* is morphologically close to to genus *Timbellus* (see Merle *et al.* 2011). In the phylogenetic tree of Barco *et al.* (2012, p. 600, 602), *Timbellus* does not belong to the clade of the Muricinae. It forms a clade having strangely *Vitularia* as sister group. Thus, its place in the subfamily Muricinae is doubtful or to be rejected.

Purpurellus cyclopterus (Millet, 1865)

Plate 9, figs 1-3

1854 *Murex cyclopterus* Millet, p. 162 (*nomen nudum*).

*1865 *Murex cyclopterus* Millet, p. 592.

1866 *Murex Veranyi* Paulucci, p. 64, pl. 2, fig. 1, pl. 3, fig. 1.

1875 *Murex (Pterynotus) cyclopterus* Millet – Tournouër, p. 147, pl. 5, fig. 2.

1964 *Pterynotus (Purpurellus) cyclopterus* Millet, 1854 [sic] – Brébion, p. 370.

1995 *Pterynotus (Purpurellus) cyclopterus* (Millet, 1866) – Bałuk, p. 216, pl. 22, figs 9-11.

2000 *Pterynotus veranyi* (Paulucci [sic], 1866) – Chirli, p. 18, pl. 9, figs 4-10.

2006 *Pterynotus (Purpurellus) cyclopterus* (Millet, 1866) – Bałuk, p. 207, pl. 11, fig. 5.

2007 *Purpurellus veranyi* (Paulucci, 1866) – Landau *et al.*, p. 18, text-fig. 4, pl. 4, figs 3-5, pl. 5, figs 1-5 (*cum syn*).

2011 *Purpurellus veranyi* (Paulucci, 1866) – Merle *et al.*, p. 142, pl. 118, figs 3-9.

2013 *Purpurellus veranyi* (Paulucci, 1866) – Goret *et al.*, p. 10, pl. 2, fig. 6.

2016 *Purpurellus cyclopterus* (Millet, 1865) – Landau *et al.*, p. 224, pl. 1, fig. 3 (*cum syn*).

2017 *Purpurellus cyclopterus* (Millet, 1865) – Vicián *et al.*, p. 268, pl. 2, figs 3,4.

Material and dimensions – Maximum height 23.1 mm, width 12.6 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0750 (5 juveniles), LC (4 + 7 juveniles), FVD (7 juveniles). **Sceaux-d’Anjou**: NHMW 2016/0103/0746-0748 (3), NHMW 2016/0103/0749 (6), RGM.1348089 (20), RGM.1348118 (2 + 9 fragments), RGM.1348122 (2 + 5 juveniles), RGM.1348176 (3 adult fragment + 7 juveniles), RGM.1348189 (2 juveniles), RGM.1348943 (1 juvenile), RGM.718078 (4 adults + 31 juveniles), LC (3), FVD (6). **Renauleau**: NHMW 2016/0103/1410 (5), LC (10), FVD (8).

Discussion – As discussed by Landau *et al.* (2016, p. 224), the correct date for Millet’s ‘*Indicateur du Maine-et-Loire ou indications par commune de ce que chacune d’elles renferme. Tome 2. Angers*’ is 1865. The 1866 reference is a reprint of the 1865 palaeontology section. Therefore, *Murex cyclopterus* Millet, 1865 must take priority over the more often used name *Murex veranyi* Paulucci, 1866. We cannot apply Article 23.9.1.2 (ICZN 1999) to consider Millet’s name a *nomen oblitum*, as Tournouër (1875), Cossmann & Peyrot (1924) and Bałuk (1995) all used Millet’s name as the valid name of a taxon.

Purpurellus cyclopterus (Millet, 1865) is remarkably long lived and widely distributed, but uncommon wherever it is found. For further discussion see Landau *et al.* (2007, p. 19).

In the French upper Miocene deposits Millet (1854, p. 162) and Brébion (1964, p. 370) recorded *P. cyclopterus* from the Assemblage I deposits of Thorigné and Sceaux-d’Anjou, to which we add St-Clément-de-la-Place and Renauleau.

Distribution – Lower Miocene: Atlantic, Aquitaine Basin, France (Landau *et al.*, 2007; Merle *et al.*, 2011). Middle Miocene: Atlantic (Langhian), Loire Basin (Tournouër, 1875; Glibert, 1952; Merle *et al.*, 2011), Aquitaine Basin, France (Cossmann & Peyrot, 1924); Proto-Mediterranean (Langhian and Serravallian), Italy (Bellardi, 1873), Karaman Basin, Turkey (Landau *et al.*, 2016); Pa-

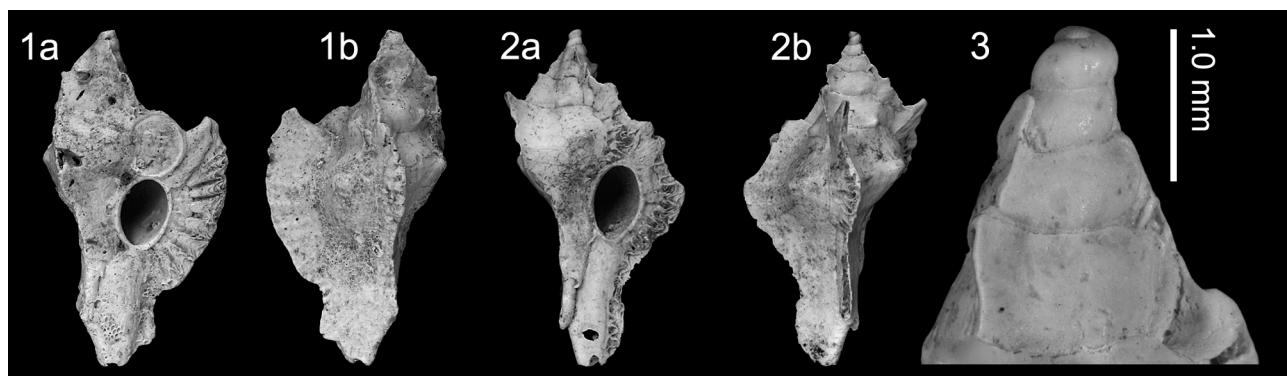


Plate 9. *Purpurellus cyclopterus* (Millet, 1865); 1. NHMW 2016/0103/0746, height 23.1 mm, width 12.6 mm; 2. NHMW 2016/0103/0747, height 19.4 mm, width 10.6 mm; 3. NHMW 2016/0103/0748 (juvenile), detail of protoconch. La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ratethys, Hungary (Vicián *et al.*, 2017), Poland (Bałuk, 1995), Romania (NHMW). Upper Miocene: Atlantic (Tortonian), north western France (Millet, 1865; Tournouër, 1875; Brébion, 1964; Merle *et al.*, 2011), Cabela, Portugal (Pereira da Costa, 1867); Proto-Mediterranean: Italy (Bellardi, 1873; Sacco, 1904; Montanaro, 1935). Lower Pliocene: western Mediterranean, France (Goret *et al.*, 2013; central Mediterranean (Chirli, 2000). Upper Pliocene: western Mediterranean, Estepona Basin (Muñiz-Solis & Guerra-Merchán, 1994); central Mediterranean, Italy (Ruggieri *et al.*, 1959; Malatesta, 1974; Cavallo & Repetto, 1992; Andreoli & Marsigli, 1992).

Genus *Paziella* Jousseau, 1880

Type species (by original designation) – *Murex pazi* Crosse, 1869, present-day, Caribbean.

1880 *Paziella* Jousseau, p. 335.

Note – *Paziella* is morphologically close to the genus *Poirieria* (see Merle *et al.* 2011, *inter alii*). In the phylogenetic tree of Barco *et al.* (2015), *Poirieria* does not belong to the clade of the Muricinae. It belongs to the clade of the Pagodulinae having the Hausrinae as sister group. Thus, as already stated by Merle *et al.* (2011), the place of *Paziella* is doubtful or to be rejected in Muricinae.

Subgenus *Flexopteron* Shuto, 1969

Type species (by original designation) – *Flexopteron philippinensis* Shuto, 1969, upper Miocene, Philippines.

1969 *Flexopteron* Shuto, p. 111.

Note – It is with interest that we describe the presence of two quite different *Paziella* (*Flexopteron*) Shuto, 1969 species in the northwestern French upper Miocene Assemblage I fauna. Merle *et al.* (2011, p. 170) reviewed all known fossil species and recognised only two species in the European Miocene, both middle Miocene. This is

therefore the last known record of this thermophile genus in Europe, which today is not represented in the Atlantic.

Paziella (*Flexopteron*) *gallica* nov. sp.

Plate 10, fig. 1; Plate 11, figs 1-3

Type material – Holotype MNHN.F.A66717, height 8.7 mm, width 4.7 mm; paratype 1 NHMW 2016/0103/0777, length 7.7 mm, width 4.3 mm; paratype 2 NHMW 2016/0103/0778, height 6.8 mm, width 3.8 mm; paratype 3 NHMW 2016/0103/0779, juvenile; paratype 4 NHMW 2016/0103/1666, length 6.8 mm, width 4.0 mm, **St-Clément-de-la-Place**. Paratype 5 RGM.1349108, height 7.4 mm, width 4.2 mm, Paratype 6 RGM.1349109, height 7.2 mm, width 4.6 mm, **Sceaux-d'Anjou**.

Other material – Maximum height 8.7 mm, width 4.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0780 (8), LC (16), FVD (12). **Sceaux-d'Anjou**: NHMW 2016/0103/0782 (9), RGM.734971 (44), RGM.134813852 (3), RGM.1348161 (5), RGM.1348253 (2), RGM.1348795 (9), RGM.1348907 (10), RGM.1352594 (2), LC (6), FVD (4).

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Flexopteron* species of small size, broadly fusiform with scalate spire, low paucispiral protoconch of 1.5 whorls, last whorl inflated mid-whorl, P1 slightly stronger, P2-P6 subequal, s1 developed on last half whorl, ADP and MP developed on moderate length siphonal canal, outer lip thickened, bearing D1-D4 well-developed, D5 weak at inner edge, smooth columella.

Description – Shell small, broadly fusiform, with moderate height scalate spire. Protoconch low paucispiral,

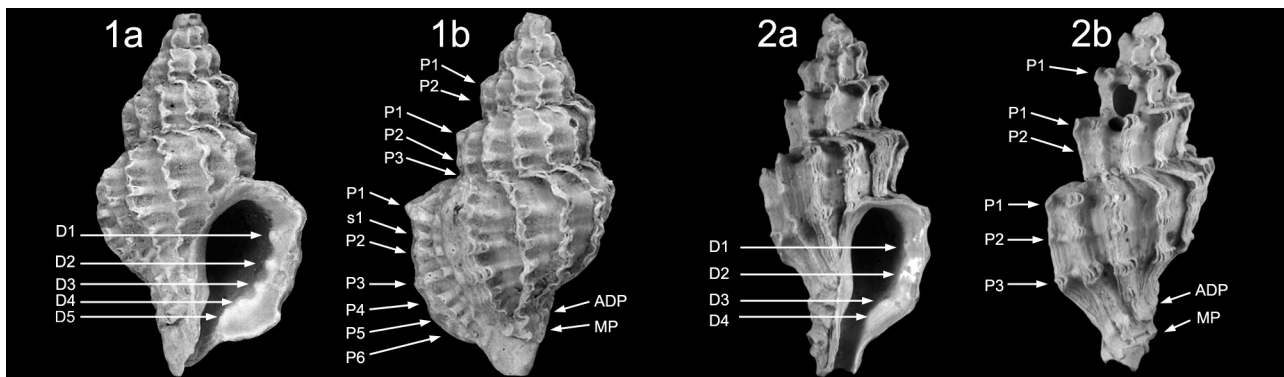


Plate 10. 1. *Paziella* (*Flexopteron*) *gallica* nov. sp., holotype MNHN.F.A66717, height 8.7 mm, width 4.7 mm; 2. *Paziella* (*Flexopteron*) *gracilentata* nov. sp., holotype MNHN.F.A66718, height 5.8 mm, width 2.6 mm. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

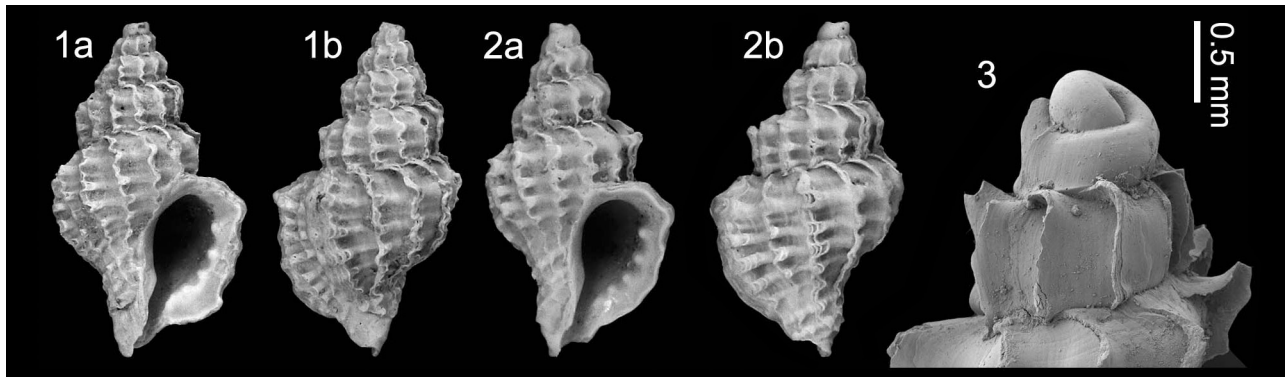


Plate 11. *Paziella (Flexopteron) gallica* nov. sp.; 1. **Holotype** MNHN.F.A66717, height 8.7 mm, width 4.7 mm; 2. **Paratype 2** NHMW 2016/0103/0778, height 6.8 mm, width 3.8 mm; 3. **Paratype 3** NHMW 2016/0103/0779 (juvenile), detail of protoconch. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

composed of 1.5 smooth whorls, with large nucleus, first whorl slightly oblique, coiled at about about 30° to main shell axis. Junction with teleoconch abrupt, marked by scar. Teleoconch of 4-5 angular whorls with shallow broad subsutural platform, sharply angled at shoulder, weakly convex to almost straight-sided below to suture. Suture mainly obscured by axial lamellae. Axial sculpture consisting of ten sharp lamellae, somewhat fimbriated at their intersections with spiral cords. Spiral sculpture; P1-P3 developed on spire whorls, with P3 placed immediately above suture. Last whorl inflated mid-whorl, strongly constricted at base; P1 slightly stronger, P2-P6 subequal, s1 developed on last half whorl. Siphonal canal ADP, MP developed. Aperture ovate; anal canal not developed; siphonal canal moderate length, straight, narrow, open, bent slightly abaxially. Outer lip thickened, outer edge scalloped by spiral sculpture, internally flattened, concave, bearing D1-D4 well-developed, D5 weak at inner edge. Columella broadly excavated, smooth. Columellar callus thickened, sharp edged, hardly expanded, forming narrow callus rim.

Discussion – Merle *et al.* (2011) recognised distinct species groups within the suguens *Flexopteron* based on shell characters. *Paziella (Flexopteron) gallica* nov. sp. does not fit exactly into any of the groups (2011, table 6). Secondary spiral sculpture is much reduced, so that only s1 is developed on the last half whorl. In this character it fits best within Group 2 (of Merle *et al.*, 2011), which does not have any European Neogene members, but it differs in having cords on the siphonal canal that are absent in Group 2 species. The shape and sculpture are superficially similar to species within Group 4 (of Merle *et al.*, 2011), but they differ in having well developed secondary spiral sculpture. The European Neogene species known until now belong within Group 8; *P. (F.) goniosstoma* (Parsch in Hörnes, 1853) from the middle Miocene Paratethys differs in being larger shelled, P1 forms a long recurved spine at the shoulder, secondary sculpture s1-s3 are developed and the siphonal canal is smooth. *Paziella (Flexopteron) citima* (Bellardi, 1873) from the lower-middle Miocene Proto-Mediterranean of Italy is similar

to *P. (F.) goniosstoma*, differing in being broader shelled and developing less of a spine at the shoulder on P1.

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

***Paziella (Flexopteron) gracilentia* nov. sp.**

Plate 10, fig. 2; Plate 12, figs 1-4

Type material – Holotype MNHN.F.A66718, height 5.8 mm, width 2.6 mm; paratype 1 MNHN.F.A66719, length 6.2 mm, width 2.8 mm; paratype 2 NHMW 2016/0103/0773, height 7.7 mm, width 3.4 mm; paratype 3 NHMW 2016/0103/0774, height 6.9 mm, width 2.9 mm; paratype 4 NHMW 2016/0103/0775, juvenile; paratype 5 RGM.1348163, height 7.1 mm, width 3.1 mm; paratype 6 RGM.1348164, height 7.4 mm, width 3.4 mm, **St-Clément-de-la-Place**. Paratype 7 RGM.1349110, height 5.5 mm, width 2.0 mm, Paratype 8 RGM.1349111, height 5.4 mm, width 2.5 mm, **Sceaux-d’Anjou**.

Other material – Maximum height 7.7 mm, width 3.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0776 (42), LC (34), FVD (31). **Sceaux-d’Anjou**: NHMW 2016/0103/0781 (11), RGM.718079 (50+), RGM.1348134 (9), RGM.1348908 (19), RGM.1352595 (15), LC (2), FVD (3).

Etymology – Latin ‘*gracilentus, -a, -um*’, meaning slender. *Paziella* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Flexopteron* species of small size, slender fusiform with tall scalate spire, tall paucispiral protoconch of 1.5 obtusely carinate whorls, last whorl slender, P1-P3 only, no secondary sculpture, ADP and MP developed on moderately long siphonal canal, outer lip thickened, bearing weak D1-D4, smooth columella.

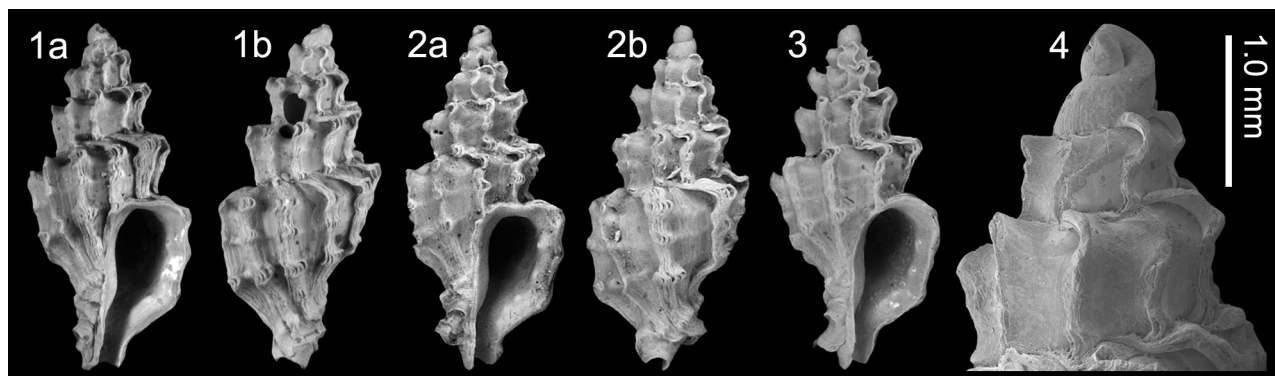


Plate 12. *Paziella (Flexopteron) gracilentata* nov. sp.; 1. **Holotype** MNHN.F.A66718, height 5.8 mm, width 2.6 mm.; 2. **Paratype 2** NHMW 2016/0103/0773, height 7.7 mm, width 3.4 mm; 3. **Paratype 3** NHMW 2016/0103/0774, height 6.9 mm, width 2.9 mm; 4. **Paratype 4** NHMW 2016/0103/0775 (juvenile), detail of protoconch. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Description – Shell small, slender fusiform, with high scalate spire. Protoconch tall paucispiral, composed of 1.5 smooth, elevated, somewhat uncoiled whorls sub-obsolete carinate and angled in upper quarter, with large nucleus. Junction with teleoconch abrupt, marked by scar. Teleoconch of four tall, angular whorls with shallow, narrow subsutural platform, sharply angled at shoulder, straight-sided below tapering into suture. Suture mainly obscured by axial lamellae. Axial sculpture consisting of ten sharp, elevated lamellae, somewhat fimbriated at their intersections with spiral cords. Spiral sculpture; P1-P2 developed on spire whorls. Last whorl slender, moderately constricted at base; P1-P3 only, P2 slightly weaker, no secondary sculpture. Siphonal canal ADP, MP developed. Aperture ovate; anal canal not developed; siphonal canal moderately long, straight, narrow, open, hardly bent abaxially. Outer lip thickened, outer edge weakly scalloped by spiral sculpture, internally flattened, bearing weak D1-D3, weak D4 at inner edge. Columella shallowly excavated, smooth. Columellar callus thickened, sharp edged, hardly expanded, forming narrow callus rim.

Discussion – *Paziella (Flexopteron) gracilentata* nov. sp. is a most unusual species, more slender than any of its congeners and with the spiral sculpture much reduced, so that only P1-P3 are developed on the last whorl and no secondary spiral sculpture is present. Despite the reduced nature of the primary spirals, the siphonal canal carries a relatively prominent ADP and MP. The outer lip denticles are also reduced, D1-D4 present only, of which D4 is weak in many specimens. Groups 1 and 2 (of Merle *et al.*, 2011) have the most reduced spiral sculpture, but in these groups the reduction is in the secondary sculpture and neither of these groups have spirals on the siphonal canal. The closest species seems to be *P. (F.) septemcostata* (Rouault, 1850) from the lower Eocene Aquitaine Basin of France. One of the specimens figured by Merle *et al.* (2011, text-fig. 59, fig. D) also has only P1-P3 and D1-D4 developed, but that species is less slender and has no cords on the siphonal canal.

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

Subfamily Aspellinae Keen, 1971

Note – The placement of *Dermomurex* Monterosato, 1890 in the subfamily Muricinae is doubtful, as molecular data presented by Barco *et al.* (2010) showed the subfamily to be polyphyletic. Merle *et al.* (2011) distinguished an aspelloid group including *Dermomurex* and *Aspella*. Later, Bouchet *et al.* (2017) and Houart (2018) attempted to give a status to the Aspellinae, because Barco *et al.* 2010 individualised a clade including to *Dermomurex* species. We agree with this position and find it better to place these genera in this subfamily than in the Muricinae.

Genus *Dermomurex* Monterosato, 1890

Subgenus *Dermomurex* Monterosato, 1890

Type species (by typification of replaced name) – *Murex scalarinus* Bivona, 1832 [= *Murex scalaroides* de Blainville, 1829], present-day, Mediterranean. *Nom. nov. pro Poweria* Monterosato, 1884, *non* Bonaparte, 1840 [Pisces].

1890 *Dermomurex* Monterosato, p. 181.

For generic synonymy see Ceulemans *et al.* (2016, p. 38).

Dermomurex (Dermomurex) distinctus (de Cristofori & Jan, 1832)

Plate 13, figs 1-3

*1832 *Murex distinctus* de Cristofori & Jan, p. 11.

1836 *Murex distinctus* Jan – Philippi, p. 209, pl. 11, fig. 32.

1853 *Murex distinctus* Jan – Hörnes, p. 246, pl. 25, fig. 7.

- 1871 *Murex distinctus* Jan – d’Ancona, p. 25, pl. 2, fig. 4.
- 1885 *Murex rutogus* de Gregorio, p. 285 (nov. nom. pro. *Murex distinctus* de Cristofori & Jan, 1832).
- 1904 *Murex (Aspella) scalarioides [sic]* Blainv. – Sacco, p. 20, pl. 5, figs 30, 31 [non *Dermomurex (s.s.) scalaroides* (de Blainville, 1829)].
- 1935 *Aspella scalarioides [sic]* var. *distincta* Jan – Montanaro, p. 52, pl. 4, fig. 1 [non *Dermomurex (s.s.) scalaroides* (de Blainville, 1829)].
- 1952 *Aspella scalarioides [sic]* Blainville, 1826 – Gilbert, p. 295, pl. 6, fig. 7 [non *Dermomurex (s.s.) scalaroides* (de Blainville, 1829)].
- 1959 *Aspella (Aspella) scalarioides [sic]* (Blainville) – Ruggieri *et al.*, p. 29, pl. 7, fig. 34 [non *Dermomurex (s.s.) scalarioides* (de Blainville, 1829)].
- 1964 *Aspella scalarioides [sic]* Blainville, 1826 – Brébion, p. 375 [non *Dermomurex (s.s.) scalaroides* (de Blainville, 1829)].
- 1971 *Murex distinctus* De Cristofori & Jan, 1832 – Pinna, p. 431, p. 77, fig. 3.
- 1975 *Dermomurex (Takia) distinctus* (Cristofori & Jan) – Vokes, p. 128, pl. 5, figs 5, 6.
- 1978 *Murex distinctus* De Cristofori & Jan, 1832 – Pinna & Spezia, p. 147, pl. 31, fig. 3.
- 2000 *Dermomurex distinctus* (Jan, 1832) – Chirli, p. 7, figs 1-7.
- 2011 *Dermomurex (s.s.) distinctus* (Cristofori & Jan, 1832) – Merle *et al.*, p. 215, pl. 166, figs 5-8.
- 2017 *Dermomurex (s.s.) distinctus* (Cristofori & Jan, 1832) – Vicián *et al.* (?partim), p. 268, pl. 2, figs 7, 8 [? figs 5-6].

Material and dimensions – Maximum height 16.7 mm, width 8.5 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0721-0723 (3), NHMW 2016/0103/0724 (19), RGM.1348239352 (3), RGM.1349221 (1), LC (19 + 28 juveniles), FVD (15). **Sceaux-d’Anjou**: NHMW 2016/0103/1707 (3), RGM.1348091 (1), RGM.1348096 (1), RGM.1348120 (1), RGM.1348150 (4), RGM.1348185 (2 juveniles), RGM.1348196 (1), RGM.718085 (37), LC (2), FVD (1). **Renauleau**: NHMW 2016/0103/1411 (16), LC (17), FVD (28).

Discussion – Landau *et al.* (2007, p. 22) argued that *Murex distinctus* de Cristofori & Jan, 1832, which had been considered a synonym of *M. scalaroides* de Blainville, 1829 by Houart (2001) amongst others, was indeed a different species, and that *M. distinctus* should be placed in the subgenus *Takia* Kuroda, 1953, whereas *M. scalaroides* belonged in *Dermomurex (s.s.)* Monterosato, 1890. This was based on Vokes’ (1975) distinction between the two genera: *Takia* differing from *Dermomurex (s.s.)* in having a lower spire, a moderately long siphonal canal, and in having six varices on the last teleoconch whorl. In comparison, *Dermomurex (s.s.)* has a high spire, a short siphonal canal, and three to six varices on the last whorl. This is illustrated by Vokes (1975, pl. 5, figs 5 & 8). Merle *et al.* (2011) discussed in depth the differences between the various subgenera of *Dermomurex* and revised Vokes’ generic concepts. They considered *M. distinctus* should also be placed in *Dermomurex (s.s.)* rather than *Takia*, and indeed all the species included in *Takia* by these authors have a far longer and more slender siphonal canal than *M. distinctus*. We therefore accept this placement. Despite being consubgeneric, the two are different species and apart from the differences in the number of axial varices, *D. (s.s.) distinctus* has stronger spiral cords, giving the sculpture a widely reticulated aspect and the last whorl is more inflated and more strongly constricted at the base, whereas the last whorl in *D. (s.s.) scalaroides* is more fusiform (see Merle *et al.*, 2011, pl. 166). Recently Vicián *et al.* (2017) recorded this species from the Paratethian middle Miocene of Hungary. One of the specimens is undoubtedly *D. (s.s.) distinctus* (2017, pl. 2, figs. 7, 8). The other (2017, pl. 2, figs. 5, 6) looks trivari-cate. It could be a teratological specimen of that species, or possibly *Dermomurex (Trialatella) jani* (Doderlein, 1862). Members of the genus *Trialatella* Berry, 1964 differ in having only three varices per whorl on the last whorl as opposed to six and the spiral sculpture on the last whorl is weaker. A further middle Miocene consubgener *D. (T.) kilikiensis* Landau, Harzhauser, İslamoğlu & Silva, 2013 was described from the eastern Proto-Mediterranean of Turkey. It differs from *D. (T.) jani* in having a protoconch composed of 2.5 as opposed to 1.5 whorls and has a more solid, squatter teleoconch, the intervarical ribs are more

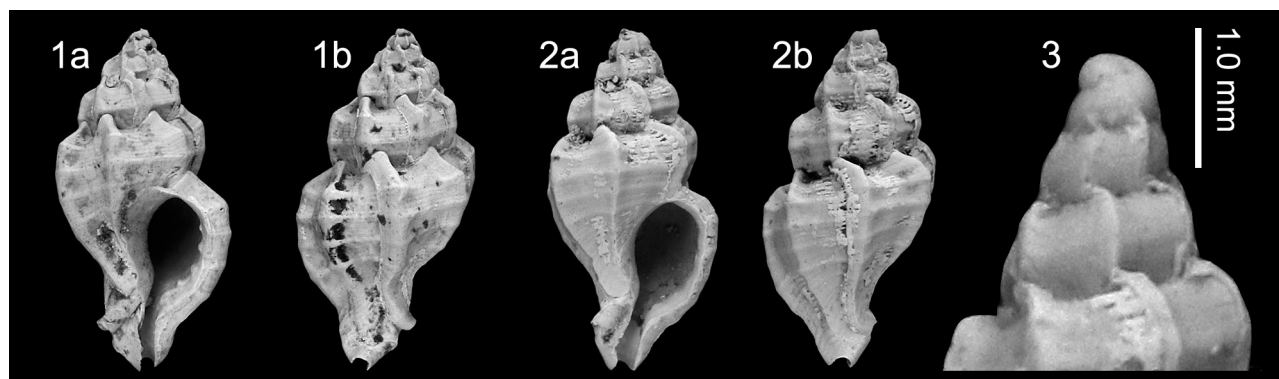


Plate 13. *Dermomurex (s.s.) distinctus* (de Cristofori & Jan, 1832); 1. NHMW 2016/0103/0721, height 16.7 mm, width 8.5 mm; 2. NHMW 2016/0103/0722, height 12.1 mm, width 5.7 mm; 3. NHMW 2016/0103/0723, height 8.8 mm, width 3.9 mm (juvenile), detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

strongly developed on the spire whorls and the intervarical node on the last whorl is more prominent.

Distribution – Middle Miocene: Atlantic, Loire Basin (Glibert, 1952; Merle *et al.*, 2011); Paratethys, Austria (Hörnes, 1853; Merle *et al.*, 2011); Paratethys, Hungary (Vicián *et al.*, 2017). Upper Miocene: Atlantic, NW France (Brébion, 1964; Merle *et al.*, 2011); Proto-Mediterranean Sea, Italy (d’Ancona, 1871; Montanaro, 1935). Lower Pliocene: central Mediterranean, Italy (Chirli, 2000; Merle *et al.*, 2011). Upper Pliocene: central Mediterranean, Italy (Sacco, 1904; Ruggieri *et al.*, 1959; Vokes, 1975; Merle *et al.*, 2011).

Dermomurex (Dermomurex) tenellus (Mayer, 1869)

Plate 14, figs 1-3

- *1869 *Murex tenellus* Mayer, p. 83, pl. 3, fig. 5.
- 1964 *Aspella tenella* Mayer, 1869 – Brébion, p. 376.
- 1975 *Dermomurex (Dermomurex) tenellus* (Mayer) – Vokes, p. 128, pl. 2, figs 1, 2.
- 2011 *Dermomurex (s.s.) tenellus* (Mayer, 1869) – Merle *et al.*, p. 215, text-fig. 73A, pl. 165, figs 7-9.
- 2016 *Dermomurex (Dermomurex) tenellus* (Mayer, 1869) – Ceulemans *et al.*, p. 38, pl. 1, fig. 6 (*cum syn.*).

Material and dimensions – Maximum height 20.5 mm, width 9.0 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0716-0718 (3), NHMW 2016/0103/0719 (19), RGM.1348166 (1), RGM.1348239353 (7), LC (11), FVD (14). **Sceaux-d’Anjou**: NHMW 2016/0103/0720 (13), RGM.1348092 (7), RGM.1348097 (14), RGM.1348141 (1), RGM.1348145 (1), RGM.1348149 (8), RGM.1348183 (3), RGM.1348195 (2), RGM.1348250 (2), RGM.1348910 (6), RGM.718083 (50+), LC (4), FVD (6). **Renauleau**: NHMW 2016/0103/1412 (6), LC (33), FVD (15).

Discussion – *Dermomurex (Dermomurex) tenellus* (Mayer, 1869) is characterised by its beaded spiral cords. The strength of the beading and number of beads is rather

variable. We illustrate two specimens; one with extremely fine beading (Pl. 14, fig. 1), the other with coarse beading (Pl. 14, fig. 2). The protoconch is worn, but is clearly paucispiral, composed of about 1.5 whorls, with a large nucleus. For further discussion see Ceulemans *et al.* (2016, p. 38).

Brébion (1964, p. 376) recorded this species from Assemblage I localities (Sceaux d’Anjou, Thorigné, St-Clément-de-la-Place), to which Ceulemans *et al.* (2016, p. 39) add the Assemblage III locality of Le Pigeon Blanc.

Distribution – Lower Miocene (Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1924). Middle Miocene: Loire Basin, France (Benoist, 1880; Cossmann, 1903; Glibert, 1952; Vokes, 1975; Merle *et al.*, 2011). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964; Merle *et al.*, 2011). Lower Pliocene: Atlantic, NW France (Ceulemans *et al.*, 2016).

Subfamily Coralliophilinae Chenu, 1859

Genus *Hirtomurex* Coen, 1922

Type species (by original designation) – *Fusus lamellosus* Philippi, 1836, present-day, Mediterranean.

1922 *Hirtomurex* Coen, p. 69.

Hirtomurex* aff. *squamosus (Bivona Ant. in Bivona And., 1838)

Plate 15, fig. 1

- aff. 1838 *Fusus squamosus* Bivona Ant. in Bivona And., p. 320, fig. 22.
- 1964 *Coralliophila* nov. sp. Brébion, p. 394, pl. 9, fig. 19.
- aff. 1985 *Coralliophila squamosa* (Bivona, 1838) – Bouchet & Warén, p. 153, figs 357-361 (*cum syn.*).
- aff. 1985 *Coralliophila basileus* (Dautzenberg & H. Fischer, 1896) – Bouchet & Warén, p. 154, figs 362-366.

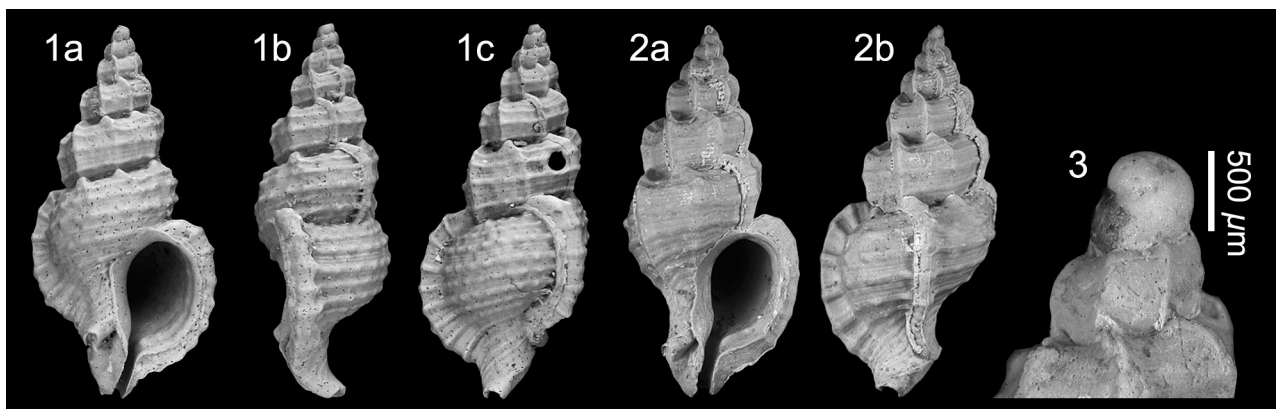


Plate 14. *Dermomurex (s.s.) tenellus* (Mayer, 1869); 1. NHMW 2016/0103/0716, height 16.5 mm, width 8.2 mm; 2. NHMW 2016/0103/0717, height 14.5 mm, width 6.0 mm; 3. NHMW 2016/0103/0718, height 11.3 mm, width 5.6 mm. Le Grand Chauverau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

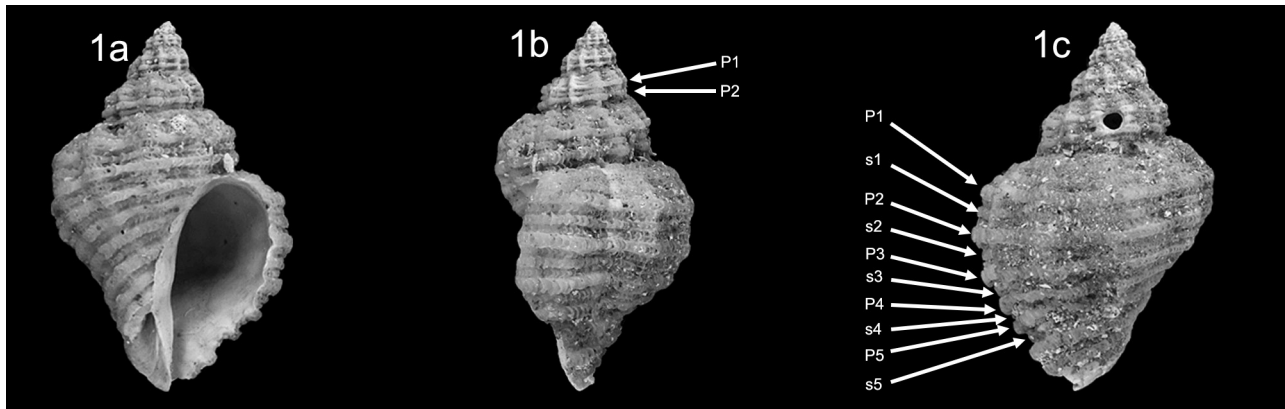


Plate 15. *Hirtomurex* aff. *squamosus* (Bivona Ant. in Bivona And., 1838). 1. NHMW 2016/0103/1678, height 21.3 mm, width 13.3 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

2016 *Hirtomurex* aff. *squamosus* (Bivona Ant. in Bivona And., 1838) – Ceulemans *et al.*, p. 49, pl. 3, fig. 8 (figures 8 and 9 on plate 3 reversed; *lapsus*).

Note – According to Houart (2018), the placement of the genus *Lindapterys* Petuch, 1987 in the subfamily Ergalataxinae is doubtful.

Material and dimensions – Height 21.3 mm, width 13.3 mm. **Sceaux-d'Anjou:** NHMW 2016/0103/1678 (1).

Discussion – A single well preserved specimen is at hand from the Sceaux-d'Anjou locality. It is characterised by its strongly convex shouldered whorls separated by a deeply impressed suture, sculpture composed of ten rounded axial ribs, roughly equal in width to their interspaces overrun by rounded spiral cords of alternating strength, three major cords present on spire whorls; the adapical cord delimiting the shoulder, the abapical just appearing at the suture. The last whorl is expanded, the shoulder rounded, placed high, cords P1-P5 strongly developed, s1-s5 developed in interspaces, separated by narrow grooves.

It is likely to be conspecific with the stratigraphically younger specimens from the lower Pliocene Assemblage III locality of Le Pigeon Blanc illustrated by Brébion (1964, pl. 9, fig. 19) and Ceulemans *et al.* (2016, pl. 3, fig 8; not 9 as stated; *lapsus*, see above in chresonymy) identified as *Hirtomurex* aff. *squamosus* (Bivona Ant. in Bivona And., 1838). This species was fully discussed in Ceulemans *et al.* (2016, p. 49) and as in that paper the material available is insufficient to come to any firm conclusions.

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

Subfamily Ergalataxinae Kuroda, Habe & Oyama, 1971

Incertae sedis in the subfamily Ergalataxinae

Genus *Lindapterys* Petuch, 1987

Type species – By original designation: *Lindapterys vokesae* Petuch, 1987, Miocene, Florida, USA.

Lindapterys alata (Millet, 1865)

Plate 16, figs 1-3

1854 *Ranella Alata* Millet, p. 163 (*nomen nudum*).

*1865 *Ranella alata* Millet, p. 594.

1874 *Triton alatus* Millet – Tournouër, p. 300, pl. 9, fig. 8.

1886 *Triton (Colubraria) alatum* Millet – Dollfus & Dautzenberg, p. 104.

1938 *Eupleura alata* Millet – Peyrot, p. 195.

1938 *Eutritonium (Colubraria) alatum* Millet – Peyrot, p. 202.

1952 *Eupleura alata* Millet, 1866 [*sic*] – Glibert, p. 309, pl. 7, fig. 7.

1964 *Eupleura alata* Millet, 1854 [*sic*] – Brébion, p. 394.

1994 *Lindapterys alata* (Millet, 1854 [*sic*]) – Lozouet *et al.*, p. 42, text-fig. 1c-d, pl. 1, figs 11-16.

Material and dimensions – Maximum height 14.0 mm, width 5.6 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0764 (8 juveniles), LC (2), FVD (4 juveniles). **Sceaux-d'Anjou:** NHMW 2016/0103/0766 (16), RGM.1348098 (1), RGM.1348115 (2 + 3 subadults), RGM.1348879 (2 + 2 juveniles), RGM.734963 (7 + 9 juveniles), LC (3), FVD (3). **Renauleau:** NHMW 2016/0103/1420-1421 (2), NHMW 2016/0103/0765 (6), LC (13 + 9 juveniles), FVD (5).

Discussion – The genus includes a small number of Miocene to present-day species with a very characteristic shell form. All members have paucispiral protoconchs of about 1.5 whorls suggesting non-planktotrophic development, all are small sized, and all are very to exceedingly uncommon in the assemblages in which they occur. The genus was reviewed by Lozouet *et al.* (1994) who recognised two, possibly three European fossil spe-

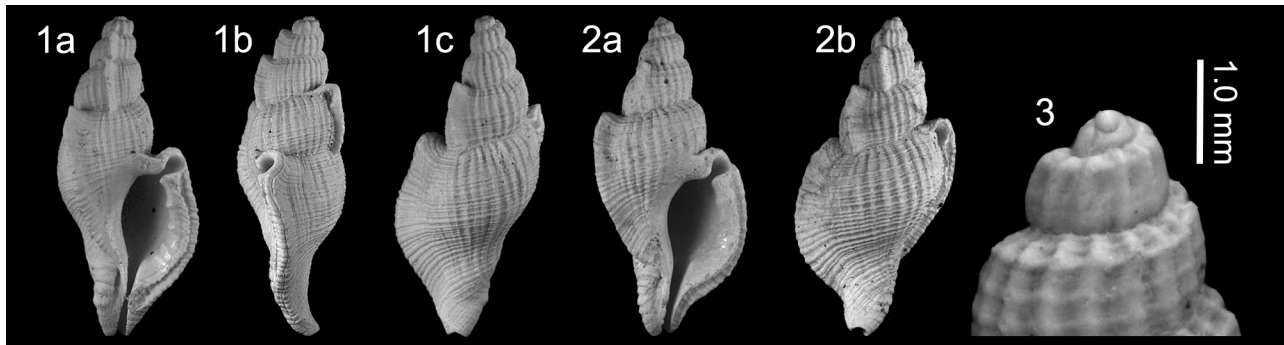


Plate 16. *Lindapterys alata* (Millet, 1865). 1. NHMW 2016/0103/1420, height 13.7 mm, width 5.4 mm; 1. NHMW 2016/0103/1421, height 12.5 mm, width 5.5 mm; 3. NHMW 2016/0103/1422, height 10.5 mm, detail of protoconch. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

cies: *Lindapterys* cf. *poppelacki* (Hörnes, 1853) from the lower Miocene Aquitaine Basin of France, *L. poppelacki* (Hörnes, 1853) from the middle Miocene Paratethys, and *L. alata* (Millet, 1865) from the upper Miocene of northwestern France. The *L. poppelacki* species group are distinguished from *L. alata* in having predominantly axial sculpture, whereas in *L. alata* the axial and spiral elements are of roughly equal strength forming an evenly and finely reticulated surface pattern. More recently a further species *L. cervantesorum* Goret, Ledon & Pons, 2013 was described from the western Mediterranean of NE Spain, extending the stratigraphic range of the genus into the lower Pliocene. The Catalan species belongs to the *L. poppelacki* species group with predominantly axial sculpture, which is even more strongly developed than in *L. poppelacki*. The genus *Lindapterys* is a tropical genus that has been described from the present-day coast of Somalia, *L. soderieae* Callea, Volpi, Borri and Martignoni, 2001. That species differs from *L. alata* in being larger (14.5–16.5 mm in height), in having weaker axial sculpture, and in having cancellate instead of clathrate sculpture.

In the French upper Miocene deposits Millet (1854, p. 163) and Brébion (1964, p. 394) recorded *L. alata* from the Assemblage I deposits of Renauleau, Sceaux-d'Anjou, Thorigné and St-Clément-de-la-Place.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Tournouër, 1874; Dollfus & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1952). Upper Miocene: Atlantic (Tortonian), NW France (Millet, 1854, 1865; Tournouër, 1874; Brébion, 1964; Lozouet *et al.*, 1994).

Subfamily Muricopsinae Radwin & D'Attilio, 1971
Genus *Favartia* Jousseume, 1880

Type species (by original designation) – *Murex breviculus* G.B. Sowerby II, 1834, present-day, Philippines.

1880 *Favartia* Jousseume, p. 335.

For generic synonymy see Ceulemans *et al.* (2016, p. 40).

Favartia milleti Ceulemans, Van Dingenen, Merle & Landau, 2016

Plate 17, figs 1–3

- 1854 *Murex lineatus* Millet, p. 163 (*nomen nudum*).
1865 *Murex lineatus* Millet, p. 593 (*non Murex lineatus* Gmelin, 1791; junior synonym of *Buccinum linea* Martyn, 1784: valid name, ICZN, Opinion 479).
1964 *Aspella* (*Favartia*) *absona lineata* Millet, 1854 – Brébion, p. 377, pl. 9, figs 5, 6.
*2016 *Favartia milleti* Ceulemans, Van Dingenen, Merle & Landau, p. 40, pl. 1, fig. 6.

Material and dimensions – Maximum height 9.0 mm, width 5.4 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0725–0727 (3), NHMW 2016/0103/0728 (18), RGM.1348165 (15), RGM.1348254 (1 juvenile), RGM.1348334 (10), RGM.1348831 (1), LC (50+), FVD (39). **Sceaux-d'Anjou**: NHMW 2016/0103/0729 (29), RGM.1348094 (16), RGM.1348101 (3), RGM.1348127 (3), RGM.1348131 (2 juvenile), RGM.1348144 (3), RGM.1348151 (8), RGM.1348184 (8), RGM.1348194 (1), RGM.1348375 (1), RGM.1348513 (7), RGM.1348944 (4), RGM.718084 (50+), LC (15), FVD (18). **Renauleau**: LC (6).

Discussion – *Favartia milleti* Ceulemans, Van Dingenen, Merle & Landau, 2016 is characterised by its strongly scalate spire. The protoconch is paucispiral (Pl. 17, fig. 3). The spire whorls are sculptured by two narrow, elevated spiral cords crossed by about six to eight axial lamellae. The last whorl is short, with a shallow, flat to weakly concave subsutural platform, sharply angled at the shoulder, convex below and constricted at the base. P1–P5 are narrow, strongly developed, P1, P2 and P3 are hooked at the labial varix. P6 is weaker, forming a short erect spine at the aperture. ADP and MP are also strongly developed, forming an open spine at their extremities. Over the entire surface the lamellae are spinose where they cross the spiral cords. The aperture is ovate and the siphonal canal is open and moderately long. For further discussion see Ceulemans *et al.* (2016, p. 40).

Brébion (1964, p. 379) recorded this species from the Assemblage I localities of Thorigné and Sceaux-d'Anjou (to

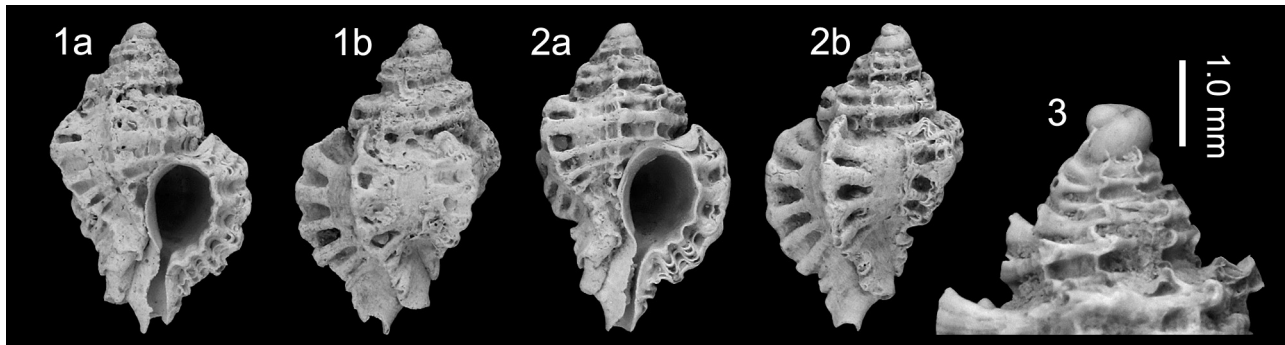


Plate 17. *Favartia milleti* Ceulemans, Van Dingenen, Merle & Landau, 2016; 1. NHMW 2016/0103/0725, height 7.8 mm, width 4.7 mm; 2. NHMW 2016/0103/0726, height 7.6 mm, width 4.7 mm; 3. NHMW 2016/0103/0727, height 7.9 mm, width 4.3 mm, detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

which we add St-Clément-de-la-Place), Assemblage III (Le Girondor, Le Pigeon Blanc, Palluau, La Dixmérie) and Assemblage IV (Gourbesville).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964).

Favartia suboblonga (d'Orbigny, 1852)

Plate 18, figs 1-3

- 1833 *Murex oblongus* Grateloup, pl. 100 (*non M. oblongus* Brocchi, 1814).
 *1852 *Murex suboblongus* d'Orbigny, p. 73 (*nom. nov. pro Murex oblongus* Grateloup, 1833, *non* Brocchi, 1814).
 1964 *Aspella (Favartia) incisa* var. *excisa* Grateloup, 1833 – Brébion, p. 377.
 1999 *Favartia suboblonga* (D'Orbigny, 1852) – Merle, p. 300, text-figs 39, 40, pl. 5, figs 7-9, pl. 6, figs 1-4.
 2007 *Favartia suboblonga* (d'Orbigny, 1852) – Landau *et al.*, p. 46, text-fig. 12, pl. 12, figs 5-8 (*cum syn.*).
 2013 *Favartia suboblonga* (d'Orbigny, 1852) – Landau *et al.*, p. 161, pl. 24, fig. 5.

2013 *Favartia suboblonga* (d'Orbigny, 1852) – Goret *et al.*, p. 17, text-fig 13 a, b, pl. 4, fig. 6.

2016 *Favartia suboblonga* (d'Orbigny, 1852) – Ceulemans *et al.*, p. 40, pl. 1, figs 8, 9 (*cum syn.*).

Material and dimensions – Maximum height 13.3 mm, width 9.4 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0730-0732 (3), NHMW 2016/0103/0733 (4), LC (7), FVD (4). **Sceaux-d'Anjou:** NHMW 2016/0103/0734 (36), RGM.1348095 (20), RGM.1348113 (1), RGM.1348139 (3), RGM.1348142 (2), RGM.1348153 (9), RGM.1348178 (12), RGM.1348193 (3), RGM.1348514 (6), RGM.718082 (50+), RGM.739217 (8 juveniles), LC (12), FVD (15). **Renau-leau:** NHMW 2016/0103/0735 (16), LC (49), FVD (25). **Beugnon:** RGM.1348464 (1).

Discussion – The complicated taxonomic history of this species was discussed by Landau *et al.* (2007, p. 47). Two closely similar species occur: *F. suboblonga* (d'Orbigny, 1852) and *F. excisa* (Grateloup, 1833). The type locality for *Murex excisus* is St-Paul-lès-Dax, Atlantic lower Miocene, Aquitanian, of France (Merle, 1999, p. 289). Both *Favartia excisa* and *F. suboblonga* have a planktonic-type protoconch consisting of about 3.5 whorls. The main difference between *F. excisa* and *F. suboblonga* is the low growth of the secondary spiral cords s2 and s3 in *F. excisa* (see Merle, 1999, p. 304). The rela-

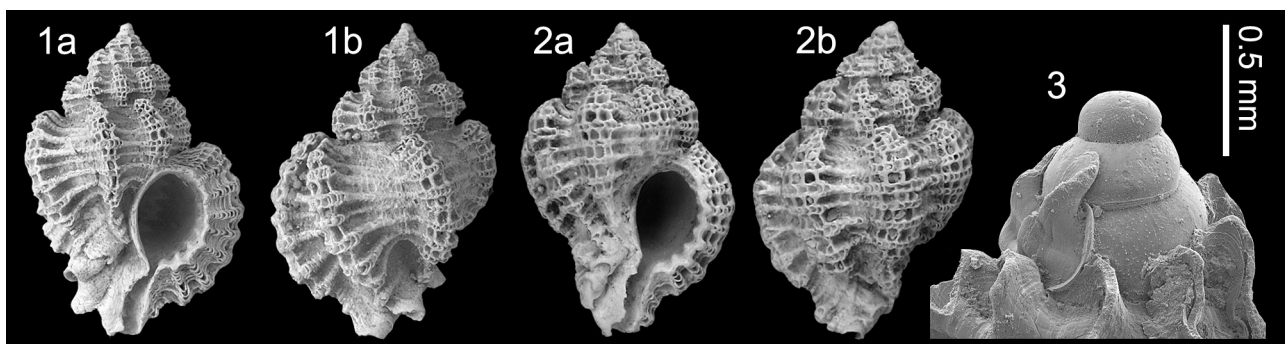


Plate 18. *Favartia suboblonga* (d'Orbigny, 1852); 1. NHMW 2016/0103/0730, height 7.8 mm, width 4.7 mm; 2. NHMW 2016/0103/0731, height 8.3 mm, width 5.3 mm; 3. NHMW 2016/0103/0732, height 4.8 mm (juvenile), detail of protoconch (SEM). Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

tive frequency of the presence of secondary cords in the two species is as follows: for *F. suboblonga*, s1 (0%), s2 (99%), s3 (33%), s4 (0%), s5 (86%), s6 (88%); for *F. excisa*, s1 (0%), s2 (1%), s3 (1%), s4 (1%), s5 (1%), s6 (11%). Therefore more than 80% of specimens of *F. suboblonga* have s2-s5 developed, whereas less than 1% of *F. excisa* do (Merle, 1999). *Favartia excisa* occurs in the French Atlantic Late Oligocene, Chattian to late lower Miocene, Burdigalian. *Favartia suboblonga* coexisted with *F. excisa* in the French Atlantic lower Miocene, Aquitanian, and persisted into the middle Miocene, Langhian (Merle, 1999). All the late Miocene and Pliocene European shells identified by authors as *F. excisa* and *F. incisa* are, in our opinion also, *F. suboblonga*.

The French specimens from the upper Miocene Tortonian Assemblage I deposits are smaller than the typical *Favartia suboblonga* from the Mediterranean Pliocene, and the aperture is smaller and rounder, however Merle (1999, p. 302) noted some degree of intraspecific variability in the size of the shells within other French Miocene populations. The Assemblage III specimens from Le Pigeon Blanc are also relatively small (Ceulemans *et al.*, 2016).

Favartia suboblonga differs from *Favartia absona* (de Cristofori & Jan, 1832) in having a higher spire, broader, rounded, rather than spinose varices and in having the siphonal canal much shorter and strongly dorsally recurved, whereas that in *F. absona* is almost straight.

Brébion (1964, p. 379) recorded this species from Assemblage I localities of Thorigné, and Sceaux d'Anjou (to which we add St-Clément-de-la-Place and Renauleau), the Assemblage III locality of Palluau (to which Ceulemans *et al.*, 2016, p. 41, added Le Pigeon Blanc), and Assemblage IV (Gourbesville).

Distribution – Middle Miocene (Langhian and Serravallian): Atlantic, Loire Basin, France (Glibert, 1952), Aquitaine Basin (Cossmann & Peyrot, 1924); Paratethys, Austria (Hörnes, 1853), Poland (Bałuk, 1995), Romania (Boettger, 1902; Zilch, 1934); Proto-Mediterranean Sea (Serravallian), Karaman Basin (Landau *et al.*, 2013). Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964); Proto-Mediterranean Sea: Italy (Montanaro, 1935). Lower Pliocene: Atlantic, NW France (Brébion, 1964);

western Mediterranean, France (Goret *et al.*, 2013); central Mediterranean, Italy (Chirli, 2000). Upper Pliocene: western Mediterranean, Estepona Basin (Landau *et al.*, 2007); central Mediterranean, Italy (Sacco, 1904; Cavallo & Repetto, 1992; Andreoli & Marsigli, 1992). Upper Pliocene-Pleistocene: Atlantic NW France (Brébion, 1964).

Genus *Muricopsis* Bucquoy & Dautzenberg, 1882

Type species– *Murex blainvillei* Payraudeau, 1826 (= *Murex cristatus* Brocchi, 1814), by original designation, present-day, Mediterranean.

1882 *Muricopsis* Bucquoy & Dautzenberg in Bucquoy, Dautzenberg & Dollfus, p. 19.

For generic synonymy see Ceulemans *et al.* (2016, p. 41).

Muricopsis cristata (Brocchi, 1814)

Plate 19, figs 1-3

- *1814 *Murex cristatus* Brocchi, p. 394, pl. 7, fig. 15.
- non 1837 *Murex cristatus* Br. – Dujardin, p. 296, pl. 19, fig. 10 (= *Muricopsis dujardini* Peyrot, 1938).
- 1854 *Fusus asperimus* Millet, p. 162 (*nomen nudum*).
- non 1952 *Muricidea cristata inermis* Philippi, 1836 – Glibert, p. 299, pl. 6, fig. 11 (= *Muricopsis dujardini* Peyrot, 1938).
- 1865 *Fusus asperimus* Millet, p. 591 (*non* Brown, 1827).
- 1964 *Muricopsis cristatus* var. *inermis* Philippi, 1836 – Brébion, p. 380, pl. 9, fig. 7.
- 2007 *Muricopsis* (*Muricopsis*) *cristata* (Brocchi, 1814) – Landau *et al.*, p. 42, pl. 11, figs 10, 11 (*cum syn.*).
- 2013 *Muricopsis* (*Muricopsis*) *cristata* (Brocchi, 1814) – Landau *et al.*, p. 160, pl. 24, fig. 2 (*cum syn.*).
- 2016 *Muricopsis cristata* (Brocchi, 1814) – Ceulemans *et al.*, p. 41, pl. 2, fig. 1 (*cum syn.*).

Material and dimensions – Maximum height 17.8 mm, width 8.1 mm. **St-Clément-de-la-Place**: NHMW 2016/

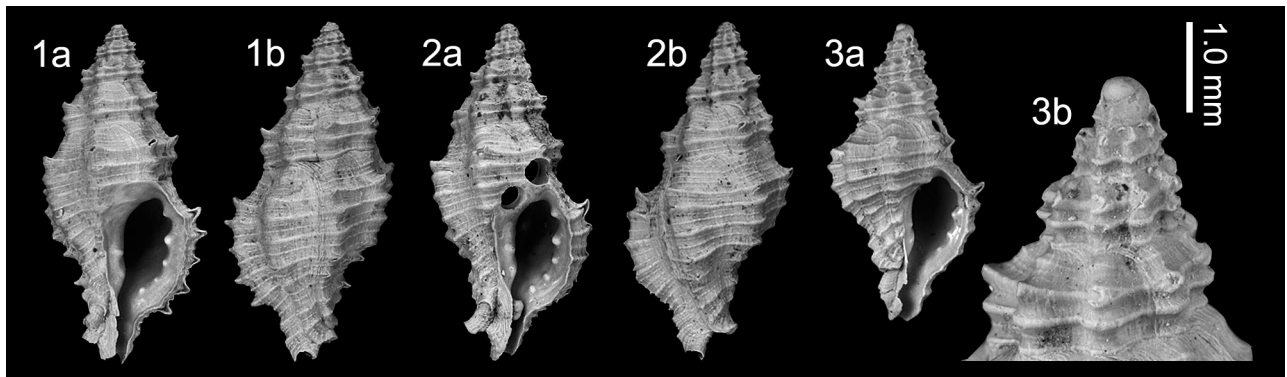


Plate 19. *Muricopsis cristata* (Brocchi, 1814); 1. NHMW 2016/0103/0736, height 16.9 mm, width 8.0 mm; 2. NHMW 2016/0103/0737, height 15.9 mm, width 7.2 mm; 3. NHMW 2016/0103/0738, height 8.7 mm, width 4.5 mm (juvenile), detail of protoconch. Le Grand Chauvèreau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

0103/0736-0738 (3), NHMW 2016/0103/0739 (50+), RGM.1348857 (1), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/0740 (50+), RGM.1348093 (50+), RGM.1348100 (2), RGM.1348104 (50+), RGM.1348105 (35 juveniles and fragments), RGM.1348124 (27), RGM.1348137 (2), RGM.1348138 (1), RGM.1348146 (50+), RGM.1348181 (50+), RGM.1348186 (38), RGM.1348909 (6), RGM.734970 (50+), RGM.718094 (1 juvenile), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1661 (22), LC (50+), FVD (37).

Discussion – *Muricopsis cristata* (Brocchi, 1814) is a highly polymorphic species, with many synonyms in the fossil and Recent literature (see Houart, 2001, p. 92). All the specimens from Assemblage I are of the spiny *cristata* form, as opposed to those from the lower Pliocene Assemblage III locality of Le Pigeon Blanc which are all of the smooth *inermis* Philippi, 1836 morphotype (*non Murex inermis* Dujardin, 1837 = *Muricopsis dujardini* Peyrot, 1938).

We note that the upper Miocene specimens from Assemblage I are typical of *M. cristata*, whereas Peyrot (1938) separated the middle Miocene Langhian specimens from the Loire Basin as *M. dujardini*. That species differs from *M. cristata* in being smaller, less elongated and by the late appearance of the secondary spiral sculpture sl, 4-6, which do not appear until 10 mm height. The protoconch of the Assemblage I specimens is paucispiral, consisting of about 1.5 whorls, similar to that reported by Merle (1999) for *M. dujardini*. For further discussion and comparison see Ceulemans *et al.* (2016, p. 43).

Brébion (1964, p. 382) recorded this species from Assemblage I (Renauleau, Thorigné, Sceaux-d'Anjou, St-Michel, Beaulieu), to which we add St-Clément-de-la-Place, Assemblage II (Apigné, Le Temple du Cerisier), Assemblage III (Le Girondor, Le Pigeon Blanc, Palluau, La Dixmérie, La Gauvinière) and Assemblage IV (Gourbesville).

Distribution – Middle Miocene: Paratethys (Langhian-Serravallian): Austria (Hörnes, 1856; Hörnes & Auinger, 1885; Schultz, 1998), Czech Republic (Hörnes, 1856; Hörnes & Auinger, 1885), Hungary (Kókay, 1966; Strausz, 1966), Poland (Friedberg, 1912; Krach, 1981; Bałuk, 1995), Romania (Hörnes, 1856; Hörnes & Auinger, 1885); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964); Proto-Mediterranean Sea: Italy (Montanaro, 1935; Venzo & Pelosio, 1963). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016); western Mediterranean, Estepona Basin (Landau *et al.*, 2007), France (Goret *et al.*, 2013); central Mediterranean, Italy (Chirli, 2000), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, NW France (Brébion, 1964), Mondego Basin (Landau *et al.*, 2013); central Mediterranean (Sacco, 1904; Ruggieri & Greco, 1965; Palla, 1967; Malatesta, 1974; Caprotti, 1976; Chirli, 1988; Cavallo & Repetto, 1992; Andreoli & Marsigli, 1992). Upper Pliocene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: western Medi-

terranean, Balearic Islands (Cuerda Barceló, 1987); central Mediterranean, Italy (Cerulli-Irelli, 1911; Bevilacqua, 1928; Malatesta, 1960). Present-day: Atlantic, southern Portugal and the Canaries, Mediterranean, intertidal to 120 m, on rocks and dead coral (Houart, 2001).

Incertae sedis in the subfamily Muricopsinae

Genus *Attiliosa* Emerson, 1968

Type species (by original designation) – *Coralliophila incompta* Berry, 1960, present-day, Gulf of California.

1968 *Attiliosa* Emerson, p. 380.

Note – In the phylogenetic tree of Barco *et al.* (2010, 2012), *Attiliosa* is placed as sister group of the Muricopsinae. However, new data including new taxa would be necessary to confirm the place of *Attiliosa* as sister group of the Muricopsinae.

Attiliosa gallica nov. sp.

Plate 20, fig. 1

Type material – Holotype NHMW 2016/0103/1703, height 11.2 mm, width 6.6 mm.

Other material – Known from holotype only.

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

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Attiliosa* species of small size, paucispiral protoconch, axial ribs that broaden markedly on last whorl, spiral cords only strongly developed below periphery, labial varix modest, seven lirae within outer lip, columella smooth except for abapical ridge at edge of siphonal canal, strongly developed umbilical slit.

Description – Shell small for genus, broadly fusiform. Protoconch paucispiral, composed of 1.5 smooth convex whorls, with large nucleus. Teleoconch of four whorls. Suture impressed, undulating. Spire whorls with shallow subsutural ramp, roundly shouldered, weakly convex below, tapering inward slightly to suture. Axial sculpture of nine prosocline ribs, sharp and much narrower than interspaces on early whorls, broadening on last two whorls, equal in width to interspaces on last whorl. No obvious varices formed, but residual varices visible, especially around P1. Spiral sculpture of narrow cords, probably of primary and secondary strength, but not easily distinguished; P1 delimiting shoulder on spire whorls, weaken-

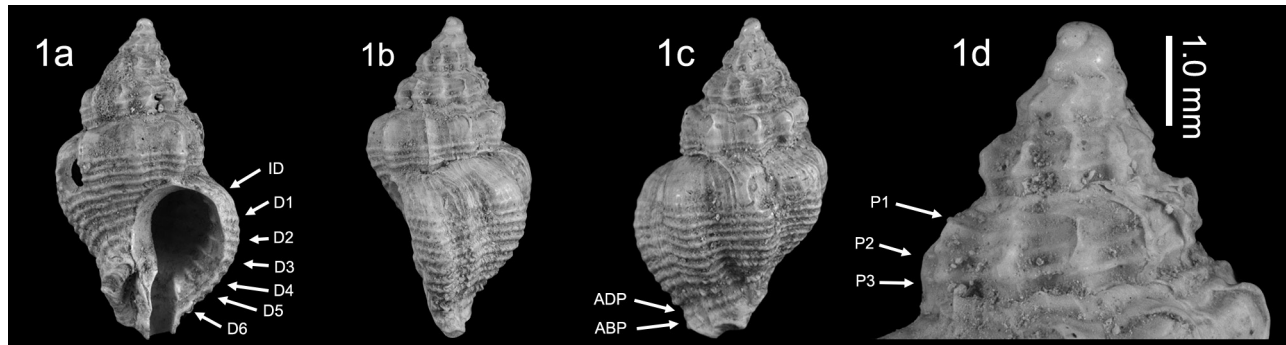


Plate 20. *Attiliosa gallica* nov. sp.; 1. **Holotype** NHMW 2016/0103/1703, height 11.2 mm, width 6.6 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

ing abapically. Weak, close-set axial growth lines cover surface, giving imbricated appearance under magnification. Last whorl with shallow convex subsutural ramp, rounded at high-placed shoulder, weakly constricted at base; ribs broad, slightly swollen at shoulder, cords strongly developed only below periphery; P1 subobsolete. Aperture ovate; outer lip moderately thickened by labial varix, bearing seven lirae within that extend deep into aperture; anal canal not developed; siphonal canal of medium length and width, open, slightly posteriorly recurved. Columella excavated in adapical portion. Columellar callus slightly thickened, sharply delimited, forming narrow callus rim, smooth except for ridge and two small tubercles at edge of siphonal canal. Siphonal fasciole short, rounded, bearing ADP and ABP, delimiting well-developed umbilical slit.

Discussion – Like almost everything in the Tortonian Assemblage I fauna of NW France, the species is small for the genus. Despite being represented by a single specimen, it is excellently preserved, undoubtedly adult, and distinct enough to warrant description. *Attiliosa gallica* nov. sp. is characterised by its scalate spire and inflated last whorl, sculpture of broad rounded ribs and narrow spiral cords that are only strongly developed below the whorl periphery, ovate aperture, modestly thickened outer lip, lirae within, absence of anal sinus, and smooth columella with a fold or ridge at the edge of the siphonal canal.

This species shows close convergence in shell characters with members of the buccinid genus *Hesperisternia* Gardner, 1944, a late Oligocene to present-day tropical and subtropical American genus (Vermeij, 2006). However, there are several shell characters seen in the specimen from Sceaux-d'Anjou that suggest placement in *Attiliosa* rather than *Hesperisternia*: 1) the aperture is rounded abapically and lacks an anal sinus; *Hesperisternia* species all have a deep narrow anal groove. 2) Two weak denticles are present on the columella on ridge bordering siphonal canal; in *Hesperisternia* there is a prominent fold in this position, but no tubercles. 3) The siphonal canal is short and strongly umbilicate; in *Hesperisternia* the canal tends to be longer and the umbilical slit, if present, is weaker. 4) Residual varices can be seen in the Sceaux-d'Anjou specimen, particularly around P1

(Pl. 20, fig. 1d); In *Hesperisternia*, the axial sculpture makes ridges that can be strong, but not true varices as in the muricids. 5) The spiral sculpture is probably composed of primary and secondary cords (Pl. 20, fig. 1d), but these are not easily distinguished in the single specimen available; in *Hesperisternia* the cords are of primary to tertiary strength.

Attiliosa gallica co-occurs with *Attiliosa pouweri* nov. sp. (see below) in the Assemblage I deposits of NW France, but that species is immediately distinguished by its more regularly fusiform shell shape and its spiral sculpture composed of regularly alternating strength cords that cover the entire whorl surface on the last whorl. Nevertheless, the protoconch and early teleoconch sculpture of the two species is remarkably similar (compare Pl. 20, fig. 1d with Pl. 21, fig. 4a). These same characters; the *Hesperisternia*-like shape and cords that are only developed below the periphery of the last whorl also distinguish *A. gallica* from its other European Neogene congeners such as *A. villae* (Michelotti, 1847) and *Attiliosa* sp. 1 and 2 in Merle *et al.* (2011, pl. 152, figs 1-3, 9).

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

Attiliosa pouweri nov. sp.

Plate 21, figs 1-4

- 1964 *Ocinebrina scalaris* Brocchi, 1814 – Brébion, p. 383, pl. 9, figs. 8, 9 (*non* Brocchi, 1814).
2011 *Attiliosa* sp. 3 – Merle *et al.*, p. 204, pl. 152, figs 10-11.

Type material – Holotype MNHN.F.A70995, height 11.0 mm, width 6.4 mm; paratype 3 RGM.1349035, height 12.5 mm, width 7.5 mm; paratype 4 RGM.1349036, height 13.6 mm, width 8.0 mm; paratype 5 RGM.1349037, height 12.8 mm, width 7.8 mm; paratype 6 NHMW 2016/0103/1845, height 13.0 mm, width 7.2 mm; paratype 7 NHMW 2016/0103/1846, height 13.3 mm, width 7.4 mm; paratype 8 NHMW 2016/0103/1847, height 13.3 mm, width 7.2 mm, **Sceaux-d'Anjou**. Paratype 1, NHMW 2016/0103/0784, height 12.6 mm, width 7.4 mm;

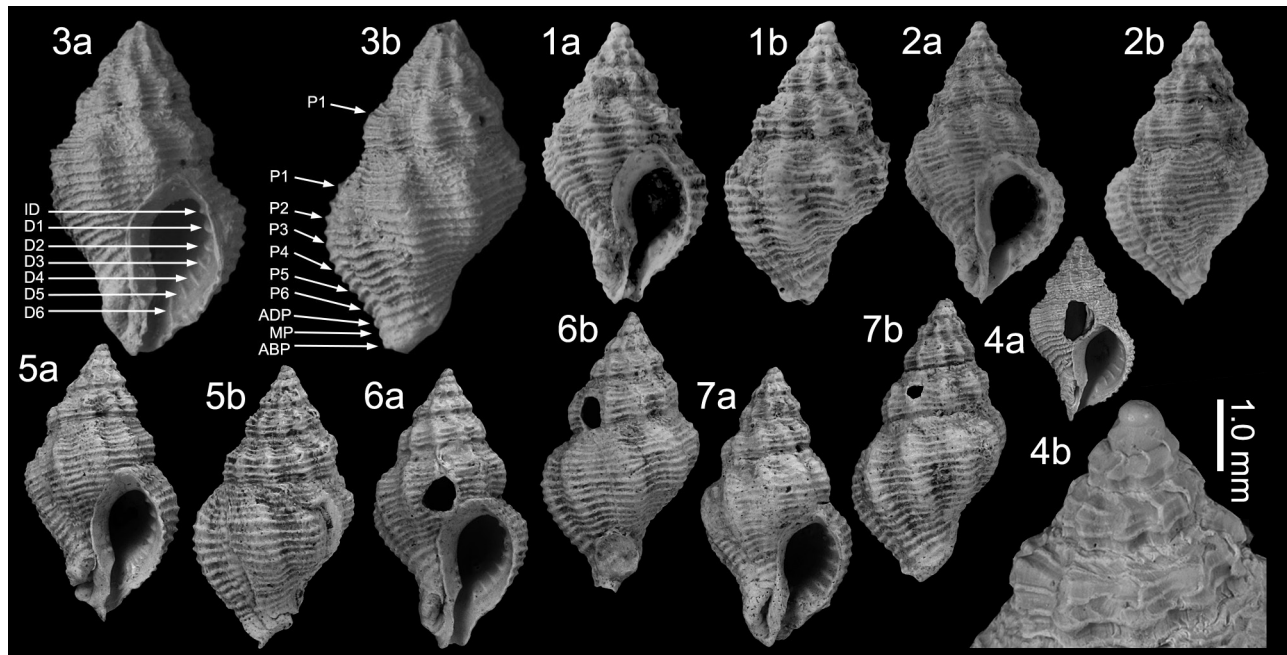


Plate 21. *Attiliosa pouweri* nov. sp.; 1. **Holotype** MNHN.F.A70995, height 11.0 mm, width 6.4 mm (photo P. Loubry); 2. Ledon coll., height 13.0 mm, width 7.3 mm (photo P. Loubry). La Presselière, Sceaux-d'Anjou; 3. **Paratype 1** NHMW 2016/0103/0784, height 12.6 mm, width 7.4 mm; 4. **Paratype 2** NHMW 2016/0103/1363, height 11.3 mm, 4b, detail of protoconch. Le Grand Chauverau, St-Clément-de-la-Place. 5. **Paratype 5** NHMW 2016/0103/1845, height 13.0 mm, width 7.2 mm; 6. **Paratype 6** NHMW 2016/0103/1846, height 13.3 mm, width 7.4 mm; 7. **Paratype 7** NHMW 2016/0103/1847, height 13.3 mm, width 7.2 mm, La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

paratype 2 NHMW 2016/0103/1363, height 11.3 mm (juvenile), **St-Clément-de-la-Place**.

Other material – Maximum height 12.6 mm, width 7.4 mm. **St-Clément-de-la-Place**: LC (1 + 1 juvenile). **Sceaux-d'Anjou**: NHMW 2016/0103/1736 (3), RGM.1348157 (2), RGM.1348826 (1); RGM.734966 (50+), RGM.1352225 (3), FVD (1). **Renauleau**: LC (3).

Etymology – Named after Ronald Pouwer, curator of fossil molluscs, Naturalis Biodiversity Center (Leiden, The Netherlands). *Attiliosa* gender feminine.

Locus typicus – La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France. The locality of Apigné (Rennes, Ille-et-Vilaine, NW France) given by Merle *et al.* (2011, p. 204) is a *lapsus*.

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Attiliosa* species of small to medium size and relatively slender for genus, with primary and secondary spiral sculpture of equal strength on last whorl, non-spinous.

Description – Shell small to medium-sized for genus, fusiform, relatively slender biconic, medium height spire about 60°. Protoconch paucispiral, composed of 1.5 smooth whorls with large nucleus. Teleoconch of four roundly shouldered whorls, with concave subsutural

ramp, separated by impressed undulating suture. Spiral sculpture on penultimate whorl; three cords on subsutural ramp, P1-P3, all of almost equal strength; spiral sculpture made scabrous by close set axial growth lines. Axial sculpture of seven rounded ribs, half width of their interspaces. Last whorl 72% of total height; subsutural platform concave bearing five narrow cords; shoulder rounded, P1-P6 and s1-s6 all of equal strength making it difficult to separate primary from secondary sculpture; base weakly constricted; siphonal fasciole ADP, MP, ABP narrow, rounded, of roughly equal strength; narrow umbilical groove. None of the spiral sculpture spinous at aperture. Aperture 46% of total height, ovate; anal canal not developed; siphonal canal short, open twisted slightly abaxially; outer lip thickened by labial varix, sharp edged, denticulate within, ID-D6 narrow, elongate, of roughly equal strength. Columella roundly excavated. Columellar callus and parietal callus continuous, thickened, sharply delimited weakly expanded, bearing three coarse tubercles abapically.

Discussion – This species was illustrated by Merle *et al.* (2011, p. 204, pl. 152, figs 10-11) as *Attiliosa* sp. 3 based on material from the Assemblage I (La Presselière, Sceaux-d'Anjou) and not Apigné as stated (*lapsus*). It differs from all its European congeners in having the primary and secondary spiral sculpture of equal strength on the last whorl. It is also rather slender and the axial ribs are relatively subdued and non-nodular compared to many congeners. As can be seen in the series illustrated

(Pl. 21, figs 1-7), there is little intraspecific variation; one of the specimens (Merle *et al.*, 2011, pl. 152, fig. 11) is weakly spinous at the shoulder.

The most similar species is *Attiliosa* sp. 2 (Merle *et al.*, 2011, pl. 152, fig. 9) from a lower Miocene assemblage from the Aquitaine Basin that differs in having a broader shell, the primary cords are stronger than the secondaries and slightly spinous at the aperture. The siphonal canal is also twisted a little more strongly abaxially. In the present-day faunas, *A. goreensis* Houart, 1993 from West Africa also has scabrous sculpture, but is broader shelled, with broader axial ribs equal in width to their interspaces, a more expanded aperture abapically and a wider umbilicus. Brébion (1964, p. 384) recorded this species from the Assemblage I locality of Sceaux-d'Anjou, to which we add St-Clément-de-la-Place and Renauleau.

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964; Merle *et al.*, 2011).

Subfamily Ocenebrinae Cossmann, 1903
Genus *Hadriana* Bucquoy & Dautzenberg, 1882

Type species (by original designation) – *Hadriana craticulata* Bucquoy & Dautzenberg, 1882, present-day, Mediterranean.

1882 *Hadriana* Bucquoy & Dautzenberg, in Bucquoy, Dautzenber & Dollfus, p. 16, 33.

***Hadriana brevituba* (Millet, 1865)**

Plate 22, figs 1-7

- 1854 *Fusus brevitubus* Millet, p. 162 (*nomen nudum*).
- *1865 *Fusus brevitubus* Millet, p. 590.
- 1964 *Hadriana craticulata* Linné, 1790 [*sic*] – Brébion, p. 389 [*non Murex craticulatus* Linnaeus 1758, now accepted as *Turriturris craticulatus* (Linnaeus, 1758 Buccinoidea (Fasciolaridae)). It is likely Brébion was referring to *Murex craticulatus* Brocchi, 1814, now accepted as *Hadriana craticulata* Bucquoy & Dautzenberg, 1882].
- 1964 *Hadriana brevituba* Millet, 1854 [*sic*] – Brébion, p. 391, pl. 9, fig. 17.
- 2016 *Hadriana brevituba* (Millet, 1865) – Ceulemans *et al.*, p. 47, pl. 3, fig. 6.

Material and dimensions – Maximum height 14.1 mm, width 6.8 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0226 (1), NHMW 2016/0103/0713-0714 (3), NHMW 2016/0103/0227 (50+), RGM.1348169 (35), RGM.1348856 (2), RGM.1349159 (13), RGM.1349220 (6), RGM.1352446 (50+), LC (50+), FVD (50+). **Sceaux-d'Anjou**: NHMW 2016/0103/1667-1669 (3), NHMW 2016/0103/0678 (50+), RGM.1348111 (24), RGM.1348128 (7), RGM.134814659 (5), RGM.1348179 (4), RGM.1348190 (8), RGM.1348766 (7), RGM.1348792 (15), RGM.1348793 (31), RGM.1348906 (13), RGM.718089 (50+), RGM.1349170 (6), LC (50+), FVD (50+). **Renauleau**: NHMW 2016/0103/1670 (18), LC (20), FVD (14).

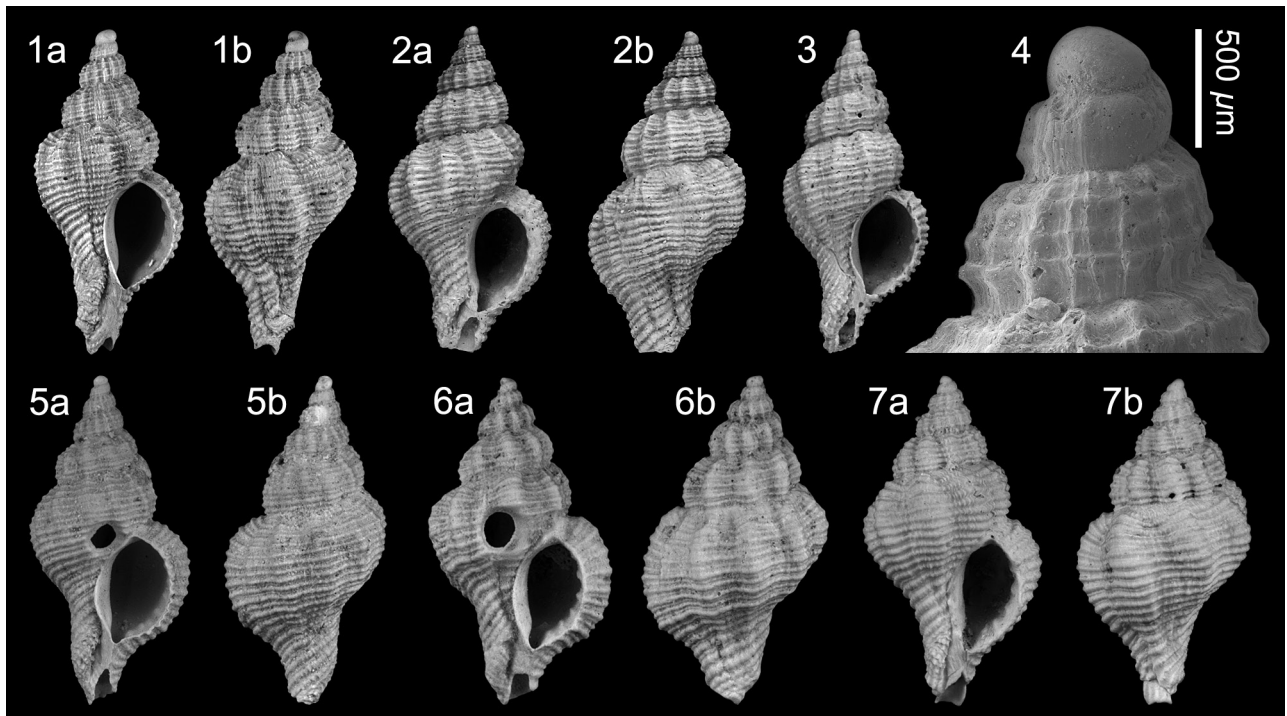


Plate 22. *Hadriana brevituba* (Millet, 1865); 1. NHMW 2016/0103/0226, height 9.3 mm, width 4.1 mm; 2. NHMW 2016/0103/0714, height 14.0 mm, width 6.6 mm; 3. NHMW 2016/0103/0715, height 12.6 mm, width 5.4 mm; 4. NHMW 2016/0103/0713, detail of protoconch (juvenile). Le Grand Chauvereau, St-Clément-de-la-Place. 5. NHMW 2016/0103/1667, height 12.3 mm, width 5.8 mm; 6. NHMW 2016/0103/1668, height 11.3 mm, width 5.8 mm; 7. NHMW 2016/0103/1669, height 10.2 mm, width 4.7 mm. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Discussion – *Hadriana brevituba* (Millet, 1865) is characterised by its relatively small sized, elongate-fusiform shell and its straight sealed siphonal canal. The protoconch was missing in the material from Le Pigeon Blanc described by Ceulemans et al. (2016), but it is well preserved in the shell illustrated from St-Clément-de-la-Place and is of paucispiral type, composed of about 1.5 whorls with a large nucleus. The small size and protoconch are the only constant characters in this species. The degree of inflation of the last whorl, length of the siphonal canal, which is sealed in fully adult specimens (open in subadult or damaged specimens), number of axial ribs (8-14), width of the spiral cords and the development of the denticles within the outer lip are all variable. It is likely that the referred to, but not illustrated, by Brébion (1964, p. 389) as *Hadriana craticulata* Linné, 1790 [sic] are this species. The present-day Mediterranean and adjacent Atlantic *H. craticulata* Bucquoy & Dautzenberg, 1882 differs in being larger-shelled, having more shouldered whorls and a bent siphonal fasciole, which may or may not be sealed. Brébion (1964, p. 392) recorded this species from Assemblage I localities (Thorigné, Sceaux-d’Anjou, St-Michel), to which we add St-Clément-de-la-Place, and the Assemblage IV locality of Gourbesville. Ceulemans et al. (2016) added the Assemblage III locality of Le Pigeon Blanc.

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

Genus *Heteropurpura* Jousseume, 1880

Type species (by original designation) – *Murex polymorphus* Brocchi, 1814. Pliocene, Italy.

1880 *Heteropurpura* Jousseume, p. 335.

Note – Vokes (1964) considered *Heteropurpura* Jousseume, 1880 a synonym of *Ocenebra* Gray, 1847. However, *Heteropurpura* differs in having strongly carinate

whorls, numerous ‘split’ denticles, narrowly elongate within the aperture and narrow spines. We therefore consider it a separate genus.

Heteropurpura polymorpha (Brocchi, 1814)

Plate 23, figs 1-3

- *1814 *Murex polymorphus* Brocchi, 1814, p. 415, pl. 8, fig. 4.
- 1924 *Ocenebra (Heteropurpura) polymorpha* var. *pliosubobtusata* Sacco – Cossmann & Peyrot, p. 515, pl. 14, fig. 24; pl. 25, fig. 4.
- 1964 *Hadriana craticulata* Linné, 1790 [sic] – Brébion, p. 389, pl. 7, figs 14, 16, ?15 (*non* Bucquoy & Dautzenberg, 1882).
- 2007 *Heteropurpura polymorpha* (Brocchi, 1814) – Landau et al., p. 28, text-fig. 7, pl. 7, figs 6-8 (*cum syn.*).
- 2000 *Heteropurpura polymorpha* (Brocchi, 1814) – Chirli, p. 32, pl. 14, figs 7-12.
- 2011 *Heteropurpura polymorpha* (Brocchi, 1814) – Landau et al., p. 22, pl. 10, figs 9, 10 (*cum syn.*).

Material and dimensions – Maximum height 18.7 mm, width 10.3 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0761-0762 (1), NHMW 2016/0103/0763 (2 + 3 juveniles), LC (5), FVD (3). **Sceaux-d’Anjou**: NHMW 2016/0103/1323 (1), RGM.1348158 (1), RGM.1348191 (1), RGM.1348794 (1), RGM.1349038 (8).

Discussion – Landau et al. (2007, p. 29) doubted the presence of true *Heteropurpura polymorpha* (Brocchi, 1814) in the Miocene. They ascribed the records of *Murex polymorphus* var. *barcinonensis* Almera & Bofill, 1893 (p. 194, pl. 6, figs 42-43) from the upper Miocene of Catalonia, Spain to *H. inflexa* (Doderlein, 1862) and the Italian upper Miocene record of *Ocenebra polymorpha* var. *pliopervaricosa* Sacco, 1904 (Montanaro, 1935, pl. 3, fig. 10), based on a juvenile specimen, of uncertain determination. They noted that the specimen illustrated by Cossmann & Peyrot (1924, pl. 14, fig. 24; pl. 25, fig. 4) from the Atlantic middle Miocene Aquitaine Basin of France as *Ocenebra (Heteropurpura) polymorpha* var. *pliosub-*

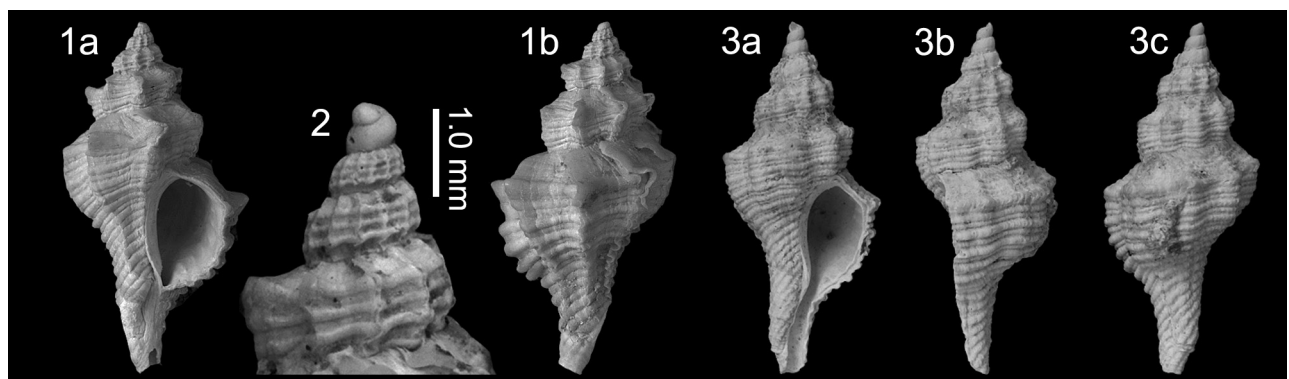


Plate 23. *Heteropurpura polymorpha* (Brocchi, 1814); 1. NHMW 2016/0103/0761, height 18.7 mm, width 10.3 mm; 2. NHMW 2016/0103/0762, detail of protoconch (juvenile). Le Grand Chauvereau, St-Clément-de-la-Place. 3. NHMW 2016/0103/1323, height 13.6 mm, width 5.9 mm, La Presselière, Sceaux-d’Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

obtusata Sacco, 1904 was smaller than typical Pliocene *H. polymorpha*, higher spired, with more numerous axial ribs, without offering an identification.

The Assemblage I specimens at hand, like almost everything from Assemblage I fauna, are small, with a maximum size of 18.7 mm, whereas Pliocene populations are typically between 25 mm and 35 mm in height (Chirli, 2001, Landau *et al.*, 2007, 2011). The spire is high, but within the range of variability seen in *H. polymorpha*. We therefore consider these Atlantic middle-upper Miocene specimens early forms of *H. polymorpha*.

As in our earlier publication (Landau *et al.*, 2007, p. 28), we reiterate the aptness of the trivial name ‘*polymorpha*’. The two specimens figured here vary in the number and strength of axial varices and in one specimen the siphonal canal is sealed, in the other, which is subadult, it is not. A similar range in shape and sculpture is seen in other populations (Chirli, 2000; Silva, 2001; Landau *et al.*, 2007), although having a sealed canal is unusual, but occurs in the occasional specimen from other assemblages as well (Sacco, 1904, pl. 5, fig. 10). The protoconch is tall, paucispiral, consisting of about 1.5 whorls with a bulbous protoconch, similar to that figured for Pliocene specimens (Landau *et al.*, 2007, pl. 7, fig. 7a, b). The protoconch described as 2.25 whorls and not 1.5 whorls by those authors is a *lapsus* (2007, p. 28).

Distribution – Middle Miocene: Atlantic, Aquitaine Basin (Cossmann & Peyrot, 1924). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, Guadalquivir Basin, Spain (González-Delgado, 1989; Landau *et al.*, 2011); western Mediterranean: north-eastern Spain (Almera & Bofill, 1893; Martinell, 1979); central Mediterranean, Italy (Bellardi, 1873; Pavia, 1975; Chirli, 2000), Tunisia (Fekih, 1975). Upper Pliocene: Atlantic, Mondego Basin, Portugal (Silva, 2001), western Mediterranean, Estepona (Muñiz-Solis & Guerra-Merchán, 1994; Landau *et al.*, 2007); central Mediterranean (Sacco, 1904; Ruggieri *et al.*, 1959; Malatesta, 1974; Caprotti, 1976; Cavallo & Repetto, 1992).

Genus *Jaton* Pusch, 1837

Type species (by original designation): – *Murex decus-*

satus Gmelin, 1791, present-day, West Africa.

1837 *Jaton* Pusch, p. 135.

Jaton dufrenoyi (Grateloup, 1845)

Plate 24, figs 1-2

*1845 *Murex Dufrenoyi* Grateloup, pl. 30, fig. 9.

2016 *Jaton dufrenoyi* (Grateloup, 1845) – Ceulemans *et al.*, p. 44, pl. 2, figs 5-7 (*cum syn.*).

Material and dimensions – Maximum height 19.1 mm, width 11.3 mm. **Sceaux-d’Anjou**: RGM.1349034 (1). **Renauleau**: NHMW 2016/0103/1774 (1), NHMW 2016/0103/1487 (2), LC (5).

Discussion – *Jaton dufrenoyi* (Grateloup, 1845) is similar to *J. sowerbyi* (Michelotti, 1841), but differs by its slightly more fusiform shell shape, and by its smaller, more elongate, and less rounded aperture. Moreover, all the specimens we have examined from Saucats (Le Peloua), France (NHMW coll.) have denticles within the outer lip, whereas all specimens we have examined of *J. sowerbyi* have a smooth outer lip. The primary cords P1, P2, P3, P5 and P6 are all relatively well developed, with P4 slightly weaker, sl is also more prominent than the rest of the secondary cords. The specimens from Assemblage I again illustrate the dwarfed nature of species found in these deposits. They are small compared to adult specimens from the lower Miocene Aquitanian and Burdigalian of the Aquitaine Basin that reach 28 mm in height (Cossmann & Peyrot, 1924, p. 450) and the lower Pliocene specimens from Assemblage I that attain 36.4 mm in height (Ceulemans *et al.*, 2016, p. 44), but judging by the strongly thickened outer lip and labial denticles, are fully adult.

Distribution – Lower Miocene (Aquitanian and Burdigalian): Aquitaine Basin, France (Cossmann & Peyrot, 1924; Lozouet *et al.*, 2001). Lower-middle Miocene: Proto-Mediterranean, France (Goret & Pons, 2013). Middle Miocene: Atlantic, Loire Basin, France (Glibert, 1952). Upper Miocene: Atlantic (Tortonian), NW France (this paper). Upper Pliocene: Atlantic, north western France (Ceulemans *et al.*, 2016).

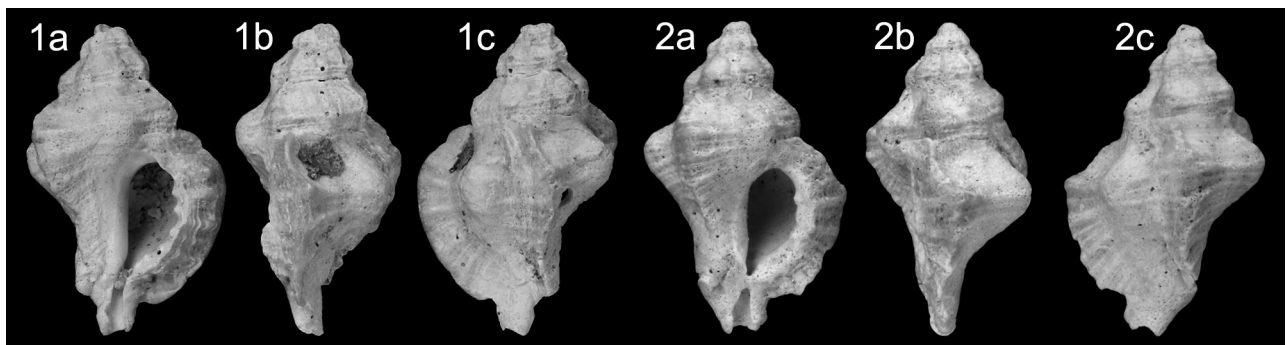


Plate 24. *Jaton dufrenoyi* (Grateloup, 1845); 1. NHMW 2016/0103/1774, height 18.1 mm, width 11.1 mm; 2. LC coll., height 16.7 mm, width 10.4 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Genus *Ocinebrina* Jousseume, 1880

Type species (by original designation) – *Murex corallinus* Scacchi, 1836, present-day, eastern Atlantic, Mediterranean.

1880 *Ocinebrina* Jousseume, p. 332.

For generic synonymy see Ceulemans *et al.* (2016, p. 45).

Note – The European Neogene *Ocinebrina* species are in need of revision. Many trivial taxa have been erected, often without adequate comparison with species in other Neogene basins and without taking into account the important intraspecific variability seen within most members of the genus. Molecular models based on extant *Ocinebrina* species and careful morphometrics of extinct species would help to revise their classification.

Ocinebrina coelata (Dujardin, 1837)

Plate 25, figs 1-3

- *1837 *Fusus coelatus* Dujardin, p. 294, pl. 19, fig. 1.
- 1886 *Murex (Ocinebra) coelata* Dujardin – Dollfus & Dautzenberg, p. 104.
- 1938 *Hadriana coelata* Dujardin – Peyrot, p. 191, pl. 4, figs 61, 68.
- 1952 *Tritonalia (Hadriana) coelata* Dujardin, 1837 – Glibert, p. 304, pl. 7, fig. 3.
- 1964 *Ocinebrina cossmanni* nom. nov. – Brébion, p. 386, pl. 9, fig. 12 (*nomen nudum*).
- ?1964 *Hadriana coelata* Dujardin, 1837 – Brébion, p. 389.

Material and dimensions – Maximum height 11.6 mm, width 5.8 mm. **Renauleau**: NHMW 2016/0103/1770-1772 (3), NHMW 2016/0103/1773 (6), LC (8), FVD (10).

Discussion – *Ocinebrina coelata* (Dujardin, 1837) from Renauleau is characterised by its slender shell, non-shouldered whorls, narrow aperture and sealed siphonal canal. Unfortunately, all specimens are worn and the protoconch is not preserved, but sculpture consists

of seven low, rounded ribs crossed by narrow cords of alternate strength. This species was originally described from the middle Miocene Langhian Loire Basin from Louans, near St-Catherine-de-Fierbois. In his revision of the Loire Basin assemblages Glibert (1952, p. 304, pl. 7, fig. 3) noted that none of the specimens he had at hand were as slender and narrow as the originally figured specimen would suggest. He figured a number of forms showing considerable variability in shell shape and shoulder strength. The specimen figured by Peyrot (1938, pl. 4, figs 61, 68), also from St-Catherine-de-Fierbois, is quite unlike the specimen figured by Dujardin (1837, pl. 19, fig. 1). It is interesting therefore that the specimens from Renauleau are all closely similar to the original figure. Brébion (1964, pl. 9, fig. 12) figured a specimen from Renauleau as *Ocinebrina cossmanni* nom. nov. (*nomen nudum*), which he introduced for *Ocenebra (Ocinebrina [sic]) cf. renierii* in Cossmann & Peyrot (1924, p. 512, pl. 15, figs 7, 8) from the middle Miocene Langhian of the Aquitaine Basin. That specimen is less slender than those from Renauleau and we consider them conspecific. Brébion (1964, p. 389) also attributed a single specimen from Thorigné to *O. coelata*, which he said was the typical form for the species as designated by Glibert (1952, figs 3a, b), not the slender form. This specimen was not figured and is therefore added in the chresonymy with some reservation.

Similarly slender specimens from the middle Miocene Paratethys were identified by Bałuk (1995, pl. 28, figs 2-3) as *Hadriana excoelata* (Cossmann & Peyrot, 1924), but twice the size of the Renauleau shells. The type locality of *Ocinebrina excoelata* is the lower Miocene Burdigalian locality of Léognan in the Aquitaine Basin, France. Lozouet *et al.* (2001, p. 56) briefly reviewed that species, adopting a broad species concept, and placed in synonymy many of the lower Miocene Aquitaine Basin *Ocinebrina* species described by Cossmann & Peyrot (1924). Lozouet *et al.* (2001) showed that *O. excoelata* has a multispiral protoconch, which suggests planktotrophic development, and hence the possibility of a wider geographic and stratigraphic range. However, none of the forms illustrated by Cossmann & Peyrot (1924) and synonymised with *O. excoelata* by Lozouet *et al.* (2001) have the elongated shell form seen in the shells from Renauleau.

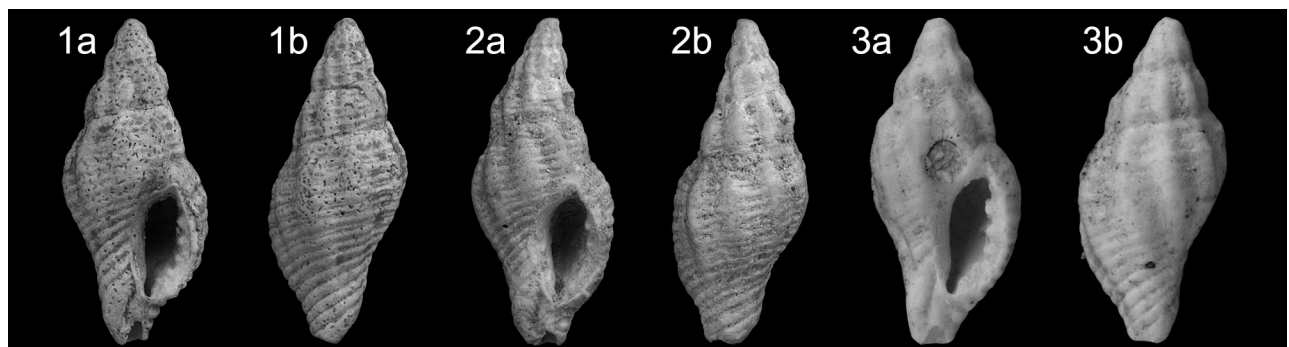


Plate 25. *Ocinebrina coelata* (Dujardin, 1837); 1. NHMW 2016/0103/1770, height 10.9 mm, width 4.7 mm; 2. NHMW 2016/0103/1771, height 11.1 mm, width 4.7 mm; 3. NHMW 2016/0103/1772, height 7.8 mm, width 3.5 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Brébion (1964, p. 389) recorded this species from the Assemblage I localities of Renauleau and St-Clément-de-la-Place (possibly Thorigné; see discussion above) and the Assemblage II locality of Apigné.

Distribution – Middle Miocene: Atlantic, Loire Basin, France (Dujardin, 1837; Dollfus & Dautzenberg, 1886; Peyrot, 1938; Glibert, 1952). Upper Miocene: Atlantic (Tortonian), NW France (Brébion, 1964).

Ocinebrina* aff. *helleri (Brusina, 1865)

Plate 26, figs 1-4

aff.*1865 *Fusus helleri* Brusina, p. 8.

aff. 2001 *Ocinebrina helleri* (Brusina, 1865) – Houart, p. 64, figs 12-13, 85, 343-347.

Material and dimensions – Maximum height 8.6 mm, width 3.8 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0767-0770 (4), NHMW 2016/0103/0771 (37), RGM.1348170 (29), RGM.1348530 (1), LC (10), FVD (14). **Renauleau:** NHMW 2016/0103/1674 (15), LC (20), FVD (22).

Description – Shell small, slender fusiform, with tall scalate spire. Protoconch paucispiral, composed of 1.5 smooth whorls. Teleoconch of 4.5 whorls with broad, flat, steeply sloping subsutural platform, weakly convex below, separated by impressed, weakly undulating suture. Axial sculpture of 8-10 low rounded ribs, half width of their interspaces. Spiral sculpture scabrous, penultimate whorl; IP developed on subsutural platform, P1-P3, s1-s2 below shoulder. Last whorl slender to moderately inflated, obtusely-angled to rounded at shoulder, moderately constricted at base, base not sharply delimited; IP, adis, abis well-developed on subsutural platform, P1-P6, s1-s6 well-developed; siphonal canal moderate length bearing ADP, MP and ABP. Aperture ovate, outer lip moderately thickened by varix, bearing weak ID, D1-D5 well-developed; anal canal rounded, poorly delimited; siphonal ca-

nal of moderate length, sealed in fully adult specimens, tip bent posteriorly.

Discussion – This unremarkable little ocinebrine is characterised by its relatively slender fusiform shape, spiral cords of alternate strength and moderate length open or sealed siphonal canal. A paucispiral protoconch of about 1.5 whorls is a generic character (Houart, 2001, p. 59). Like most of its congeners, it is rather variable in shape; in some specimens the last whorl is inflated, and the siphonal canal is sealed in fully adult specimens. It is similar to the present-day northern Adriatic *Ocinebrina helleri* (Brusina, 1865), but the maximum height is less than half that of the extant species (8.6 mm vs. 20 mm; Houart, 2001, p. 64) and the last whorl is generally more inflated in the living species. The Pliocene (Chirli, 2000) to present-day eastern Atlantic and Mediterranean *O. aciculata* (Lamarck, 1822), which can be extremely variable in shape is also similar, but differs in having primary and secondary spiral cords of equal strength and the base is often, although not always, delimited by a stronger peribasal cord. A strong peribasal cord is a character seen in numerous *Ocinebrina* species, but not in the French Assemblage I material described herein. *Ocinebrina carvalhoi* (Cox, 1936) from the Atlantic lower Piacenzian Pliocene of the Mondego Basin is also a relatively small slender ocinebrine with spiral cords of alternate strength (Landau *et al.*, 2007, pl. 8, fig. 2), but has only D1-D4 developed, the whorls are more regularly rounded separated by a more superficial suture and the base is slightly more strongly delimited. *Ocinebrina renieri* (Michelotti, 1847) from the lower-middle Miocene Proto-Mediterranean of Italy and the shell figured as *O. cf. renieri* from the middle Miocene Aquitaine Basin of France by Cossmann & Peyrot (1924, pl. 15, figs 7, 8) differ in having a more conical spire and primary and secondaries of subequal strength.

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

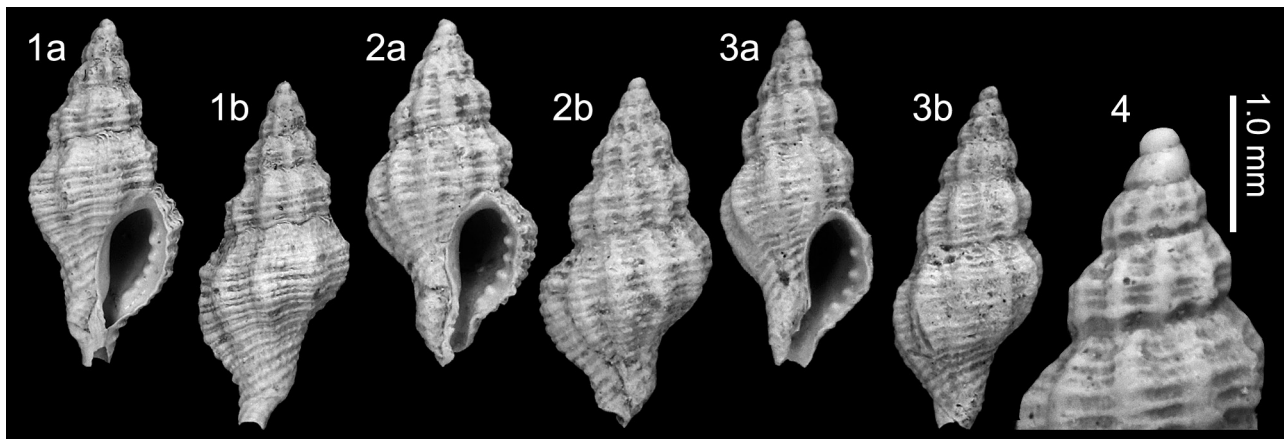


Plate 26. *Ocinebrina* aff. *helleri* (Brusina, 1865); 1. NHMW 2016/0103/0767, height 8.6 mm, width 3.8 mm; 2. NHMW 2016/0103/0768, height 6.7 mm, width 3.3 mm; 3. NHMW 2016/0103/0769, height 6.8 mm, width 2.9 mm; 4. NHMW 2016/0103/0770, height 6.8 mm, width 2.9 mm, detail of protoconch. Le Grand Chauvereau, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

***Ocinebrina houarti* nov. sp.**

Plate 27, figs 1-4

Type material – Holotype NHMW 2016/0103/0783, 8.4 mm, width 4.5 mm; paratype 1 NHMW 2016/0103/1855, length 8.5 mm, width 5.1 mm; paratype 2 RGM.719015, height 8.0 mm, width 5.1 mm; paratype 3 RGM.1349093, height 8.1 mm, width 4.9 mm; paratype 4 RGM.1349094, height 8.0 mm, width 5.0 mm; paratype 5 RGM.1349095, height 7.9 mm, width 4.9 mm; paratype 6 RGM.1349097, juvenile.

Other material – Maximum length 8.5 mm, width 5.1 mm. **St-Clément-de-la-Place:** LC (1 adult). **Sceaux-d'Anjou:** RGM.1349096 (2 + 1 juvenile).

Etymology – Named after Roland Houart, Research Associate at the Institut royal des Sciences naturelles de Belgique (Brussels) in recognition of his enormous contribution to muricid taxonomy. *Ocinebrina* gender feminine.

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

Stratum typicum – Tortonian, upper Miocene.

Diagnosis – *Ocinebrina* species of small size, paucispiral protoconch, three shouldered teleoconch whorls, strongly cancellate sculpture, small ovate aperture, outer lip denticulate within, sealed siphonal canal.

Description – Shell small, inflated, with low, strongly scalate spire. Protoconch bulbous, paucispiral, composed of 1.5 smooth whorls, with large nucleus. Boundary with teleoconch sharply delimited. Three low teleoconch whorls preserved with narrow, sub-horizontal subsutural ramp, convex below. Axial sculpture of 12 elevated, rounded ribs, about half width of their interspaces, axial sculpture slightly predominant; rib one-quarter whorl be-

fore labial varix on last whorl strongly varicose. Spiral sculpture on penultimate whorl; P1-P3 narrow, elevated. Last whorl inflated, moderately constricted at base, long smooth siphonal canal; IP on subsutural platform, P1-P6 well-developed, s1-s6 developed on last quarter whorl; sculpture forming elevated cancellate pattern, with axial component slightly predominant. Aperture ovate, outer lip regularly convex, thickened by labial varix, bearing ten elongated denticles within; anal canal shallow, rounded; siphonal canal relatively long, sealed, bent abaxially.

Discussion – Paratype 6 is a juvenile with a well preserved protoconch (Pl. 27, fig. 4). We are fairly certain this shell represents a juvenile of *Ocinebrina houarti* nov. sp., but cannot be totally certain due to the very immature state. Although the shape and sculpture of this species superficially resembles some species within the Trophoninae Cossmann, 1903, the siphonal canal is sealed, which places it in *Ocinebrina* Jousseume, 1880. *Ocinebrina houarti* is characterised by its small size for the genus, paucispiral protoconch and strongly cancellate teleoconch sculpture. The series illustrated (Pl. 27, figs 1-3) shows slight variation in the globosity of the last whorl and the length of the siphonal canal, but otherwise the species is relatively constant in shape and sculpture. It is difficult to find species with which to compare. None of the extant northeastern Atlantic *Ocinebrina* species illustrated by Houart (2001) have cancellate sculpture, neither do the lower Miocene French Atlantic species from the Aquitaine Basin illustrated by Lozouet *et al.* (2001) under *Ocenebra*, some of which we would consider to be *Ocinebrina* (i.e. *Ocenebra excoelata* Cossmann & Peyrot, 1924, *O. sublavata* (de Basterot, 1825), *O. suberinacea* (de Basterot, 1825), *O. cf. cazeauxi* Cossmann & Peyrot, 1924). Similarly, no cancellate forms occur in the Neogene of Italy (Bellardi, 1873), nor in the Miocene Paratethys (Hörnes, 1853; Hoernes & Auinger, 1885; Bałuk, 1995). *Ocinebrina houarti* is uncommon in Assemblage I and found so far only at St-Clément-de-la-Place and La Presselière.

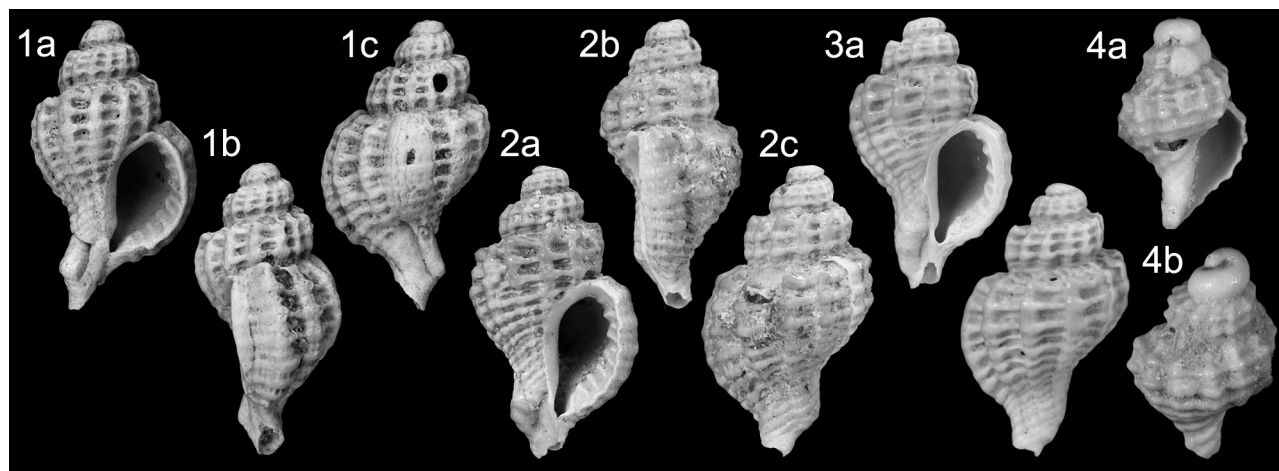


Plate 27. *Ocinebrina houarti* nov. sp.; 1. **Holotype** NHMW 2016/0103/0783, height 8.4 mm, width 4.5 mm; 2. **Paratype 1** NHMW 2016/0103/1855, length 8.5 mm, width 5.1 mm; 3. **Paratype 2** RGM.719015, height 8.0 mm, width 5.1 mm; 4. **Paratype 6** RGM.1349097. La Presselière, Sceaux-d'Anjou, Maine-et-Loire, NW France, Tortonian, upper Miocene.

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

Ocinebrina lauriatrageae Ceulemans, Van Dingenen, Merle & Landau, 2016
Plate 28, figs 1-2

- 1918 *Ocinebra* [sic] (*Ocinebrina*) *funiculosa* (Borson) – Harmer, p. 348, pl. 36, fig. 1 (not fig 2 = *Ocinebrina funiculosa*) [non *Ocinebrina funiculosa* (Borson, 1821)].
- 1964 *Ocinebrina incincta* Dollfus mss. – Brébion, p. 384, pl. 9, figs 10, 11 (*nomen nudum*).
- *2016 *Ocinebrina lauriatrageae* Ceulemans, Van Dingenen, Merle & Landau, p. 45, text-fig. 2, pl. 3, figs 2-5.

Material and dimensions – Maximum height 16.7 mm, width 9.7 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0224-0225 (2), LC (6), FVD (3). **Sceaux-d'Anjou**: NHMW 2016/0103/1706 (2), RGM.1348192 (3 subadults), RGM.1348946 (3), RGM.1349031 (4), RGM.718088 (47 subadult + juveniles). **Renaleau**: FVD (1).

Discussion – As discussed by Ceulemans *et al.* (2016, p. 47), *Ocinebrina lauriatrageae* Ceulemans, Van Dingenen, Merle & Landau, 2016, described from the lower Pliocene Assemblage III locality of Le Pigeon Blanc, bears features intermediate between those of *Ocinebrina* Jousseau, 1880 and *Ocenebra* Gray, 1847, applying to the latter the more restricted generic concept of Vermeij & Vokes (1997, p. 72) ‘a relatively small number of Miocene to present-day species from western Europe, the Mediterranean region and Tropical West Africa. These are characterized by the tendency

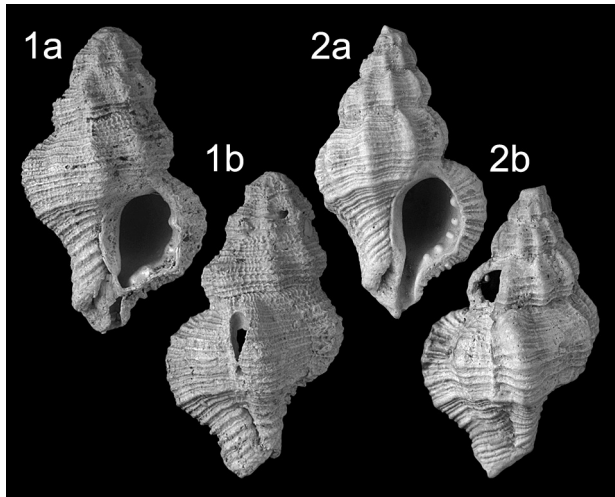


Plate 28. *Ocinebrina lauriatrageae* Ceulemans, Van Dingenen, Merle & Landau, 2016. 1. NHMW 2016/0103/0224, height 16.7 mm, width 9.7 mm; 2. NHMW 2016/0103/0225, height 12.5 mm, width 7.2 mm. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

to form three varices on the last whorl, by the presence of six to eight primary spiral cords on the last whorl, a crenulated outer lip without a labral tooth, an adherent or very lightly erect inner lip, and six weak to strong denticles on the inner side of the outer lip. In species with varices, the latter are separated from each other by a single intervarical node’. The varices are weakly developed in *O. lauriatrageae* when compared with some of its lower Miocene congeners from the Aquitaine Basin (see Lozouet *et al.*, 2001, pl. 22, figs 6-7, pl. 23, figs 1-8) but nevertheless, they are present. However, there is more than one intervarical node and there are only four well-developed denticles within the outer apertural lip. The presence of a well-delimited P4, marking an abrupt change in whorl profile from convex above the basal cord to concave below, is common to several European *Ocinebrina* species, such as the Pliocene Mediterranean and adjacent Atlantic *O. conserpta* (Bellardi, 1873), but *O. lauriatrageae* can be separated from most of its European fossil and present-day congeners by its rather slender fusiform shape, with an elevated spire and by the presence of only four denticles within the outer lip, although we note that one of the upper Miocene specimens from St-Clément-de-la-Place has five (Pl. 28, fig. 2). This species has not been recorded from the older Assemblage I deposits before, where it seems much more uncommon. Furthermore, the average size of the upper Miocene specimens is half to two-thirds that of the lower Pliocene shells (maximum height, Miocene: 16.7 mm; Pliocene: 27.3 mm).

Distribution – Upper Miocene: Atlantic (Tortonian), NW France (this paper). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016). Pleistocene: St Erth, England (Harmer, 1918).

Genus *Pteryropsis* Vokes, 1972

Type species (by original designation) – *Pteryropsis prosopeion* Vokes, 1972 (*nom. nov. pro Murex nysti* von Koenen, 1867; *non* Rouault, 1850), Miocene, Germany.

1972 *Pteryropsis* Vokes, p. 3.

Pteryropsis subcontabulata (Millet, 1854)
Plate 29, figs 1-3

- *1854 *Murex subcontabulatus* Millet, p. 163.
1865 *Murex subcontabulatus* Millet, p. 592.
1905 *Murex torquis* Dollfus, p. 367.
1906 *Murex torquis* Dollfus, p. 311.
1907 *Murex subcontabulatus* Millet – Couffon, p. 185.
1908 *Murex contabulatus* Lmk. var. – Couffon, p. 56 (*non* Lamarck, 1803).
1914 *Ocinebra erinacea* var. *minor* Harmer, p. 125, pl. 12, figs 9-11.
1915 *Murex torquis* G. Dollfus – Couffon, p. 47.
1918 *Ocinebra erinacea* var. *minor* F.W. Harmer – Har-

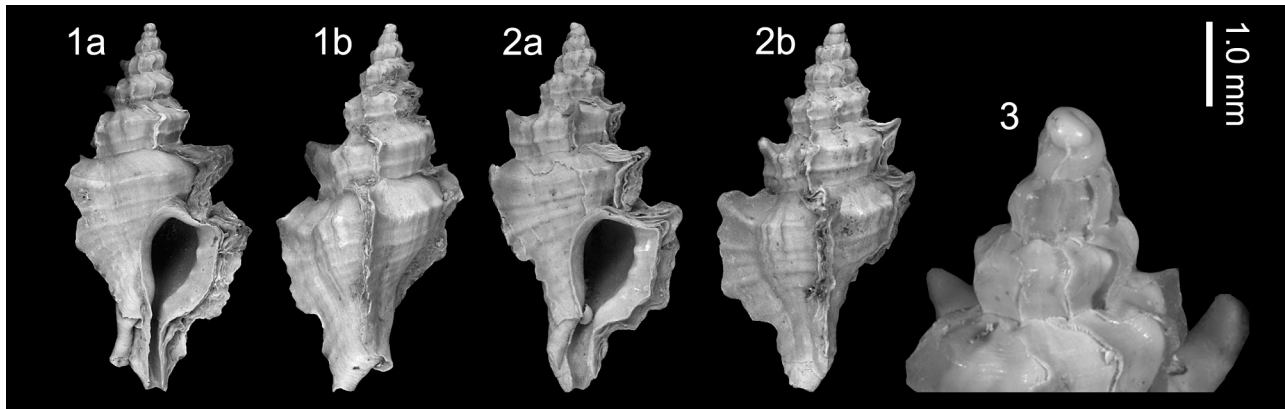


Plate 29. *Pteryagnosis subcontabulata* (Millet, 1854); 1. NHMW 2016/0103/0741, height 20.0 mm, width 9.0 mm; 2. NHMW 2016/0103/0742, height 16.2 mm, width 8.3 mm; 3. NHMW 2016/0103/0743, height 13.6 mm, width 6.6 mm (juvenile), detail of protoconch. Le Grand Chauvreaux, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

mer, p. 343, pl. 35, fig. 9.

- 1964 *Pteryagnosis* (*Pterochelus*) *canhami* (?) var. *minor*
Harmer, 1914 – Brébion, p. 367, pl. 8, figs 30, 31.
2016 *Pteryagnosis subcontabulata* (Millet, 1854) – Ceulemans *et al.*, p. 43, pl. 2, figs 2-4.

Material and dimensions – Maximum height 20.0 mm, width 9.0 mm. **St-Clément-de-la-Place:** NHMW 2016/0103/0741-0743 (3), NHMW 2016/0103/0744 (40), RGM.1348162 (11), RGM.1348333 (4 + 6 juveniles), RGM.1348632 (3), RGM.1348858 (1), RGM.1349222 (3 fragments), LC (41 + 55 juveniles), FVD (50+). **Sceaux-d’Anjou:** NHMW 2016/0103/0745 (31), RGM.1348099 (34), RGM.1348108 (3), RGM.1348109 (17), RGM.1348116 (3 subadults + 50+ juveniles), RGM.1348121 (18 juveniles), RGM.1348125 (1), RGM.1348132 (6 juvenile), RGM.1348140 (2), RGM.1348148 (38), RGM.1348180 (50+), RGM.1348182 (18), RGM.1348374 (14), RGM.1348911 (31), RGM.718076 (50+), LC (15), FVD (20). **Renauveau:** NHMW 2016/0103/1409 (1), LC (2).

Discussion – Specimens from St-Clément-de-la-Place are beautifully preserved. The protoconch is tall, paucispiral, composed of just under two whorls, with a large nucleus (Pl. 29, fig. 3); the first whorl coiled obliquely in respect to the central shell axis. As is the case for almost all the muricids, the Assemblage I specimens are somewhat smaller than those found in the younger lower Pliocene Assemblage III. For full discussion see Ceulemans *et al.* (2016, p. 43).

Brébion (1964, p. 369) recorded this species from Assemblage I localities (Thorigné, Sceaux-d’Anjou, St-Clément-de-la-Place, St-Michel), Assemblage III (Le Girondor, Le Pigeon Blanc, Palluau) and Assemblage IV (St-Jean-la-Poterie, Gourbesville).

Distribution – Upper Miocene (Tortonian): Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016); NSB, Coralline Crag, England (Harmer, 1914). Upper Pliocene: NSB, Red Crag, England (Harmer, 1914). Upper Plio-

cene-Pleistocene: Atlantic, NW France (Brébion, 1964). Pleistocene: Isle of Man, England (Harmer, 1914).

Genus *Spinucella* Vermeij, 1993

Type species (by original designation) – *Purpura tetragona* J. de C. Sowerby, 1825, Pliocene, British Isles.

1993 *Spinucella* Vermeij, p. 20.

Spinucella cf. *cancellata* (Bellardi, 1882)

Plate 30, fig. 1

cf. 1882 *Monoceros cancellatus* Bellardi, p. 191, pl. 12, fig. 3.

cf. 2007 *Spinucella cancellata* (Bellardi, 1882) – Landau *et al.*, p. 39, pl. 10, figs 5-7, pl. 11, fig. 6 (*cum. syn.*).

Material and dimensions – Height 40.2 mm (incomplete fragment with portion of spire, most of last whorl and outer lip preserved). **Renauveau:** LC (1 fragment).

Discussion – The single incomplete specimen at hand can confidently be ascribed to the genus *Spinucella* Vermeij, 1993 characterised by its spinous labial tooth placed abapically, in having the rest of the labial denticles on the inner surface of the outer lip close to the edge of the lip and its reticulated surface sculpture.

The earliest member of the genus, *S. angulata* (Dujardin, 1837), from the Langhian middle Miocene of the Loire Basin of France, is smaller shelled than the rest of its congeners, less globose, with a less expanded outer lip and stronger, more elevated axial sculpture. *Spinucella benoisti* (Degrange-Touzin, 1894) from the Serravallian middle Miocene Aquitaine Basin in France is also small shelled. Apart from the size difference, it seems to differ from the Assemblage I species in being lower spired, having a narrower aperture and less expanded outer lip, however, we have not seen that species.

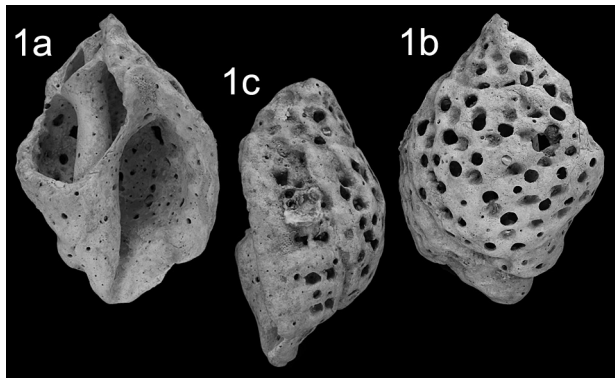


Plate 30. *Spinucella cancellata* (Bellardi, 1882); LC coll., height 40.2 mm. Renauleau, Maine-et-Loire, NW France, Tortonian, upper Miocene.

Peyrot (1938, p. 198) described but did not figure a thaid from the Langhian middle Miocene of the Loire Basin of France as *Purpura (Polytropicalicus) dautzenbergi*. We have not seen this species, which according to Peyrot is extremely uncommon and always poorly preserved, but we do not think it is the same as the species discussed here, as Peyrot wrote in his discussion of *P. (P.) dautzenbergi* ‘*Bien distincte de P. [Purpura] angulata notamment par l’absence, sur le labre, à l’origine du canal d’un dentelon conique [dans?] la présente espèce, ...* (1938, p. 198). He is referring to the spinous labral tooth characteristic to the genus *Spinucella* and present in *S. angulata* and the Assemblage I specimen, but evidently not in *P. (P.) dautzenbergi*.

Two closely similar species occur in the Mediterranean Pliocene; *Spinucella cancellata* (Bellardi, 1882) and *Spinucella monacanthos* (Brocchi, 1814). In its typical form *S. cancellata* is larger, with a more depressed spire, the last whorl is more expanded and the aperture larger, the sculpture of the spiral cords are broader and the axial elements more indistinct than in *S. monacanthos*. Unusually for the genus, the denticulation within the outer lip is mostly absent in *S. cancellata*, although the labral tooth is more strongly developed than in *S. monacanthos* (Landau *et al.*, 2007, p. 39). The single incomplete shell at hand from the Assemblage I locality of Renauleau shows signs of transport and is heavily bioeroded and perforated. The labial tooth is strongly developed as in *Spinucella cancellata*, but the rest of the denticles within the outer lip are stronger than those seen in *S. cancellata*. Despite being incomplete, the spire portion preserved suggests the shell was lower spired than *S. monacanthos*.

Spinucella plessisi (Lecointre, 1952) from the Late Pliocene to Late Pleistocene of Morocco and the Canaries is also rather variable in shape and in the development of its sculpture. Lecointre (1952) figured a range of forms from smooth, which he called *Purpura (Acanthina) crassilabrum* Lam. to strongly sculptured, which he called *Purpura (Acanthina) plessisi* and *Purpura (Acanthina) nicklesi* Lecointre, 1952. Brébion (1974, 1979a, b) and Meco (1981) synonymised all these forms. The species seems much more closely related to the Mediterranean

Spinucella-group of *S. cancellata* and *S. monacanthos* than to the North Sea Basin *Spinucella tetragona* (J. de C. Sowerby, 1825), sharing the squat shape, solid shell and large, inflated last whorl. The Moroccan material is again poorly preserved, and some of the forms illustrated by Lecointre (1952) are extremely similar to *S. cancellata*, however, *S. plessisi* seems to have an even thicker shell and the pseudo-umbilical chink is not developed. *S. plessisi* appears in the fossil record after *S. cancellata*, from which it may be descended. Cuerda Barceló (1987) figured a specimen as *Acanthina plessisi* from the Pleistocene of the Balearic Islands. Again the shell is worn; there seems to be no umbilical chink, but otherwise it is very similar to some forms of *S. cancellata*. Silva (2001) recorded *S. plessisi* from the Pliocene Mondego Basin of Portugal. The specimen figured is juvenile and poorly preserved, it has a lower spire, similar to some juvenile specimens of *S. cancellata*. Silva (2001) was unsure of the difference between *S. cancellata* and *S. plessisi*, and in view of the great variability seen in the two shells, suggested the latter might be a junior synonym. Unfortunately we have not seen any material from Morocco to give a definite opinion.

This genus is endemic to the Neogene European North Sea Basin, Atlantic frontage including the Atlantic coast of Morocco and Mediterranean. It is therefore not surprising to find it represented in the Assemblage I fauna and it may represent a further undescribed species, but we await complete specimens to better characterise the species.

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

Subfamily Typhinae Cossmann, 1903

Genus *Typhinellus* Jousseume, 1880

Type species (by original designation) – *Murex sowerbyi* Broderip, 1833 (= *Murex labiatus* de Cristofori & Jan, 1832), Pliocene to present-day, Mediterranean, eastern and western Atlantic.

1880 *Typhinellus* Jousseume, p. 335.

Typhinellus labiatus (de Cristofori & Jan, 1832)

Plate 31, fig. 1

* 1832 *Murex labiatus* de Cristofori & Jan, p. 11.

2016 *Typhinellus labiatus* (de Cristofori & Jan, 1832) – Ceulemans *et al.*, p. 48, pl. 3, fig. 7 (*cum syn.*).

Material and dimensions – Maximum height 24.2 mm, width 12.1 mm. **St-Clément-de-la-Place**: NHMW 2016/0103/0221 (1), NHMW 2016/0103/0222 (11), RGM.1348231 (3 subadult + 6 juveniles), RGM.1348332 (1 + 3 juveniles), RGM.1349223 (1 fragment), LC (10 + 13 juveniles), FVD (10). **Sceaux-d’Anjou**: NHMW 2016/0103/0223 (4), RGM.1348110 (8), RGM.1348126 (1 +

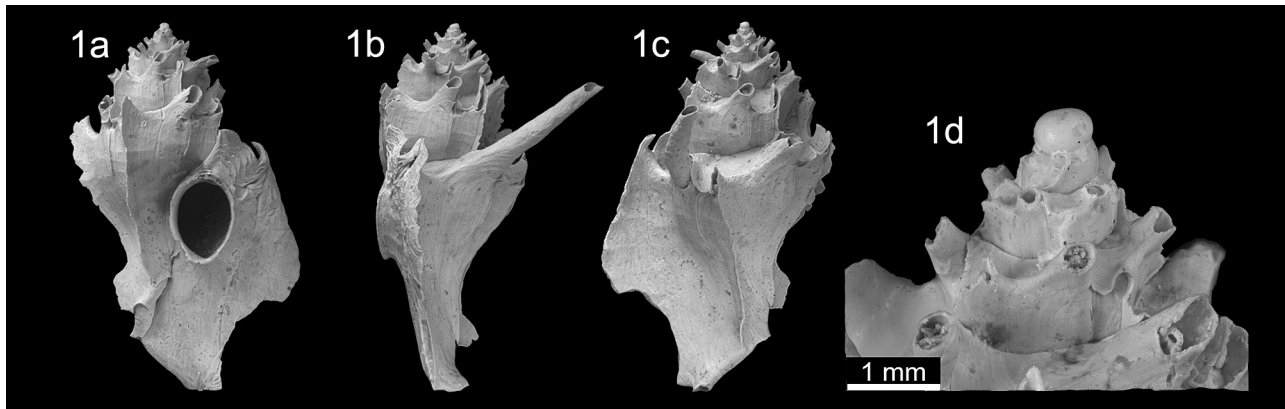


Plate 31. *Typhinellus labiatus* (de Cristofori & Jan, 1832). 1. NHMW 2016/0103/0221, height 24.2 mm, width 12.1 mm; 1d. detail of protoconch. Le Grand Chauvère, St-Clément-de-la-Place, Maine-et-Loire, NW France, Tortonian, upper Miocene.

3 fragments), RGM.1348177 (2), RGM.718081 (4 + 30 subadult and juveniles), LC (2), FVD (3). **Renaleau:** NHMW 2016/0103/1408 (16), LC (44), FVD (25).

Discussion – Houart (2015) described the Caribbean specimens as a distinct species *Typhinellus jacolombi*. *Typhinellus labiatus* differs from the Caribbean species in having a generally smaller shell, which is narrower compared to its length, with a length/width ratio of 1.68–1.77 compared to 1.50–1.72 in *T. jacolombi* and in having a different spiral sculpture morphology. *Typhinellus labiatus* has the primary cords IP to MP with s2 in all shells and an occasional s4. *Typhinellus jacolombi* n. sp., always has a s2 spiral cord, often s3, less often s4 and rarely s5 and abs. Lastly, *T. labiatus* has a less broad and less expanded apertural wing abapically and a more constricted last teleoconch whorl (Houart, 2015, p. 431). Therefore, the Caribbean Miocene to present-day specimens identified in the literature as *T. labiatus* are transferred to *T. jacolombi* Houart, 2015.

Brébion (1964, p. 375) recorded *T. labiatus* from Assemblage I localities (Thorigné, Sceaux-d'Anjou, St-Clément-de-la-Place, Beaulieu), Assemblage II (Apigné, Le Temple du Cerisier) and Assemblage III (Le Girondor, Le Pigeon Blanc, Palluau, La Dixmérie).

The specimens from the Assemblage I localities are small compared to those recorded from Assemblage III by Ceulemans *et al.* (2016); the average height half that of the shells from Le Pigeon Blanc.

Distribution – Middle Miocene: northeastern Atlantic (Langhian): Loire Basin, France (Glibert, 1952); Paratethys (Langhian-Serravallian): Austria (Hörnes, 1853; Hörnes & Auinger, 1885; Schultz, 1998), Hungary (Strausz, 1966), Poland (Bałuk, 1995), Romania (Csepregy-Meznerics, 1956); Proto-Mediterranean Sea (Serravallian): Karaman Basin, Turkey (Landau *et al.*, 2013). Upper Miocene: Atlantic (Tortonian and Messinian): Atlantic, NW France (Brébion, 1964). Lower Pliocene: Atlantic, NW France (Brébion, 1964; Ceulemans *et al.*, 2016); western Mediterranean, France (Goret *et al.*, 2013); western Mediterranean, Estepona Basin, Spain (Landau *et al.*, 2007);

central Mediterranean, Italy (Chirli, 2000), Tunisia (Fekih, 1975). Lower-upper Pliocene: central Mediterranean (Sacco, 1904; Ruggieri *et al.*, 1959; Caprotti, 1976; Cavallo & Repetto, 1992; Andreoli & Marsigli, 1992). Lower Pleistocene: central Mediterranean, Italy (Cerullirelli, 1911). Present-day: Mediterranean, adjacent Atlantic coast, West Africa to São Tomé and Príncipe (Houart *et al.*, 2011).

Discussion

In this paper we record thirty species of Muricidae (of which four are left in open nomenclature), representing 18 genera. This is an increase from the 22 species recorded by Brébion (1964) from the Assemblage I localities of NW France. Five are described as new: *Paziella (Flexopteron) gallica* nov. sp., *Paziella (Flexopteron) gracilentia* nov. sp., *Attiliosa gallica* nov. sp., *Attiliosa pouweri* nov. sp. and *Ocinebrina houarti* nov. sp.

Of the 30 muricid species recorded here, 12 (40%) occur exclusively in northwestern French Assemblage I-III deposits and are therefore restricted stratigraphically and geographically. If we include the middle Miocene, 15 (50%) are restricted to northwestern France. Stratigraphically (see Fig. 1), 14 (47%) of the species found in the Assemblage I deposits are found in the middle Miocene Langhian of the Loire Basin (see Glibert, 1952). 14 species (47%) are also present in the Assemblage III (sensu Van Dingenen *et al.*, 2015) of northwestern France. None of the species are found in the North Sea Basin Pliocene. 10 species (33%) are relatively cosmopolitan in the European Pliocene, found in the Atlantic and Mediterranean. Only two (6%) are still living in European Atlantic and/or Mediterranean waters.

We were able to identify or interpret most of the species recorded by Brébion (1964) with a few exceptions:

Hexaplex (Muricanthus) rudis Borson, 1821 – Brébion, p. 363. Now considered *Hexaplex (Trunculariopsis) rudis* (Borson, 1821). This species was not figured by Brébion,

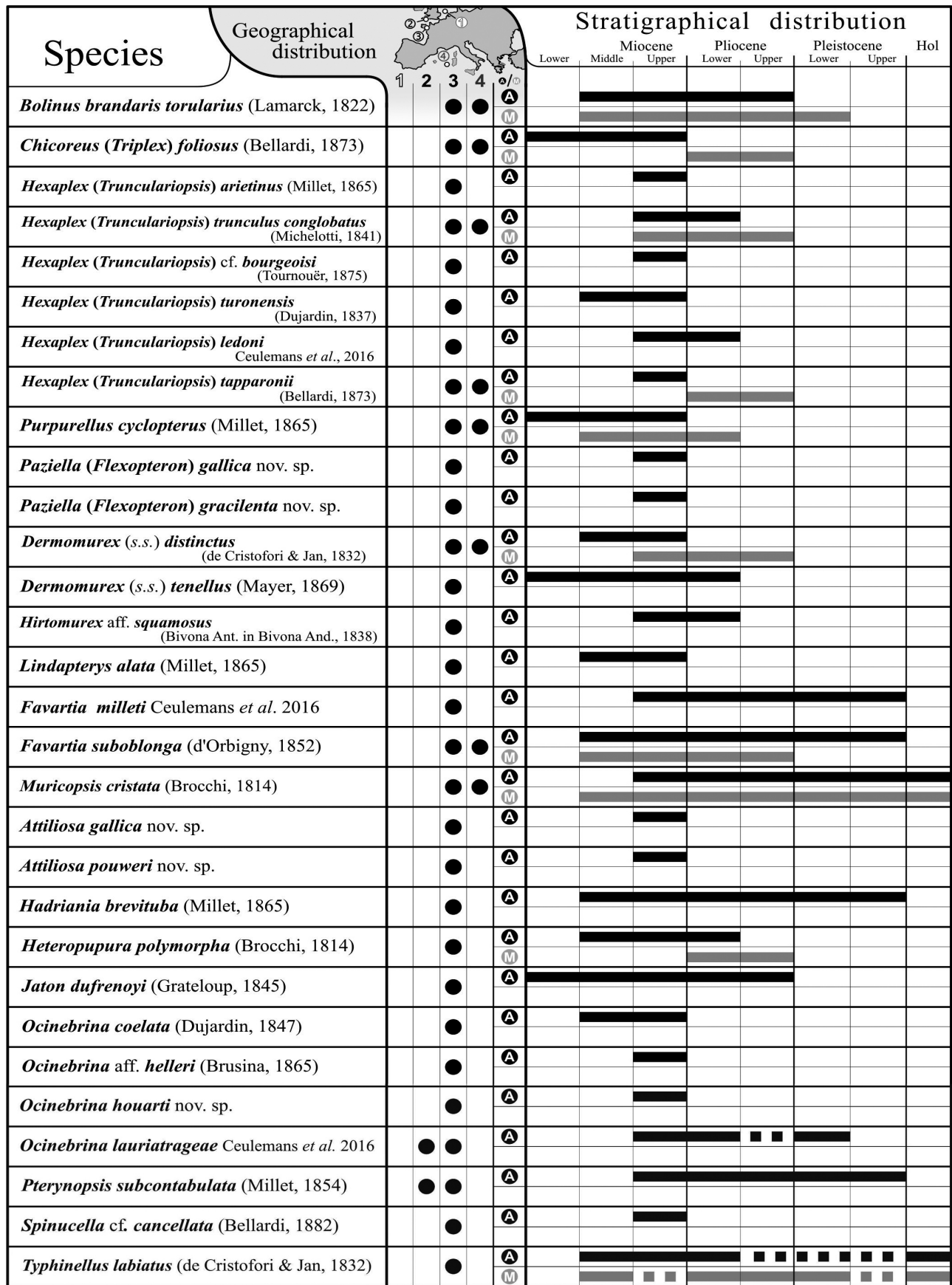


Figure 1. Geography, stratigraphy and distribution of species found in the upper Miocene Tortonian Assemblage I localities of northwestern France. For geographic distribution 1 = North Sea Basin, 2 = Atlantic coasts British Isles, 3 = NW France, 4 = Mediterranean. For stratigraphic distribution black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

who recorded it only from the locality of Thorigné. Unfortunately, none of the collections at hand have material from this locality. The species is known to range into the late Miocene (Bellardi, 1873; Merle *et al.*, 2011) and may well be present in Assemblage I, but considering the difficulties encountered in ascribing Assemblage I species to the subgenus, we provisionally exclude it, pending confirmation.

Ocinebrina sublassignei Peyrot, 1938 – Brébion, p. 382. This species was recorded from Sceaux-d'Anjou, but not figured. We have not seen any specimen resembling the type figured by Peyrot (1938, pl. 4, figs 62, 69) in the vast collections from that locality consulted. We therefore exclude it, pending confirmation.

Ocinebrina imbricata Brocchi, 1814 – Brébion, p. 387, pl. 9, fig. 13. This species was recorded by Brébion from Thorigné. The photograph is difficult to interpret, but it is unlikely to be that species. It is excluded pending confirmation.

The generic composition is not unusual for European Miocene Atlantic assemblages, with a strong presence of small-shelled genera. Species of the larger shelled genera are almost without exception damaged and abraded, showing signs of transport. This suggests the large-shelled species did not live in this environment. The dwarfism seen in the fauna, or what Lauriat-Rage (1981) called 'nanisme' was already commented on in part 1 and 2 of this series (Landau *et al.*, 2017, 2018).

In the muricid assemblage ten species (33%) occur exclusively in the northwestern French Assemblages I-III. This is a lower level of endemism than noted in previous parts of this series, in which endemics within the Patellogastropoda, Vetigastropoda and Caenogastropoda accounted for 63% of the species within the assemblage (Landau *et al.*, 2017, 2018). Almost all the Assemblage I muricid species, in which the protoconch is known, are of the non-planktotrophic type. This would favour greater endemism, but this does not seem to be the case in muricids.

The muricid generic composition is moderately strongly thermophilic, with a considerable number of genera present that do not extend southwards to the latitude of NW France today. Many of the genera present, such as *Bolinus*, *Hexaplex*, *Dermomurex*, *Muricopsis*, *Hadriana*, and *Typhinellus* do not extend further north than southern Portugal (about 38° latitude) (Houart, 2001). Others, such as *Attiliosa*, *Favartia*, *Purpurellus*, *Lindapterys* and *Jaton* are fully tropical genera, and occur today further south off the coast of West Africa. The muricid fauna in the lower Pliocene Assemblage III of northwestern France was also found to be thermophilic compared to that found as those latitudes today (Ceulemans *et al.*, 2013), but contained fewer frankly tropical elements (i.e. *Attiliosa*, *Purpurellus* and *Lindapterys*), suggesting some cooling of Sea Surface Temperatures (SSTs) between the late Miocene and early Pliocene.

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

Acknowledgements

We would like to thank Carlos Marques da Silva of the University of Lisbon, Portugal, for his advice and help with graphics and to Daniel Ledon, France, for donating type material. To Roland Houart, Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium for his thorough review. Ronald Pouwer, fossil mollusc curator at the Naturalis Biodiversity Center in Leiden (The Netherlands), for making the RGM collections available to us. Special thanks should be given to Mr. Hammoneau, Mr. Justeau, and family Lherbette for allowing us to collect on their property.

References

- Adams, H. & Adams, A. 1853-1858. *The Genera of Recent Mollusca; Arranged According to their Organization*. John van Voorst, London, 2 vols. [Vol. 1: 1-256, pls 1-32 (1853); 257-484; Vol. 2: 1-92, pls 33-72 (1854); 93-284, pls 73-96 (1855); 285-412, pls 97-112 (1856); 413-540, pls 113-128 (1857); 541-660, pls 129-138 (1858)].
- Agassiz, L. 1846. *Nomenclatoris Zoologici Index Universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis homonymis plantarum nec non variis annotationibus et emendationibus*. Soloduri, Sumptibus Jent et Gassman: i-x, 1-1135.
- Almera, J. & Bofill, A. 1893. Moluscos fósiles de los terrenos terciarios superiores de Cataluña. Familia Muricidos Fleming. *Boletín de la Comisión del Mapa Geológico de España* 19 (1892): 114-243.
- Ancona, C. d' 1871. Malacologia pliocenica Italiana, descritta ed illustrata da Cesare d'Ancona, 1. Generi: *Strombus*, *Murex*, *Typhis*. *Comitato Geologico, Memorie per Servire alla Descrizione della Carta Geologica d'Italia* (1871): 305-363.
- Andreoli, G. & Marsigli, S. 1992 [1991]. Contributo alla conoscenza della malacofauna pliocenica modenese (Introduzione e parte I – famiglia Muricidae). *Natura Modenese* 1: 3-20.
- Annoscia, E. 1970. Contributi alle conoscenze del Neogene dell'Italia meridionale, 1. Molluschi delle argille figuline di Venosa (Potenza). *Giornale de Geologia* (2)35: 207-242.
- Bałuk, W. 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland, 2. *Acta Geologica Polonica* 45: 1-255.
- Bałuk, W. 2006. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part V Addenda et corrigenda ad Prosobranchia. *Acta Geologica Polonica* 56: 177-220.
- Barco, A., Claremont, M., Reid, D.G., Houart, R., Bouchet, P., Williams, S.T., Cruaud, C., Couloux, A. & Oliverio, M. 2010. A molecular phylogenetic framework for the Muricidae, a diverse family of carnivorous gastropods. *Molecular Phylogenetics and Evolution* 56: 1025-1039.

- Barco, A., Schiaparelli S., Houart R., Oliverio M. 2012. Cenozoic evolution of Muricidae (Mollusca, Neogastropoda) in the Southern Ocean, with the description of a new subfamily. *Zoologica Scripta* 41: 596-616.
- Barco, A., Marshall, B., Houart, R. & Oliverio, M. 2015. Molecular phylogenetics of Haustriinae and Pagodulinae (Neogastropoda: Muricidae) with a focus on New Zealand species. *Journal of Molluscan Studies* 81(4): 476-488.
- Basterot, B. de 1825. *Mémoire géologique sur les environs de Bordeaux. Première partie, comprenant les observations générales sur les mollusques fossiles, et la description particulière de ceux qu'on rencontre dans ce bassin*. Paris (J. Tastu): 100 pp. (reprinted from *Mémoires de la Société d'Histoire Naturelle de Paris* 2: 1-100).
- Bellardi, L. 1873. I molluschi dei terreni terziarii del Piemonte e della Liguria, 1. Cephalopoda, Pteropoda, Heteropoda, Gasteropoda (Muricidae e Tritonidae). *Memorie della Reale Accademia delle Scienze di Torino* (2)27: 33-294 (reprint 264 pp.) (June 10, 1873).
- Bellardi, L. 1882. I molluschi dei terreni terziarii del Piemonte e della Liguria, 3. Gasteropoda (Buccinidae, Cyclopsidae, Purpuridae, Coralliophilidae, Olividae). *Memorie della Reale Accademia delle Scienze di Torino* (2)34 (1883): 219-469 (reprint 253 pp.) (December 10, 1882).
- Benoist, E.A. 1880. Etude sur les espèces de la sous-famille des Muricinae observées dans le Miocène du Sud-Ouest de la France. *Actes de la Société Linnéenne de Bordeaux* 34: 145-173.
- Berry, S.S. 1960. Notices of new eastern Pacific Mollusca. *Leaflets in Malacology* 1(19):115-122.
- Berry, S.S. 1964. Notices of new Eastern Pacific Mollusca, 4. *Leaflets in Malacology* 1: 147-154.
- Bevilaqua, A. 1928. Studi sulla fauna fossile marina pliocenica e quaternaria dell'Isola di Rodi (Egeo). *Atti della Società Italiana di Scienze Naturale e del Museo Civico di Storia Naturale di Milano* 67: 150-178.
- Bivona-Bernardi, A. 1832. Caratteri di un nuovo genere di conchiglie fossili, estratti dalle Collettanee di Storia naturale, opera manoscritta del barone Antonino Bivona Bernardi. *Effemeridi Scientifiche e Letterarie per la Sicilia* 1: 55-62, pl. 1; 2: 3-8, pl. 2.
- Bivona-Bernardi, A. 1838. Generi e specie di molluschi descritti dal Barone Antonio Bivona e Bernardi. Lavori postumi pubblicati dal figlio Andrea dottore in medicina con note ed aggiunte. *Giornale di Scienze Lettere e Arti per la Sicilia* 61: 211-227 [stated date March 1838]; 63: 319-324 [stated date september 1838].
- Blainville, H.M.D. de 1828-1830. Malacozoaires ou animaux mollusques. [in] *Faune Française*. 320 p., 48 pl. [livr. 18 (1828): 1-80; livr. 2 (1829): 81-176; livr. 23 (1829): 177-240; livr. 28 (1830): 241-320], Paris (Levrault).
- Boettger, O. 1902. Zur Kenntnis der Fauna der mittelmiozänen Schichten von Kostež im Krassó-Szörényer Komitat. Mit einem Situationsplan der Fundpunkte, 2. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt* 51 (1901): 1-200.
- Bonaparte, C.L. 1832-1841. *Iconografia della fauna italica per le Quattro classi degli Animali Vertebrati*. 3 vols. Tipografia Salviucci, Roma, 286 + 270 + 556 pp.
- Borson, S. 1820-1825. Saggio di orittografia piemontese. *Memorie della Reale Accademia di Scienze di Torino* 25: 180-299 (1820); 26: 297-364 (1821); 29: 251-318 (1825).
- Bouchet, P., Rocroi, J.P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61(1-2): 1-526.
- Bouchet, P. & Warén, A. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). *Bollettino Malacologico* Suppl. 1: 121-296.
- Braun, A. 1843. Vergleichende Zusammenstellung der lebenden und diluvialen Molluskenfauna des Rheinthals mit der tertiären des Mainzer Beckens. *Amtlicher Bericht über die zwanzigste Versammlung der Gesellschaft Deutscher Naturforscher und Aerzte zu Mainz im September 1842*: 142-150.
- Brébion, P. 1964. Les gastéropodes du Redonien et leur signification, 1-2. – Thèse de doctorat ès-Sciences. Paris (Faculté des Sciences de l'Université de Paris: 775 pp., 15 pls. (27 June 1964, unpublished).
- Brébion, P. 1974. Révision des Acanthines du Plio-Pleistocène marocain et critique de l'origine chilo-péruvienne de ces gastéropodes. *Comptes rendus de l'Académie des Sciences de Paris* (D)278: 1901-1904.
- Brébion, P. 1979a. Iconographie critique des gastéropodes marins du Pliocène supérieur et du Quaternaire marocains atlantiques. *Bulletin du Muséum national d'Histoire naturelle de Paris* (4)1(C): 137-149.
- Brébion, P. 1979b. Étude biostratigraphique et paléocéologique du Quaternaire marocain. *Annales de Paléontologie (Invertébrés)* 65: 1-42.
- Brocchi, G. 1814. *Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente*, 1-2. Milano (Stamperia Reale): 1-240 (1); 241-712 (2), 16 pls.
- Broderip, W.J. 1833. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. *Proceedings of the Zoological Society of London* 2: 173-179.
- Brown, T. 1827. *Illustrations of the conchology of Great Britain and Ireland. Drawn from nature*. Edinburgh (W.H. Lizars), London (D. Lizars & S. Highley): 144 pp.
- Brusina, S. 1865. Conchiglie dalmate inedite. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* 15: 3-42.
- Bucquoy, E., Dautzenberg, P. & Dollfus, G. 1882-1886. *Les mollusques marins du Roussillon*. Tome Ier. Gastropodes. Paris, J.B. Baillière & fils 570 p., 66 pl. [1-40, pl. 1-5 (February 1882); 41-84, pl. 6-10 (August 1882); 85-135, pl. 11-15 (February 1883); 136-196, pl. 16-20 (August 1883); 197-222, pl. 21-25 (January 1884); 223-258, pl. 26-30 (February 1884); 259-298, pl. 31-35 (August 1884); 299-342, pl. 36-40 (September 1884); 343-386, pl. 41-45 (February 1885); 387-418, pl. 46-50 (August 1885); 419-454, pl. 51-60 (January 1886); 455-486, pl. 56-60 (April 1886); 487-570, pl. 61-66 (October 1886)].
- Callea, A., Volpi, C., Borri, M. & Martignoni, R. 2001. A new species of the genus *Lindapterys* Petuch, 1987 (Gastropoda: Muricidae) from Somalia. *Tropical Zoology* 14(2): 211-221.
- Caprotti, E. 1976. Malacofauna dello stratotipo piacentiano

- (Pliocene de Castell'Arquato). *Conchiglie* 12: 1-56.
- Caretto, P.G. 1963. Nuovi dati sulla estensione della formazione a facies piacentiana a ovest della città di Asti. *Atti della Società Italiana di Scienza Naturale e del Museo Civico di Storia Naturale di Milano* 102: 3-31.
- Caretto, P.G. 1967. Studio morfologico con l'ausilio del metodo statistico e nuova classificazione dei gasteropodi pliocenici attribuibili al *Murex brandaris* Linneo. *Memoria della Società Italiana di Scienza Naturali e del Museo Civico di Storia Naturale di Milano* 16: 1-60.
- Cataliotti-Valdina, J. 1975. La faune malacologique du Pliocène des Alpes-Maritimes, 1. *Annales du Muséum d'Histoire Naturelle de Nice* 3: 55-77.
- Cavallo, O. & Repetto, G. 1992. Conchiglie fossili del Roero. Atlante iconografico. *Associazione Naturalistica Piemontese Memorie* (Associazione Amici del Museo 'Federico Eusebio') 2: 1-251.
- Cerulli-Irelli, S. 1911. Fauna malacologica mariana, 5. Cancellariidae, Marginellidae, Mitridae, Fusidae, Chrysodomidae, Buccinidae, Nassidae, Columbidae, Muricidae, Tritonidae, Cassidae, Cypraeidae, Chenopodidae. *Paleontographia Italica* 17: 280-325.
- Ceulemans, L., Landau, B.M. & Van Dingenen, F. 2014. *Carinofusus* gen. nov. from the Mio-Pliocene transition of western France. *Vita Malacologica* 12: 23-30.
- Ceulemans, L., Van Dingenen, F. & Landau, B.M. 2016. The lower Pliocene gastropods of Le Pigeon Blanc (Loire Atlantique, Northwest France), 3 – Muricidae. *Vita Malacologica* 15: 35-55.
- Chenu, J.C. 1859. *Manuel de conchyliologie et de paleontologie conchyliologique*. 1. vii + 508 pp., Paris (Masson).
- Chirli, C. 1988. *Malacofauna pliocenica di Poggibonsi, Cava delle Piaggiole*. Poggibonsi (Lalli Ed.): 1-89.
- Chirli, C. 2000. *Malacofauna Pliocenica Toscana, 2 Superfamiglia Muricoidea*. Firenze (C. Chirli): 142 pp.
- Chirli, C. & Richard, C. 2008. *Les mollusques plaisanciens de la Côte d'Azur*. Tarnelle (C. Chirli): 128 pp.
- Cleavelly, R.J., 1974. The Sowerbys, the Mineral Conchology, and their fossil collections. *Journal of the Society for the Bibliography of Natural History* 6: 418-481.
- Coen, G., 1922. Del genere *Pseudomurex* (Monterosato, 1782). *Atti della Società italiana di scienze naturali* 61: 68-71.
- Cossmann, M. 1903. *Essais de paléonconchologie comparée*, 5. Paris (Cossmann): 215 pp., 9 pls.
- Cossmann, M. 1921. Rectifications de nomenclature. *Revue Critique de Paléozoologie et Paléophytologie* 25(2): 79-80.
- Cossmann, M. & Peyrot, A. 1909-1935 (after 1924 continued by A. Peyrot). Conchologie néogénique de l'Aquitaine. *Actes de la Société Linnéenne de Bordeaux*, 63: 73-293 (1909); 64: 235-400 (1910), 401-445 (1911); 65: 51-98 (1911). 99-333 (1912); 66: 121-232 (1912), 233-324 (1913); 68: 5-210, 361-435 (1914); 69: 157-365 (1917); 70: 5-180 (1918), 181-491 (1919) 73: 5-321 (1922); 74: 257-342 (1923); 75: 71-318 (1924); 77: 51-256 (1925); 78: 199-256 (1926); 79: 5-263 (1928); 82: 73-126 (1931); 83: 5-116 (1931); 84: 5-288 (1933); 85: 5-71 (1933); 86: 257-353 (1935). Also published as a 6 volume book with different pagination as Édition in-8°, *Extrait des Actes de la Société Linnéenne de Bordeaux ('Ouvrages couronnés par l'Académie des Sciences, Arts et Belles-Lettres de Bordeaux')*, 1: 1-220 (1909); 221-428 (1911); 429-718 (1912); 2: 1-204 (1913); 205-496 (1914); 3: 1-384 (1917); 385-695 (1919); 4: 1-322 (1922); 323-610 (1924); 5: 1-206 (1927); 207-465 (1928); 6: 1-294 (1931); 295-541 (1932).
- Couffon, O. 1907. Le Miocène en Anjou. *Bulletin de la Société d'Études Scientifiques d'Angers* N.S. 36 (1906): 157-196.
- Couffon, O. 1908. Le Miocène en Anjou. (Supplément). *Bulletin de la Société d'Études Scientifiques d'Angers* N.S. 37 (1907): 50-58.
- Couffon, O. 1915. Contribution à l'étude des faluns de l'Anjou, 4. Miocène supérieur, gisement de Saint-Michel-et-Chanveaux. *Bulletin de la Société d'Études Scientifiques d'Angers* N.S. 44 (1914): 31-56.
- Cox, L.R. 1936. Pliocene Mollusca from Portugal. *Memórias e Notícias da Universidade de Coimbra* 9: 47-75.
- Cristofori, J. de & Jan, G. 1832. *Catalogus in quatuor sectiones divisus rerum naturalium in museo exstantium Josephi de Christofori et Georgio Jan Plurinum Acad. Scient. et Societ. Nat. Cur. Sodalium ecc*, 2(1). *Conchylia fossilia ex formatione telluris tertiaria in collectione nostra exstantia*. 16 pp., Parma (Carmignani).
- Crosse, H. 1869. Diagnoses molluscorum novorum. *Journal de Conchyliologie* 17: 183-188.
- Csepregy-Meznerics, I. 1956. Die Molluskenfauna von Szob und Letkés. *Magyar Állami Földtani Intézet Évkönyve (Annales de l'Institut de Géologie Publique de Hongarie)* 45: 361-477.
- Cuerda Barceló, J. 1987. *Molluscos marinos y salobres del Pleistoceno Balear*. Palma de Mallorca (Publ. Caja de Baleares 'Sa Nostra'): 421 pp.
- Damarco, P. 1993. The paleontological reserve of the Andona and Botto valleys, 2. *World Shells* 4: 74-76.
- Dautzenberg, P. & Fischer, H. 1896. Dragages effectués par l'Hirondelle et par la Princesse Alice 1888-1895. 1. Mollusques Gastropodes. *Mémoires de la Société Zoologique de France* 9: 395-498, pls 15-22.
- Degrange-Touzin, A. 1894. Étude préliminaire des coquilles fossiles des faluns des environs d'Orthez et de Salies-de-Béarn (Basses-Pyrénées). *Actes de la Société Linnéenne de Bordeaux* 47: 333-457, pls 8-9.
- Doderlein, P. 1862. *Cenni geologici intorno la giacitura dei terreni miocenici superiori dell'Italia centrale*. Estratto dagli Atti del X° Congresso degli Scienziati Italiani, 1862, Siena: 25 pp. Also published as: 1864, Atti del Decimo Congresso degli Scienziati Italiani: 83-107, 223 (errata).
- Dollfus, G. 1905. Faune Malacologique du Miocène Supérieur de Gourbesville (Manche) – Étage Rédonien. *L'Association Française pour l'Avancement des Sciences. Congrès de Cherbourg 1905*: 358-371.
- Dollfus, G. 1906. Faune malacologique du miocène supérieur de Beaulieu (Mayenne) – Étage Rédonien. *L'Association Française pour l'Avancement des Sciences. Congrès de Lyon 1906*: 304-315.
- Dollfus, G. & Dautzenberg, P. 1886. Étude préliminaire des coquilles fossiles des faluns de la Touraine. *La Feuille des Jeunes Naturalistes* 16(189): 101-105.
- Draparnaud, J.P.R. 1805. *Histoire naturelle des mollusques terrestres et fluviatiles de la France*. Paris, i-viii + 1-34.
- Dujardin, F. 1837. Mémoire sur les couches du sol en Touraine et description des coquilles de la craie et des faluns. *Mé-*

- moire de la Société Géologique de la France 2: 211-311.
- Emerson, W.K. 1968. Taxonomic placement of *Coralliophila incompta* Berry, 1960, with the proposal of a new genus, *Attiliosa*. (Gastropoda: Muricacea). *The Veliger* 10: 379-381.
- Erünal-Erentöz, L. 1958. Mollusques du Néogène des Bassins de Karaman, Adana et Hatay (Turquie). Première these, 1ère partie. *Publications de l'Institut d'Étude et du Recherches Minières de Turquie* (C)4: 1-232.
- Fekih, M. 1975. Paleocologie du Pliocène marin au nord de la Tunisie. *Annales des Mines et de la Géologie* 27: 1-195.
- Ferrero Mortara, E.L., Montefameglio, L., Pavia, G. & Tampieri, R. 1981. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, 1. *Museo Regionale di Scienze Naturali di Torino, Cataloghi* 6: 1-327.
- Fontannes, F. 1879-1880. *Les invertébrés du bassin tertiaire du Sud-Est de la France. Les mollusques pliocènes de la Vallée du Rhône et du Roussillon*, 1. *Gastéropodes des formations marines et saumâtres*. Paris (Georg, Lyon & F. Savy): viii + 276 pp., 12 pls (pp. 1-76 published in 1879, remainder in 1880).
- Friedberg, W. 1911-28. *Mięczaki miocénskie ziem Polskich (Mollusca Miocaenica Poloniae)*, 1. *Ślimaki i łódkonogi*, 1. *Gastropoda et Scaphopoda*. Lwow (Muzeum Imienia Dzieduszyckich): 631 pp. (issued in parts: 1, 1-112, pls 1-5 (1911); 2, 113-240, pls 6-14 (1912); 3, 241-360, pls 15-20 (1914); 4, 361-440, pls 21-26 (1923); 5, 441-631, pls 27-38 (1928). Reprinted 1951-55 with slightly different title and pagination, Warszawa (Wydawnictwa Geologiczne).
- Gardner, J.A. 1944. The molluscan fauna of the Alum Bluff Group of Florida. Part VII. Stenoglossa (in part). [*Xancus*, *Busycon*, *Nassariidae*, *Fusinidae*, etc.]. *United States Geological Survey Professional Paper* 142-G: 437-491, pls 49-51.
- Garilli, V., Galletti, L., & Parrinello, D. 2017. Distinct protoconchs recognised in three of the larger Mediterranean *Cerithium* species (Caenogastropoda: Cerithiidae). *Molluscan Research* 38(2): 105-118.
- Glibert, M. 1952. Gastropodes du Miocène moyen du Bassin de la Loire, 2. *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* 2(46): 241-450.
- Gmelin, J.F. 1791. *Caroli a Linnei systema natura per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis etc. Editio decima tertia, aucta, reformata, cura J.F. Gmelin*, 1(6). *Vermes testacea*. Lipsiae (G.E. Beer): 3021-4120.
- González-Delgado, J.A. 1989. Estudio sistemático de los gasterópodos del Plioceno de Huelva (SW de España), 4. Neogastropoda (Muricacea, Buccinacea). *Studia Geologica Salmanticensia* 26: 269-315.
- Goret, B., Ledon, D. & Pons, J. 2013. Les Muricidae (Gastropoda, Muricoidea) du Pliocène Inférieur de Catalogne (France, Espagne). *Palaeontos* 23: 1-52.
- Goret, B. & Pons, J. 2013. Les Muricidae (Gastropoda, Muricoidea) du Miocène de Montpeyroux (Hérault – France). *Palaeontos* 23: 53-70.
- Gratoloup, J.P.S. de 1828-35. Tableau des coquilles fossiles qu'on rencontre dans les terrains calcaire tertiaires (faluns) des environs de Dax, dans le Département des Landes, 1-12. *Bulletins d'Histoire Naturelle de la Société Linéenne de Bordeaux* 2(9): 72-109 (1828a) (1); 2(10): 123-158 (1828b) (2); 2(10): 192-204 (1828c) (3). *Actes de la Société Linéenne de Bordeaux* 5(27): 192-204 (1832a) (4); 5(29): 263-282 (1832b) (5); 5(30): 314-344 (1832c) (6); 6(32): 31-48 (1833a) (7); 6(33): 90-100 (1833b) (8); 6(34): 159-164 (1833c) (9); 6(35): 188-212 (1834a) (10); 6(37): 270-320 (1834b) (11); 7(39): 101-114 (1835) (12).
- Gratoloup, J.P.S. de 1845-1847. *Conchyliologie fossile des terrains tertiaires du Bassin de l'Adour (environs de Dax)*, 1. *Univalves*. Atlas. Bordeaux (Th. Lafargue): All plates published 1845, except plates 2, 4, 11 (1847). Note: For dates of the plates we follow Lesport, J.F., Cluzaud, A. & Verhecken, A. 2012. Les publications du Docteur Jean-Pierre Sylvestre de Gratoloup sur les mollusques fossiles du Bassin d'Aquitaine (S.-O. France): dates de parutions et commentaires. *Bulletin de la Société Linéenne de Bordeaux* (n.s.) 40: 417-485.
- Gray, J.E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London* (1847): 129-219 [November].
- Gregorio, A. de 1885. Continuazione degli studi su talune conchiglie mediterranee vivente e fossili. *Bollettino della Società Malacologica Italiana* 11: 27-203.
- Griffith, E. & Pidgeon, E. 1834. *The animal kingdom arranged in conformity with its organisation, by Baron Cuvier*, 12. *The Mollusca and Radiata* arranged by the Baron Cuvier with supplementary additions to each order. London (Whittake): 1-601.
- Harmer, F.W. 1914-1925. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's monograph of the Crag Mollusca, 1. *Monographs of the Palaeontographical Society* 1(1): 1-200 (1914); 1(2): 201-302 (1915), 1(3): 303-461 (1918), 1(4): 463-483 (1919), 2(1): 485-652 (1920), 2(2): 653-704 (1921), 2(3): 705-856 (1923), 2(4): 857-900 (1925).
- Herrmannsen, A.N. 1846-1852. *Indicis generum malacozoorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium: adjectis auctoribus, temporibus, locis systematicis atque literariis, etymus, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda*, 1-2. Cassel (T. Fischeri): 1-232 (1846), 233-637 (1847) (1); 1-352 (1847), 353-492 (1848), 493-717 (1849), supplement (1852).
- Hoernes, R. & Auinger, M. 1879-91. Die Gasteropoden der Meeres-Ablagerungen der ersten und zweiten Miocänen Mediterran-Stufe in der Österreichisch-Ungarischen Monarchie. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 12: 1-382, 50 pls. Published in parts: 1-52, pls 1-6 (1879); 53-112, pls 7-12 (1880); 113-152, pls 13-16 (1882); 153-192, pls 17-22 (1884); 193-232, pls 23-28 (1885); 233-282, pls 29-36 (1890); 283-330, pls 37-42 (1891); 331-382, pls 43-50 (1891).
- Hörnes, M. 1851-1870. Die fossilen Mollusken des Tertiär-Beckens von Wien. – *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 3-4: 1-42, pl. 1-5 (1851), 43-208, pl. 6-20 (1852), 209-296, pl. 21-32 (1853), 297-382, pl. 33-40 (1854), 383-460, pl. 41-45 (1855), 461-736, pl. 46-52 (1856) (3); 1-479, pls 1-85 (1870) (4).
- Houart, R. 1993. Description of three new species and one new subspecies of Muricidae (Muricinae and Muricopsinae) from West Africa. *Bollettino Malacologico* 29: 17-30.

- Houart, R. 2001. *A review of the Recent Mediterranean and northeastern Atlantic species of Muricidae*. Rome (Evolver srl.): 227 pp.
- Houart, R. 2015. Description of a new species of *Typhinellus* (Gastropoda: Muricidae: Typhinae) from the Western Atlantic. *Zootaxa* 4007(3): 427-432.
- Houart, R. 2018. Historique et classification des espèces actuelles de Muricidae (Neogastropoda, Muricoidea). *Novapex* 19(2): 37-66.
- Houart, R., Gori, S. & Ryall, P. 2011. New record of *Typhinellus labiatus* (Cristofori & Jan, 1832) (Gastropoda: Muricidae) from São Tomé and Príncipe and discussion about its classification and geographical distribution. *Novapex* 12: 91-97.
- ICZN [International Commission on Zoological Nomenclature], 1957. Opinion 479. Validation under the plenary powers of specific names for nine species of the Class Gastropoda occurring in the New Zealand area as published by Martyn (T.) in 1784 in the work entitled *The Universal Conchologist* (Opinion supplementary to Opinion 456). *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* 16: 365-416.
- ICZN [International Commission on Zoological Nomenclature], 1970. Opinion 911. Six misidentified type-species in the superfamily Muricea (Gastropoda). *Bulletin of Zoological Nomenclature* 27(1): 20-26.
- ICZN [International Commission on Zoological Nomenclature], 1999. International Code of Zoological Nomenclature. Fourth Edition: xxix + 306 pp., London (International Trust for Zoological Nomenclature).
- ICZN [International Commission on Zoological Nomenclature], Kadolsky, K. 2005. Case 3321. *Bythinella* Moquin-Tandon, 1856 (Mollusca, Gastropoda, Prosobranchia, Rissooidea): proposed conservation of usage by the designation of *Bulimus viridis* Poiret, 1801 as the type species. *Bulletin of Zoological Nomenclature* 62(3): 134-139.
- ICZN [International Commission on Zoological Nomenclature], 2006. Opinion 2161 (Case 3321) *Bythinella* Moquin-Tandon, 1856 (Gastropoda, Prosobranchia, Rissooidea): usage conserved by the designation of *Bulimus viridis* Poiret, 1801 as the type species. *Bulletin of Zoological Nomenclature* 63(4): 276-277.
- Inzani, A. & Bertarelli, C. 1985. La famiglia Muricidae nel Pliocene italiano. *Hobby Fauna* 1(11): 24-31, 3 pls.
- Iredale, T. 1915. A commentary on Suter's Manual of the New Zealand Mollusca. *Transactions and Proceedings of the New Zealand Institute* 47: 417-497.
- Iredale, T. 1936. Australian molluscan notes, 2. *Records of the Australian Museum* 19: 267-340, pls. 20-24.
- İslamoğlu, Y. 2004. Kasaba Miyosen havzasının Gastropoda faunası (Batı Toroslar, GB. Türkiye) (Gastropod fauna of Kasaba Miocene basin (Western Taurids, SW Turkey). *Bulletin of Mineral Research and Exploration* 128: 137-170 (in Turkish).
- Jousseume, F.P. 1880. Division méthodique de la famille des purpuridés. *Le Naturaliste* 1(2): 335-336.
- Karakus, K. & Taner, G. 1994. Samandag formasyonu'nun (Antakya Havzası) yası ve Molluska faunasına bağlı paleoekolojik özellikleri. *Türkiye Jeoloji Bülteni* 37: 87-109 (in Turkish).
- Keen, A.M. 1971. Two new supraspecific taxa in the Gastropoda. *The Veliger* 13(3): 296.
- Koenen, A. von 1867. Das marine Mittel-Oligocän Nord-Deutschlands und seine Mollusken-Fauna. *Palaeontographica* 16(2): 53-127.
- Kókey, J. 1967. Stratigraphie des Oberhelvets ('Karpätien') von Várpalota (Ungarn). *Palaeontographia Italica* 63: 75-111.
- Krach, W. 1981. The Badenian reef formations in Roztocze Lubelskie. *Prace Geologiczne* 121: 5-91, 116-140.
- Kuroda, T. 1953. New genera and species of Japanese Gastropoda (1). *Venus* 17: 179-185.
- Kuroda, T., Habe, T. & Oyama, K. 1971. *The sea shells of Sagami Bay*. Tokyo (Maruzen): xix + 741 pp. (in Japanese), 489 pp (in English), 51 pp., 121 pls.
- Lamarck, J.B.P.A. de M. 1803. Suite des mémoires sur les fossils des environs de Paris. *Annales du Muséum National d'Histoire Naturelle de Paris* 2: 217-227.
- Lamarck, J.B.P.A. de M. 1822. Histoire naturelle des animaux sans vertèbres, présentant des caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent, précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie, 7. 711 pp., Paris (de Lamarck).
- Landau, B.M. Ceulemans, L. & Van Dingenen, F. 2018. The upper Miocene gastropods of northwestern France, 2. Caenogastropoda. *Cainozoic Research* 18(2): 177-368.
- Landau, B.M., Harzhauser, M., Büyükmeriç, Y. & Breitenberger, A. 2016. Additions to the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research* 16(2): 221-229.
- Landau, B.M., Harzhauser, M., İslamoğlu, Y. & Silva, C.M. da 2013. Systematics and palaeobiogeography of the gastropods of the middle Miocene (Serravallian) Karaman Basin, Turkey. *Cainozoic Research* 11-13: 3-584.
- Landau, B.M., Houart, R & Silva, C.M. da 2007. The early Pliocene Gastropoda (Mollusca) of Estepona, southern Spain, 7. Muricidae. *Palaeontos* 11: 1-87.
- Landau, B., Silva, C.M. da & Mayoral, E. 2011. The lower Pliocene gastropods of the Huelva Sands Formation, Guadalquivir Basin, southwestern Spain. *Palaeofocus* 4: 1-90.
- Landau, B.M. Van Dingenen, F. & Ceulemans, L. 2017. The upper Miocene gastropods of northwestern France, 1. Patellogastropoda and Vetigastropoda. *Cainozoic Research* 17(1): 75-166.
- Lauriat-Rage, A. 1981. Les Bivalves du Redonien (Pliocène atlantique de France). Signification stratigraphique et paléobiogéographique. *Mémoires du Muséum national d'Histoire naturelle n.s., sér. C, Sciences de la Terre* 45: 1-173.
- Lecointre, G. 1952. Recherches sur le Néogène et le Quaternaire marin de la côte atlantique du Maroc, 2. Paléontologie. *Notes et Mémoires. Service Géologique du Maroc* 99: 5-170.
- Lesueur, C.A. 1821. Descriptions of several new species of cuttlefish. *Journal of the Academy of Natural Sciences of Philadelphia* 2: 86-101.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum charac-*

- teribus, differentiis, synonymis, locis*, 1. Editio decima, reformata. Holmiae (Laurentii Salvii): 824 pp. [facsimile reprint, British Museum (Natural History), 1956].
- Lozouet, P., Ledon, D. & Lesport, J.-F. 1994. Le genre *Lindapterys* (Neogastropoda, Muricidae): un exemple de disjonction de distribution en domaine tropical marin. *Géobios* 27: 39-50.
- Lozouet, P., Lesport, J.F., & Renard, P. 2001. Révision des Gastropoda (Mollusca) du stratotype de l'Aquitainien (Miocène inf.): site de Saucats 'Lariey', Gironde, France. *Cossmanniana* (hors série 3): 189 pp.
- MacPherson, J.H. & Gabriel, C.J. 1962. *Marine Molluscs of Victoria*. Melbourne University Press. 475 pp.
- Malatesta, A. 1960. Malacofauna pleistocenica di Grammichele (Sicilia). *Memorie per Servire alla Carta Geologica d'Italia* 12: 1-196.
- Malatesta, A. 1974. Malacofauna pliocenica Umbra. *Memorie per Servire alla Carta Geologica d'Italia* 13: 1-498.
- Martinell, J. 1979. Mesogastropoda del Plioceno del Empordà (Girona), 1. Descriptiva y sistemática. *Studia Geologica Salmanticensis* 15: 85-165.
- Martyn, T. 1784-1787. *The universal conchologist, exhibiting the figure of every known shell*. London, published by the author. 4 vols. 40 pp., 80 pls.
- Mayer, K. 1869. Description de coquilles fossiles des terrains tertiaires supérieurs (suite). *Journal de Conchyliologie* (3)9: 82-88, 282-287.
- Meco, J. 1981. Neogastropodos fosiles de Las Canarias orientales. *Anuario de Estudios Atlánticos* 27: 601-615.
- Merle, D. 1999. *La radiation des Muricidae (Gastropoda: Neogastropoda) au Paléogène: approche phylogénétique et évolutive*. Paris. Unpublished thesis, Muséum national d'Histoire naturelle: i-vi, 499 pp.
- Merle, D. 2001. The spiral cords and the internal denticles of the outer lip in the Muricidae: terminology and methodological comments. *Novapex* 2(3): 69-71.
- Merle, D. 2005. The spiral cords of the Muricidae (Mollusca: Gastropoda): importance of ontogenetic and topological correspondences for delineating structural homologies. *Lethaia* 38: 367-379.
- Merle, D., Garrigues, B. & Pointier, J.P. 2011. *Fossil and recent Muricidae of the world. Part Muricinae*. Hackenheim (ConchBooks): 648 pp.
- Michelotti, G. 1841. *Monografia del genere Murex ossia enumerazione delle principali specie dei terreni sopracretacei dell'Italia*. Vicenza (Tipografia Tremechin): 28 pp.
- Michelotti, G. 1847. Description des fossiles des terrains miocènes de l'Italie septentrionale. *Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem* (2)3: 408 pp. Also as: Ouvrage publié par la société Hollandaise des Sciences, et accompagné d'un atlas de 17 planches. Leiden (A. Arns & Compie): 408 pp.
- Millet [de la Turtaudière], P.A. 1854. *Paléontologie de Maine-et-Loire*. 144 pp., Angers (Cosnier et Lachèse).
- Millet de la Turtaudière, P.A. 1865. *Indicateur du Maine-et-Loire ou indications par commune de ce que chacune d'elles renferme*. Tome 2. 616 pp., Angers (Cosnier et Lachèse).
- Montanaro, E. 1935. Studi monografici sulla malacologia Miocenica Modenese, 1. I molluschi Tortoniani di Montegibbio. *Palaeontographia Italica* 35 (nuova serie 5): 1-84.
- Monterosato, T.A. di 1884. *Nomenclatura generica e specifica di alcune conchiglie mediterranee*. Palermo (Virzi): 152 pp.
- Monterosato, T.A. di 1890. Conchiglie della profondità del mare di Palermo. *Naturalista Siciliano* 9(6): 140-151; 9(7): 157-166; 9(8): 181-191.
- Monterosato, T.A. di 1917. Molluschi viventi e quaternari raccolti lungo le coste della Tripolitania dall'Ing. Camillo Crema. *Bollettino della Società Zoologica Italiana* (3)4: 1-28.
- Montfort, D. de 1810. *Conchyliologie systématique, ou classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Coquilles univalves, non cloisonnées*. Paris (F. Schoell): 676 pp.
- Moquin-Tandon, A. 1855-1856. *Histoire naturelle des mollusques terrestres et fluviatiles de France, contenant des études générales sur leur anatomie et leur physiologie et la description particulière des genres, des espèces et des variétés*. Paris (J.-B. Baillière). 1: 1-416 [1855]; 2: 1-646 [1856], Atlas 1-92, pls 1-54 [1855-1856].
- Muñiz Solís, R. & Guerra-Merchán, A. 1994. Estudio malacológico del Plioceno de Estepona (Málaga). La familia Muricidae, Rafinesque, 1815 (Gastropoda, Prosobranchia). *Iberus* 12: 7-44.
- Oliverio, M. & Mariottini, P. 2001. A Molecular Framework for the Phylogeny of Coralliophila and Related Muricoids. *Journal of Molecular Studies* 67: 215-224.
- Orbigny, A. d' 1852. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie stratigraphique*, 3. Paris (Victor Masson): 1-196, index 1-189.
- Palla, P. 1967. Gasteropodi pliocenici della Bassa Val d'Elsa (Toscana Occidentale). *Rivista Italiana di Paleontologia e Stratigrafia* 73: 931-1020.
- Paulucci, M. 1866. Description d'un *Murex* fossile du terrain tertiaire subapennin de la Vallée d'Elsa. *Journal de Conchyliologie* 14: 64-67.
- Pavia, G. 1975. I molluschi del Pliocene inferiore di Monteu Roero (Alba, Italia NW). *Bollettino della Società Paleontologica Italiana* 14: 99-175.
- Payraudeau, B.C. 1826. *Catalogue descriptif et méthodique des annélides et des mollusques de l'île de Corse*. Paris (Béchet, Levraut, Paschoud, Treuttel & Wurtz): 218 pp. + 8 pls.
- Pereira da Costa, F.A. 1866-1867. Molluscos fosseis. Gasteropodes dos depositos terciarios de Portugal. *Memória Comissão Geologica de Portugal* 4(1): 1-116 (1866); (2): 117-252 (1867).
- Perry, G. 1810. *Arcana; or the museum of natural history: containing the most recent discovered objects. Embellished with coloured plates, and corresponding descriptions; with extracts related to animals, and remarks of celebrated travellers; combining a general survey of nature*. London (James Stratford): [348 pp.], 84 pls unnumbered.
- Perry, G. 1811. *Conchology, or the natural history of shells: containing a new arrangement of the genera and species,*

- illustrated by coloured engravings executed from the natural specimens, and including the latest discoveries. London (William Miller): 4 pp. + unpaginated captions to 61 pls.
- Petit, R.E. 2003. George Perry's molluscan taxa and notes on the editions of his Conchology of 1811. *Zootaxa* 337: 1-72.
- Petit, R.E. 2009. George Brettingham Sowerby, I, II & III: their conchological publications and molluscan taxa. *Zootaxa* 2189: 1-218.
- Petuch, E.J. 1987. *New Caribbean molluscan faunas*. Charlottesville, Virginia: The Coastal Education and Research Foundation. 154 pp., 29 pls. + addendum, 2 pp., 1 pl.
- Peyrot, A. 1938. Les mollusques testacés univalves des dépôts Helvétiques du Bassin Ligérien. Catalogue critique, descriptive et illustré. – Actes de la Société Linnéenne de Bordeaux 89: 5-361.
- Philippi, R.A. 1836. *Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit*, 1. Berolini (Schropp): xiv + 267 pp., pls 1-12.
- Pinna, G. 1971. I Tipi delle specie di Gasteropodi terziari istituite de Giuseppe De Cristofori e Giorgio Jan nel 1832 conservati nelle collezioni del Museo Civico di Storia Naturale di Milano. *Atti Società Italiana Scienza Naturale et Museo Civico di Storia Naturale di Milano* 112: 421-440.
- Pinna, G. & Spezia, L. 1978. Catalogo dei tipi del Museo Civico di Storia Naturale di Milano, 5. I tipi dei Gasteropodi fossili. *Atti della Società Italiana di Scienze naturali Museo Civico di Storia naturale* 119: 125-180.
- Poiret, J.L.M. 1801. *Coquilles fluviatiles et terrestres observées dans le département de l'Aisne et aux environs de Paris*. Paris, xi + 119 pp.
- Pusch, G.G. 1836-1837. *Polens Paläontologie oder Abbildung und Beschreibung der vorzüglichsten und der noch unbeschriebenen Petrefakten aus den Gebirgsformationen in Polen, Volhynien und den Karpathen nebst einigen allgemeinen Beiträgen zur Petrefaktenkunde und einem Versuch zur Vervollständigung der Geschichte des europäischen Auer-Ochsen*. 1-80, pls 1-10 (1836); i-xiii, 81-218, pls 11-16 (1837), Stuttgart (E. Schweizerbart's Verlagshandlung).
- Radwin, G.E. & Atillio, A. d' 1971. Muricacean supraspecific taxonomy based on the shell and the radula. *The Echo* 4: 55-67.
- Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palermo (Rafinesque): 223 pp.
- Rouault, A. 1850. Description des fossiles du terrain éocène des environs de Pau. *Mémoires de la Société Géologique de France série 2*, 3(2): 457-502.
- Reeve, L.A. 1845. Monograph of the genus *Murex*. *Conchologia Iconica: or, illustrations of the shells of Molluscan animals*, 3. London (Reeve): 37 pls (1845-1846, 1849).
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale et principalement de celles des environs de Nice et des Alpes-Maritimes*, 4. Mollusques. Paris (Levrault): i-vii, 1-439.
- Röding, P.F. 1798. *Museum Boltenianum, sive catalogus cimeliorum e tribus regnis naturae quae olim colligera Joa. Fried. Bolten, M.D.p.d. per XL annos proto physicus Hamburgensis*, 2. *Conchylia sive Testacea univalvia, bivalvia et multivalvia*. Hamburgi (Johan. Christi. Trappii): 199 pp.
- Rouault, A. 1850. Description des fossiles du terrain éocène des environs de Pau. *Mémoires de la Société Géologique de France* 3(2): 457-502.
- Ruggieri, G., Bruno, F. & Curti, G. 1959. La malacofauna pliocenica di Altavilla (Palermo), 1. *Atti dell'Accademia di Scienze Lettere e Arti di Palermo* 18: 1-97.
- Ruggieri, G. & Greco, A. 1965. Studi geologici e paleontologici su Capo Milazzo con particolare riguardo al Milazziano. *Geologica Romana* 4: 41-88.
- Sacco, F. 1904. I molluschi dei terreni terziari del Piemonte e della Liguria, 30. Aggiunte e correzioni (con 1400 figure). Considerazioni generali. Indice generale dell'opera. Torino (C. Clausen): 203 + xxxvi pp., 31 pls.
- Sandberger, C.L.F. 1870-1875. *Die Land- und Süßwasser-Conchylien der Vorwelt*. C. W. Kreidel, Wiesbaden. 1000 pp., 36 pls.
- Scacchi, A. 1836. *Catalogus conchyliorum regni neapolitanae usque reperit*. 18 pp., Neapoli (Typis Filiatre-Sebetii).
- Schlüter, F. 1838. *Kurzgefasstes systematisches Verzeichniss meiner Conchyliensammlung nebst Andeutung aller bis jetzt von mir bei Halle gefundenen Land- und Flussconchylien*. Gebauersche Buchdruckerei, Halle. vii + 40 pp.
- Schultz, O., 1998. *Tertiärfossilien Österreichs, Wirbellose, niedere Wirbeltiere und marine Säugetiere; schöne, interessante, häufige und wichtige Makrofossilien aus den Beständen des Naturhistorischen Museums Wien und Privatsammlungen; eine Bilddokumentation*. 159 pp., Wien (Golschneck-Verlag).
- Shuto, T. 1969. Neogene gastropods from Panay Island, the Philippines. Contributions to the geology and paleontology of Southeast Asia, LXVII. *Memoirs of the Faculty of Science, Kyushu University, series D, Geology* 19(1):1-250, 43 figs., 24 pls.
- Silva, C.M. da 2001. *Gastropodes pliocénicos marinhos de Portugal: sistemática, paleoecologia, paleobiologia, paleogeografia*. Dissertação de doutoramento. Faculdade de Ciências da Universidade de Lisboa, Lisboa: 747 pp. (unpublished).
- Sowerby, G. B., I. 1822-1834. *The genera of Recent and fossil shells, for the use of Students in conchology and geology: plates of genera; also corresponding letter-press, descriptive of the characters by which each genus is distinguished. Particularly the land, fresh water & marine nature of each genus, as well as the strata in which fossil species occur*. London (G.B. Sowerby): 1 (Text). 274 pp.; 2 (Atlas), 264 pls. (see Petit, 2009 for dates of publication of parts).
- Sowerby, G.B. II 1834-41. *Murex*. [In] *The conchological illustrations, or coloured illustrations of all the hitherto unfigured Recent shells*. pls 58-67 (1834), pls 187-199 and catalogue, pp. 1-9 (1841), G.B. Sowerby, London.
- Sowerby, J. 1812-1845, continued by J. de C. Sowerby. *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth*. London (Sowerby), 1-7 (for authorship, collation and dates of parts see Cleavelly, 1974, and *Bulletin of Zoological Nomenclature* 1987, 44: 64-67).
- Stchepinsky, V. 1938. Contribution à l'étude du Sahélien de Tunisie. *Société Géologique de France* (n.s.)16(2-3), *Mémoires* 37: 1-121.
- Stimpson, W. 1865. Researches upon the Hydrobiinae and al-

- lied forms chiefly made upon materials in the museum of the Smithsonian Institution. *Smithsonian Miscellaneous Collections* 201: 1-59.
- Strausz, L. 1966. *Die Miozän-Mediterranen Gastropoden ungarns*. 692 pp., Budapest (Akadémiai Kiadó).
- Tournouër, R. 1874. Description de coquilles des faluns. *Journal de Conchyliologie* 22: 288-308.
- Tournouër, R. 1875. Etude sur quelques espèces de *Murex* fossiles du falun de Pont-Levoy en Touraine. *Journal de Conchyliologie* 23: 144-167.
- Van Dingenen, F., Ceulemans, L. & Landau, B.M. 2014. *Euroscaphella* nov. gen. (Gastropoda: Volutidae) in the Neogene of Europe, with the description of a new species: *Euroscaphella namnetensis* nov. sp. from the Mio-Pliocene transition of northwestern France. *Cainozoic Research* 14(2): 101-111.
- Van Dingenen, F., Ceulemans, L., Landau, B.M. & Silva, C.M. da, 2015. The family Nassariidae (Gastropoda: Buccinoidea) from the late Neogene of northwestern France. *Cainozoic Research* 15: 75-122.
- Venzo, S. & Pelosio, G. 1963. La malacofauna Tortoniana del Colle di Vigoleno (Preapennino Piacentino). *Palaeontographia Italica* 58: 43-213.
- Vermeij, G.J. 1993. *Spinucella*, a new genus of Miocene to Pleistocene muricid gastropods from the eastern Atlantic. *Contributions to Tertiary and Quaternary Geology* 30(1-2): 19-27.
- Vermeij, G.J. 2006. The *Cantharus* Group of pisaniine buccinid gastropods: Review of the Oligocene to Recent genera and description of some new species of *Gemophos* and *Hesperisternia*. *Cainozoic Research* 4: 71-96.
- Vermeij, G.J. & Vokes, E.H. 1997. Cenozoic Muricidae of the western Atlantic region, 12. The subfamily Ocenebrinae (in part). *Tulane Studies in Geology and Paleontology* 29: 69-118.
- Vicián, Z., Krock, H. & Kovács, Z. 2017. New gastropod records from the Cenozoic of Hungary. *Földtani Közlöny* 147(3): 265-282.
- Voigt, F.S. In: Cuvier G. (ed.). 1834. *Das Thierreich, geordnet nach seiner Organisation, Als Grundlage der Naturgeschichte der Thiere und Einleitung in die vergleichende Anatomie. Vom Barron von Cuvier. vol. 3, die Mollusken*. Leipzig, F. A. Brodhaus. 621 pp.
- Vokes, E.H. 1964. Supraspecific groups in the subfamilies Muricinae and Tritonaliinae (Gastropoda: Muricidae). *Malacologia* 2: 1-41.
- Vokes, E.H. 1972. *Pterylopsis*, new genus of Trophoninae (Gastropoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique. Sciences de la Terre* 48(9): 1-7, 2 pls.
- Vokes, E.H. 1975. Cenozoic Muricidae of the western Atlantic region. Part 6. *Aspella* and *Dermomurex*. *Tulane Studies in Geology and Paleontology* 11(3): 121-162.
- Wenz, W. 1938-1944. Gastropoda. Prosobranchia. In: Schindewolf, O.H. (ed.) *Handbuch der Paläozoologie*, 6. Berlin (Gebrüder Borntraeger): 1201-1505. (pagination from H.-J. Anderson, 1964, for Wenz's contribution to the entire work is: 1-240, figs 1-471, March 1938 (1); 241-480, figs 472-1235, October 1938 (2); 481-720, figs 1236-2083, July 1939 (3); 721-960, figs 2084-2787, August 1940 (4); 961-1200, figs 2788-3416, October 1941 (5); 1201-1505, figs 3417-4211, October 1943 (6); xii + 1507-1639, November 1944 (7).
- Wiegmann, A.F.A. & Rütke, J.F. 1832. *Handbuch der Zoologie*. 621 pp., Lüderitz, Berlin.
- Zilch, A. 1934. Zur Fauna des Mittel-Miocäns von Kostež (Bárat). Typus-Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. *Senckenbergiana* 16(4-6): 193-302.